THEME SECTION

Marine ecosystems, climate and phenology: impacts on top predators

Idea and Coordination: **William J. Sydeman**

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Contribution to the Theme Section 'Marine ecosystems, climate and phenology: impacts on top predators'

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Marine ecosystems, climate and phenology: introduction

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ABSTRACT: Mid to high-latitude marine ecosystems are characterized by strong intra-seasonal variability in productivity across multiple trophic levels. It is understood that climate variability, as well as projected climate change, is likely to cause substantial changes in the timing of key seasonal events, such as the spring phytoplankton bloom, dates of diapause for zooplankton, or nesting dates in seabirds. However, it is not well known how changes in timing across multiple trophic levels will impact predator-prey relationships. Several mechanistic hypotheses have been put forth to explain changes in fish production in relation to phenological variability of prey, including Cushing's (1990; Adv Mar Biol 26:249–293) 'match-mismatch' hypothesis, yet there have been few tests of these ideas relative to ongoing oceanographic change. In this Theme Section, we present 9 papers that relate ocean climate variability and climate change to timing of key events for zooplankton, fish, and seabirds from northern hemisphere marine ecosystems. They cover phenological variability and consequences of timing changes for species of the California Current, Gulf of Alaska, NE Atlantic Ocean, Arctic Ocean and northern Japan Sea, all cold-water ecosystems, and highlight the importance of phenology as a key response variable, as well as the complexity of ecological relationships to be impacted by marine climate change. Multi-trophic level changes in phenology of species abundance and productivity are likely to have important consequences to marine ecosystem structure and function.

KEY WORDS: Abundance · Match-mismatch · Ocean warming · Plankton · Prey · Seabirds · Timing

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Anthropogenic warming of the world's oceans is evident for most of the globe (Levitus et al. 2000, 2005), but until recently reports of impacts of climate change in marine ecosystems have lagged behind those of terrestrial counterparts. Despite the role of the oceans in driving and modulating earth's climate system, and the substantial importance of marine organisms to providing numerous ecosystem services to humanity (Cheung et al. 2009), marine climate impacts received scant attention in the latest International Panel on Climate Change (IPCC) assessment report (Richardson & Poloczanska 2008). This is surprising given that interannual and lower frequency climate variability are known to have dramatic and sometimes devastating effects on marine biota, from plankton to fish, marine birds and mammals (Hurrell et al. 2003). Therefore, it seems likely that anthropogenic warming (AW) would strongly impact marine environments and ecosystems.

In terrestrial systems, diverse studies have shown that plants and animals have shifted their ranges towards higher latitudes or altitudes in response to AW (Walther et al. 2002, Parmesan & Yohe 2003, Parmesan 2006). In marine ecosystems, range shifts have been observed for groundfish in the North Sea (Perry et al. 2005) and Bering Sea (Mueter & Litzow 2008). Moreover, in many terrestrial systems, changes in phenology, i.e. the study of 'timing' of seasonal activities (such as reproduction, migration, bud-burst) within a given year have been documented. In most cases, and in accordance with AW, timing has become earlier (Parmesan 2006). In marine systems, changes in timing have been documented, but less frequently than in terrestrial systems (Mackas et al. 2007, Richardson 2008)

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and both climate variability and climate change have been related to phenological variation.

Observed responses of individual species, however, are just a starting point in understanding change in complex marine ecological systems that may result from climate variability, ocean warming and other forms of anthropogenic climate change (e.g. change in wind strength and circulation). While organisms may respond to ocean warming by advancing — or delaying, both situations have been observed, even in the same locality (Byrd et al. 2008) — seasonal timing, there are physiological, evolutionary, and ecological reasons to expect that different species will change at varying rates (Visser et al. 2004, Visser & Both 2005, Parmesan 2006). Indeed, some studies of warming impacts in disparate communities worldwide have found that previously tight trophic coupling (i.e. feeding or mutualistic interactions) between predator and prey, herbivore and food plant, parasite and host, have been disrupted because the resource (prey or host) is not available at the right time or place, i.e. climate change has caused a 'mismatch' in phenology (Stenseth & Mysterud 2002, Gremillet et al. 2008). Changes in important ecological interactions such as predator–prey relationships could have fitness consequences, thereby ultimately affecting populations and communities. For example, a reduction in foraging efficiency could cause a decline in key demographic attributes (e.g. annual reproductive success) leading to poor recruitment and population decreases in future years. If persistent, decoupling of trophic linkages could have severe impacts on marine ecosystem organization and functions. Cushing (1990) suggested that the degree of 'match–mismatch' between predator and prey in time or space is a key influence on fisheries recruitment, affecting fish biomass and fisheries yield, and a number of studies have related the loss of groundfish in the North Atlantic (cod) to trophic mismatches with their prey (large calanoid copepods) (Beaugrand et al. 2003).

It is critical, therefore, that upper trophic level predators adjust energy-intensive phases of their life cycle (e.g. migration, reproduction) to periods of maximum food availability within each year. The overlap in predator activities/needs and prey availability is influenced by both the timing and abundance of the prey (Fig. 1). Mid-trophic-level forage fish, squids, and zooplankton should also time their breeding schedules to coincide with the intra-seasonal peak of their prey (including micro-zooplankton and phytoplankton) availability. With ocean warming, and the multiple food web links involved, severe trophic mismatches between supply and demand may develop if the timing of multiple trophic levels responds to climate change in different ways.

With this background in mind, we convened a symposium entitled 'Phenology and climate change in the North Pacific: implications of variability in the timing of zooplankton production to fish, seabirds, marine mammals, and fisheries (human)' on 2 November 2007 at the 16th Annual Meeting of the North Pacific Marine Science Organization (PICES) in Victoria, Canada. The contributions to this Theme Section by Batten & Mackas (2009), Schroeder et al. (2009), and Watanuki et al. (2009) were originally presented in that topic session. Additional papers were solicited to provide a broader survey of phenological impacts on top marine predators.

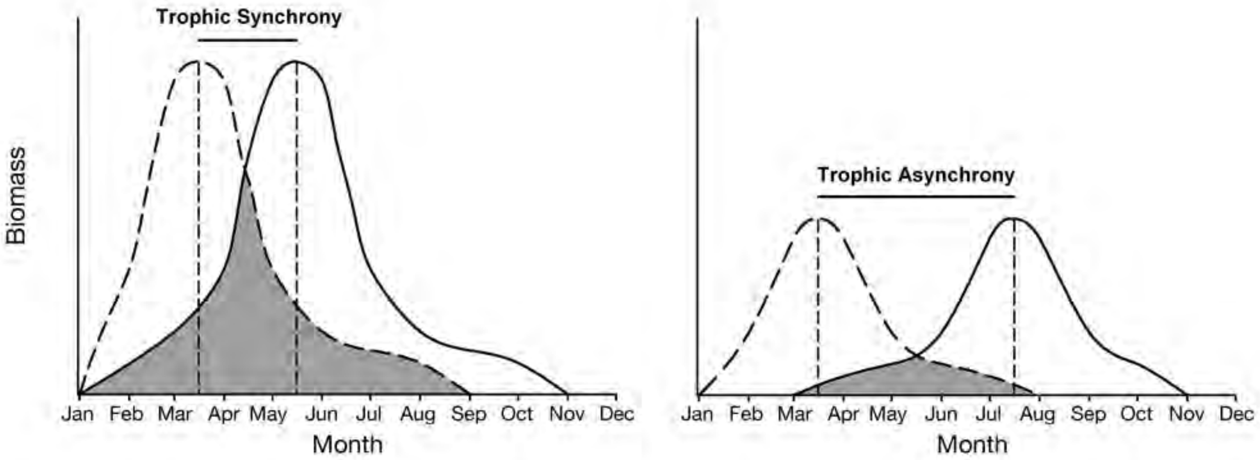

Fig. 1. Schematic of how phenology (timing) and relative abundance (biomass) affect the degree of trophic match-mismatch (after Durant et al. 2005). The key variable is the degree of trophic overlap of predator needs (continuous line) and prey availability (dashed line) in time and space. Dashed curves reflect biomass of prey (height) and seasonality of prey abundance (position of maximum). Reproductive success and other demographic traits will be high when there is great trophic overlap (grey area under curves)

Our intentions in preparing this Theme Section were 4-fold. (1) We wished to investigate the physical basis for phenological changes in marine animal populations. To demonstrate effects of AW, it is necessary to link change in populations to a physical 'state' variable; typically, this is temperature, but we also considered winds, degree of ocean stratification, currents and circulation flow rates, and date of the spring transition as potentially important links between AW and marine populations. All of the papers in this Theme Section contain data and analyses on physical-biological interactions, focused primarily on temperature and atmospheric or oceanographic drivers of temperature variation (e.g. the North Atlantic Oscillation).

(2) We wanted to describe phenological changes in space and time, with the same species in different ecosystems and habitats if possible. For zooplankton, Batten & Mackas (2009) describe changes in developmental timing for *Neocalanus plumchrus*, a dominant mesozoplankton species in the sub-arctic North Pacific. For fish, Holt & Mantua (2009) investigate recruitment variations of sablefish *Anoplopoma fimbria* and Pacific ocean perch *Sebastes alutus* in relation to various measurements of the timing of the spring transition in the California Current. In the case of seabirds, we were able to obtain studies on a total of 5 seabird species, with 3 — Cassin's auklet *Ptychoramphus aleuticus*, common murre/muillemot *Uria aalge*, and black-legged kittiwake *Rissa tridactyla*— having data from different regions and ocean systems. Studies on murres/guillemots represent research from the California Current (Schroeder et al. 2009), NE Atlantic Ocean (Votier et al. 2009), and Gulf of Alaska (Shultz et al. 2009). The work on kittiwakes represents studies from the Gulf of Alaska (Schultz et al. 2009) and Spitsbergen, Svalbard in the high Arctic Ocean (Moe et al. 2009). The work on Cassin's auklet comes from studies in the central (Schroeder et al. 2009) and northern (Bertram et al. 2009) sectors of the California Current. Cassin's auklets are planktivorous, feeding primarily on euphausiid crustaceans and large calanoid copepods (Bertram et al. 2009). A related planktivorous species, the little auk *Alle alle*, was reported on by Moe et al. (2009). Finally, Watanuki et al. (2009) and Ito et al. (2009) provide information on another member of the seabird family Alcidae, rhinoceros auklets *Cerorhinca monocerata*, which consumes both fish and zooplankton (euphausiid crustaceans). Alcids (murres, auklets, and auks) are wing-propelled divers reliant on large and perhaps persistent prey patches for successful reproduction. Thus, they are particularly appropriate subjects for studies considering the importance of prey abundance, timing of abundance, and spatial distribution of prey.

(3) We intended to examine the hypothesis that climate change is affecting trophic interactions through changes in the degree of match-mismatch between predators and prey. To study this hypothesis, a number of steps are required, including: (a) examining relationships between climate and prey, (b) investigating the seasonality of prey abundance in the environment, (c) quantifying the use of prey by predators, and (d) determining the fitness consequences of variation in prey abundance and distribution (collectively 'prey availability') (Durant et al. 2007). The papers by Bertram et al. (2009), Schultz et al. (2009), Watanuki et al. (2009) and Ito et al. (2009) provide independent measurements of prey availability in the environment, examine relationships between prey availability and ocean climate, proxied by sea surface temperature (SST) and current flows, and relate the degree of matching and mismatching in prey availability to predator needs. Watanuki et al. (2009) take this a step further in linking indices of match-mismatch in their system to variation in large-scale atmospheric pressure cells in the northern hemisphere. This paper represents one of the most comprehensive examinations of the climate change match-mismatch hypothesis to date, including data from atmospheric science to seabird ecology.

(4) We desired to develop indices of key physical-biological interactions with which to evaluate the nexus between climate change and match-mismatch in marine ecosystems. Holt & Mantua (2009) provide a comprehensive series of indices of the 'spring transition' from winter to upwelling conditions in the California Current system. Schroeder et al. (2009) make the point that wintertime upwelling conditions are important to seabird reproductive phenology, and provide indices to key physical measurements at that time of year. Batten & Mackas (2009) provide a new index of developmental timing in zooplankton, and demonstrate that the duration of peak biomass, as well as the timing of peak biomass, has changed through time. Bertram et al. (2009) and Ito et al. (2009) provide indices to the timing of prey switching in auklets, which has consequences to reproductive performance. Schroeder et al. (2009) highlight the value of considering 'variance' in addition to measures of central tendency (mean or median) in reproductive phenology as an important indicator of change.

In tackling the issue of marine climate impacts, the complexity of ecological systems must be considered. Predator–prey interactions and changes therein are a prime example of how AW of the world's oceans could alter marine ecosystem organization, structure, and ultimately the services provided to society (food). Here we have compiled a series of papers that focus on mechanistic inter-relationships and the complexities of marine ecological systems, mainly through the lens of seabirds, but also considering important fish and zooplankton populations. Seabirds are understood to be useful indicators of marine ecosystem dynamics, though there is work to be done to resolve key relationships (Durant et al. 2009). Nonetheless, we have established in this Theme Section that climate change can have broad impacts on key trophic interactions within diverse marine ecosystems. Understanding and distinguishing the impacts of natural and anthropogenic climate impacts on marine ecosystems, within the context of other human pressures (e.g. fisheries, development), is critical for restoring and sustaining healthy ocean ecosystems.

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Shortened duration of the annual *Neocalanus plumchrus* biomass peak in the Northeast Pacific

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ABSTRACT: The calanoid copepod *Neocalanus plumchrus* (Marukawa) is a dominant member of the spring mesozooplankton in the subarctic North Pacific and Bering Sea. Previous studies have shown interdecadal and latitudinal variation in seasonal developmental timing, with peak biomass occurring earlier in years and places with warmer upper ocean temperatures. Because *N. plumchrus* normally has a single dominant annual cohort, its seasonal timing can be indexed from measurements of total population biomass or by following progressive changes in stage composition. Early studies empirically found that peak upper ocean biomass occurred when about half of the pre-dormant population had reached copepodite stage 5 (C5). However, more recent comparisons derived from recent Continuous Plankton Recorder (CPR) data now show peak biomass when a larger fraction (>80%) of the population is at C5. CPR samples the surface 10 to 15 m, but comparisons to depth-resolved BIONESS data show that this discrepancy is not an artefact of sampling depth. Other causes are either a prolongation of duration of pre-dormant C5 or a narrowing of the age range making up the annual cohort. We assessed changes in cohort width using a modification of Greve's cumulative percentile method, and found that average cohort widths in the Alaska Gyre were significantly narrower in 2000–2007 than in 1957–1965 (1968–1980 were intermediate). Net tow sampling of Strait of Georgia populations showed a similar significant narrowing of cohorts in the 2003–2005 sampling period. This study provides evidence that in addition to the shift to an earlier occurrence of peak biomass reported previously, the duration of the peak has also decreased in the last decade.

KEY WORDS: *Neocalanus plumchrus* · Copepod · Biomass · Continuous Plankton Recorder

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INTRODUCTION

The calanoid copepod *Neocalanus plumchrus* (Marukawa) spends only a short fraction of the year in surface waters of the subarctic Pacific, completing its annual development cycle from early copepodite through to the sub-adult stage in about 3 mo, after which it migrates to deeper layers for prolonged seasonal dormancy, followed by maturation, mating, and spawning at depth. Recent data from Continuous Plankton Recorder (CPR) sampling, analyzed in this study, suggest that the surface abundance peak is now even narrower than shown in studies published before the CPR survey began in 2000.

Miller et al. (1984, and revised by Miller & Clemons 1988) detailed the annual life cycle of *Neocalanus plumchrus* at Ocean Station P (OSP) in the oceanic subarctic NE Pacific at 145° W, 50° N. Maturation and spawning rates were at a maximum in the autumn, even though early copepodites were not present in surface waters until the following late winter/early spring. This contrasts with the coastal populations in the Strait of Georgia (a small but deep marginal sea lying between Vancouver Island and the coast of mainland North America) which mature in late winter, with a spawning peak in February (Fulton 1973). The duration of the surface biomass peak also varied between these 2 locations, being about 60 d at OSP

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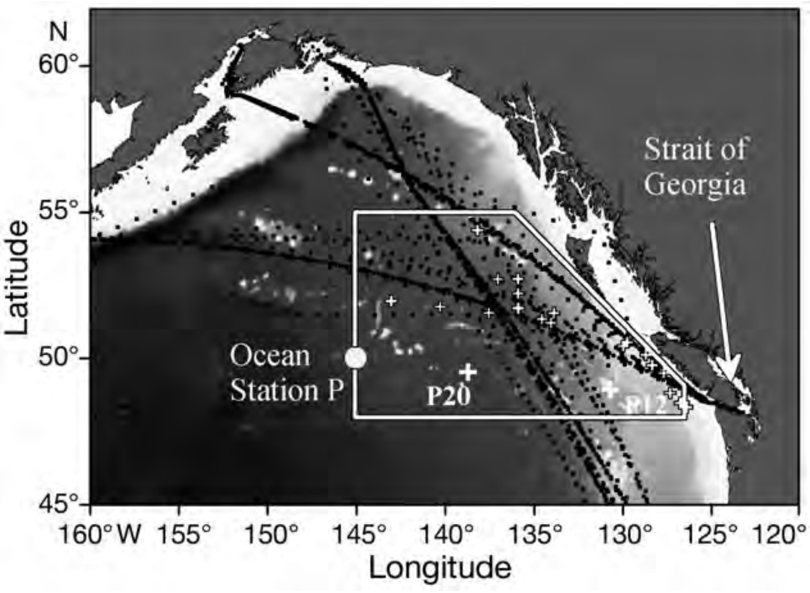

Fig. 1. Study area (polygon and the Strait of Georgia). (■) CPR samples; (✚) BIONESS sampling; (large crosses and circle) Line P stations where Tucker trawl was deployed

(Miller 1993) but often <40 d in the Strait of Georgia (Fulton 1973).

A more intensive sampling program allowed stage durations to be established for copepodite stages 1 to 4 (C1–C4; Miller 1993), and these duration estimates were used by Mackas et al. (1998), together with a time series of biomass data from OSP, to produce an index of the timing of peak biomass. Peak C2–C5 biomass was found empirically to occur when the proportion of C5 was between 35 and 65% of the total copepodite abundance; the midpoint, 50%, was therefore used to estimate the date of peak biomass. This index allowed a precise date of peak biomass to be deduced from relatively infrequent sampling by linearly interpolating the stage composition between sampling dates. The index was subsequently used to show interdecadal variation in developmental timing including an advance in the peak biomass under warm ocean conditions (Mackas et al. 1998, 2007).

The CPR began sampling the NE Pacific in 2000 and has maintained 2 transects that sample the region between the outer coast of British Columbia, Canada, and OSP 6 to 9 times per year. The '50%C5' index was applied to the CPR stage composition data and showed a similar advance in the warmer years of 2004 to 2006 versus the cooler years of 2000 to 2002 (Mackas et al. 2007). However, estimates of biomass derived from the abundance data (as well as the raw abundance data themselves) suggested that the peak in biomass was occurring at a later date than given by the stage-composition index (although the warm versus cool year advance was maintained). This study details the investigation into this discrepancy and possible implications.

MATERIALS AND METHODS

Zooplankton sampling. ***Continuous plankton recorder:*** The sampling and data analysis are as described by Mackas et al. (2007) but extended to include the subsequent additional sampling in 2005 and 2006. Two CPR transects intersect in the eastern Gulf of Alaska (Fig. 1). The 'North-South' route runs between Alaska (Prince William Sound in 2000 to 2003 or Cook Inlet in 2004 to 2006) and the west coast of the USA (Long Beach, California, in 2000 to 2003; Seattle, Washington, in 2004 to 2006) 5 to 6 times per year through spring and summer. The 'East-West' route runs between the Canada–USA border and Japan 3 times per year. The offshore study area shown in Fig. 1 has thus been sampled 6 to 9 times per year with about half of those samplings occurring in spring and early summer.

The CPR sampler and its deployment and sample processing methodologies (Richardson et al. 2006) are the same as have been used in the Atlantic since the 1940s. Briefly, a mechanical towed body (the CPR) is towed behind commercial ships at a depth of about 7 m. Water and plankton enter a small hole at the front of the sampler and are progressively caught, rolled up, and preserved between 2 ribbons of silk gauze (mesh aperture 0.27 mm). The movement of the gauze is mechanically driven by a propeller at the tail of the CPR and is proportional to distance traveled: each 10.16 cm panel of gauze filters a total of about 3.1 m^3 of water and represents an average of about 18.5 km (10 nautical miles) along the transect. At the end of each trip, the cartridges containing the mesh are offloaded and shipped to a laboratory for sectioning and labeling of the gauze, followed by identification and enumeration of retained zooplankton by species and stage.

Copepodites of *Neocalanus plumchrus* are not routinely distinguished from their congener *N. flemingeri* in the CPR analysis, although C5 copepodites were counted in 2 size ranges from 2001 onwards (>4.2 mm and 3.4 to 3.9 mm), the smaller of which are assumed to be *N. flemingeri* (Batten et al. 2003, Mackas et al. 2007). *N. flemingeri* completes its life cycle in surface waters earlier than *N. plumchrus* and is less dominant in the offshore NE Pacific (Miller & Clemons 1988). In the following analyses, only the larger C5 copepodites were included, although for C2, C3, and C4, some *N. flemingeri* may also have been present, and for data from 2000, some *N. flemingeri* C5 may also have been present.

Conversion of abundance counts to biomass was achieved by multiplying the abundance of each stage by a stage specific dry weight and summing the products for each sample. Dry weights were calculated from published lengths and the calanoid copepod length:weight relationship from Planque & Batten (2000), giving weights of C2: 21.3 µg, C3: 57.2 µg, C4: 161 µg, and C5: 488 µg. These dry weights are somewhat higher than those given by Mackas et al. (1998), but in fact the relative changes in total biomass between successive samplings is minimal if these values are adjusted.

The CPR samples the surface ~10 m layer while the net samples used in previous studies of *Neocalanus plumchrus* life history sample much more of the water column (usually down to 150 to 250 m or more). Although *N. plumchrus* copepodites are generally believed to be near-surface day and night, we first needed to exclude the possibility that the CPR has sampled a biased stage composition. If different copepodite stages inhabit different strata, then applying the Mackas et al. (1998) index to CPR data could produce an erroneous date of peak biomass.

Net tows during the 1956–1980 OSP 'weathership' time series: OSP was occupied semi-continuously as an offshore weather station from the 1950s to 1980, and the weatherships collected a variety of physical oceanographic time series (Tabata & Peart 1985, Freeland 2007). The weatherships also collected frequent zooplankton samples: vertical net tows covering the upper 150 m throughout most of the time series (Fulton 1983, Waddell & McKinnell 1995), plus weekly sampling to 2000 m in 1980 to 1981 (Miller et al. 1984, Miller & Clemons 1988). The majority of the 0 to 150 m samples were analyzed only for total wet weight biomass, but dominant species (including combined *Neocalanus plumchrus/flemingeri*) and their later developmental stages were enumerated in 1971, 1973, and 1980 (Waddell & McKinnell 1995). As noted above, Mackas et al. (1998) estimated seasonal timing of *N. plumchrus* during the weathership time series using a combination of the biomass (all years) and stage composition (1971,1973, 1980) indices, and concluded (based on those years of overlap) that peak biomass corresponded to a C5:total copepodites ratio between 35 and 65%. In this paper, we applied an additional phenology index based on cumulative integration of the biomass time series (developed by Greve et al. 2001, 2005, and described below) to examine interannual variation in cohort width (i.e. the duration of the period of high biomass).

Depth-stratified sampling with multiple net systems: After the termination of the semi-continuous weathership time series, multiple-net zooplankton sampling systems (BIONESS [B], MOCNESS [M], and/or Tucker trawl [TT]) were deployed from intensive but shorter duration research programs in the study area in late spring of several years (Fig. 1): 1984 (B), 1987 (B&M), 1988 (M), 1996 to 1997 (TT), and 2000 to 2004 (B) have provided samples of zooplankton abundance within discrete depth bands. Typical depth strata for these tows were: 0–10, 10–25, 25–50, 50–75, 75–100, 100–150, and 150–250 m per haul (for additional details, see Mackas et al. 1993, Miller 1993, Goldblatt et al. 1999). Although contemporaneous depth-stratified and CPR sampling was too limited for direct comparison, these data do enable us to compare the depth preferences of the different copepodite stages. B samples from May or June within the study area were used (Table 1), and only from the depth bands listed above. Separate densities of C2 to C5 (*Neocalanus plumchrus* plus *N. flemingeri* for C2 to C4) copepodites were calculated for each depth band, integrated over the 250 m sampling depth, and then the proportion of each stage occurring within each depth band was calculated for each year.

Analysis. ***Estimation of peak biomass:*** The estimation of the date of peak biomass from stage composition CPR data follows the methodology of Mackas et al. (1998). The proportion of the C2–C5 community present as C5 on each sampling date was calculated. Linear interpolation was used to deduce the date at which 50% of the population were at the C5 stage (since this date usually occurred between samplings).

Estimation of cohort width: Greve and colleagues have developed and applied an alternative method for indexing zooplankton seasonal phenology (examples in Greve et al. 2001, 2005 and Valdés et al. 2006) that relies on cumulative integration through each year of the bell-shaped curve of abundance versus date or biomass versus date. 'Start-of-season' is defined as the date at which the cumulative curve crosses a lower threshold (15th or 25th percentile), 'middle-of-season'

Table 1. Summary of BIONESS hauls in each year used in the analyses

Year	Period	Number of hauls
1986	14–15 June	5
1987	6–9 June	5
1993	25 June	2
2000	18–22 June	7
2001	4–11 June	10
2002	5–6 May	2
2003	18–19 June	2
2004	27–31 May	4

as the date for the 50th percentile, and 'end-of-season' as the 75th or 85th percentile. For our purposes, the 'duration-of-season' estimate (number of days between the 25th and 75th percentiles) provides a useful index of cohort width.

Sampling at OSP was often very frequent (a few days apart) and a 3 point running median was used to smooth the time series. Bongo net sampling has also occurred in the adjacent Strait of Georgia (Fig. 1) sporadically over the last few decades with sufficient temporal resolution to calculate cohort width occurring in the years 1966–1968, 1976, 1996–1998, and 2003–2005 (Fulton 1973, Bornhold 2000, R. El-Sabaawi pers. comm.). Sampling occurred between 6 and 23 times per year (i.e. at least as frequently as the CPR sampling) and was typically a vertical net haul from 100 m to the surface.

Cohort widths were calculated for each year of biomass data from the Strait of Georgia, OSP weathership, and NE Pacific CPR time series as the number of days between the 25th and 75th percentile of the cumulative abundance (interpolating where necessary between successive samplings).

Model of population abundance, biomass, and stage composition versus cohort age composition: To examine the effects of varying cohort width and/or relative stage duration on the relationship between biomass-based and stage-composition-based timing indices, we reapplied a time-step spreadsheet model of growth, survival, and stage progression that was originally developed by Miller (1993) and subsequently applied by Mackas et al. (1998, 2007). Input parameters for the model are daily growth and survival rates versus copepodite stage, durations (days) of the 5 pre-dormant copepodite stages, and starting width of the copepodite cohort (SD in days of the bell-shaped abundance versus age-at-date curve). Outputs are total and stage-specific biomass and abundance versus date. Our original application (Mackas et al. 1998) had used a uniform weight-specific growth rate (7.3% d^{-1}), a mortality rate that declined from 13% d^{-1} at the start of C1 to 3% d^{-1} at mid-C5, stage durations from Miller (1993), and a Gaussian cohort with width parameter (SD) of 12 d. Here we report the effects of altering 2 of these parameters: a narrowing of the cohort width (SD reduced from 12 to 4 d), and increasing the pre-dormant duration of C5 from 25 to 35 d.

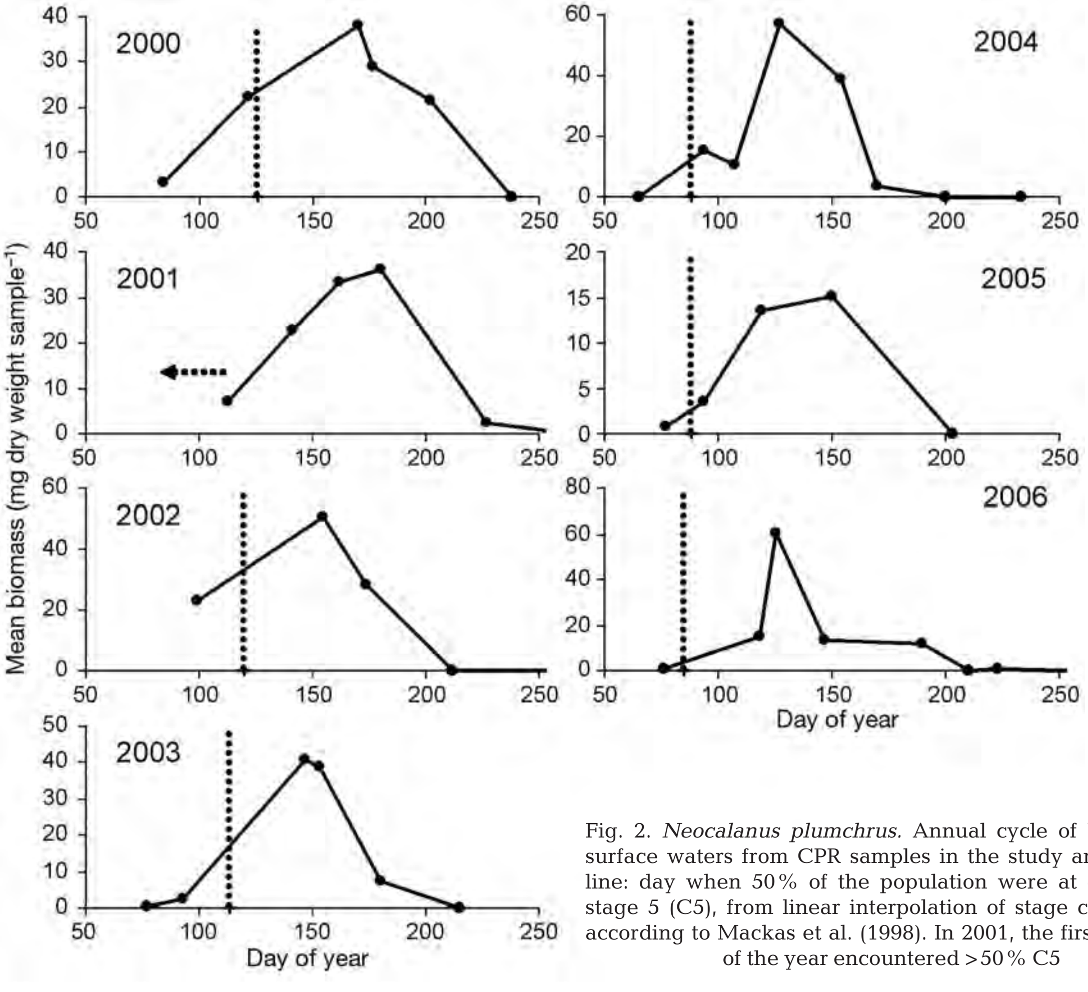

Fig. 2. *Neocalanus plumchrus.* Annual cycle of biomass in surface waters from CPR samples in the study area. Dotted line: day when 50% of the population were at copepodite stage 5 (C5), from linear interpolation of stage composition according to Mackas et al. (1998). In 2001, the first sampling of the year encountered >50% C5

RESULTS

The discrepancy in the estimates of peak biomass timing between the stage composition method (shown by the dashed lines) and the estimated sample biomass method is demonstrated in Fig. 2.

Because intervals between successive samplings of the study area by the CPR were between 6 and 67 d (mean of 29 d), it is not possible to pinpoint the date of peak biomass from the sample biomass method (hence the appeal of the stage composition method); however, it is clear that in each year, the stage composition method gave a date far in advance of the maximum observed sample biomass. An alternative way of viewing the CPR data is shown in Fig. 3, where the proportion of the community at pre-migrant C5 is plotted against the total biomass. Mackas et al. (1998) found the biomass peak to occur when C5 copepodites comprised between 35 and 65 % of the C2–C5 abundance. The CPR data in Fig. 3 show that peak biomass was not reached until most (>80 %) of the population were at the pre-migrant stage in each year.

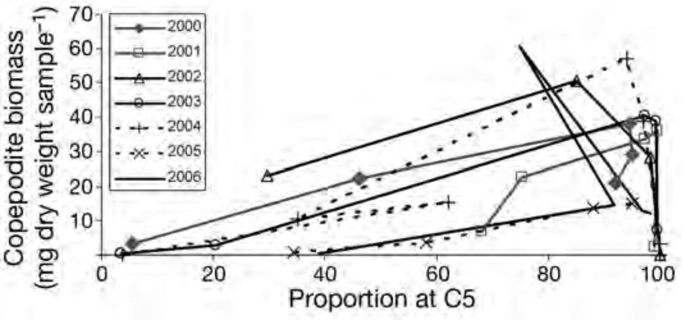

Fig. 3. *Neocalanus plumchrus.* Proportion of the C2–C5 community at C5 against the mean total copepodite biomass (mean dry weight in mg per CPR sample, ~3 m^3), from CPR data. If peak biomass were to occur when the population was around 50 % C5 (as in the Mackas et al. 1998 index), then bell-shaped curves with maxima centered near 50 % would be expected. Instead, peak biomass occurs when the population is >80 % C5

It was first necessary to establish whether there was a bias in the stage composition sampled by the CPR that could be responsible for this difference. Mean abundance of each copepodite stage in each depth band was calculated from the B data by averaging all years. Most of the copepodites in the water column at the time the B was sampling were C5, with the other stages making up only about 8 % on average. In 1986, 1993, and 2002, all copepodites were C5. Minor differences occurred in the proportions of each stage at each depth band (Fig. 4A) but the depth distribution of each stage (C2 to C5) was highly correlated with the depth distribution of each other stage ($p < 0.01$ in all cases). The depth band containing the highest number of copepodites was the 10 to 25 m layer, with at least 63 % of each stage occurring in this stratum. The surface layer comprised <13 % of each stage on average. However, when means were calculated separately for each year, it became apparent that there were 2 distinct patterns, each occurring in multiple years. In 3 of the years (2000, 2001, and 2002) only about half of the copepodites were in the 10 to 25 m layer, with substantially more occurring in the surface 10 m layer. This was most obvious in the C5 (younger stages being

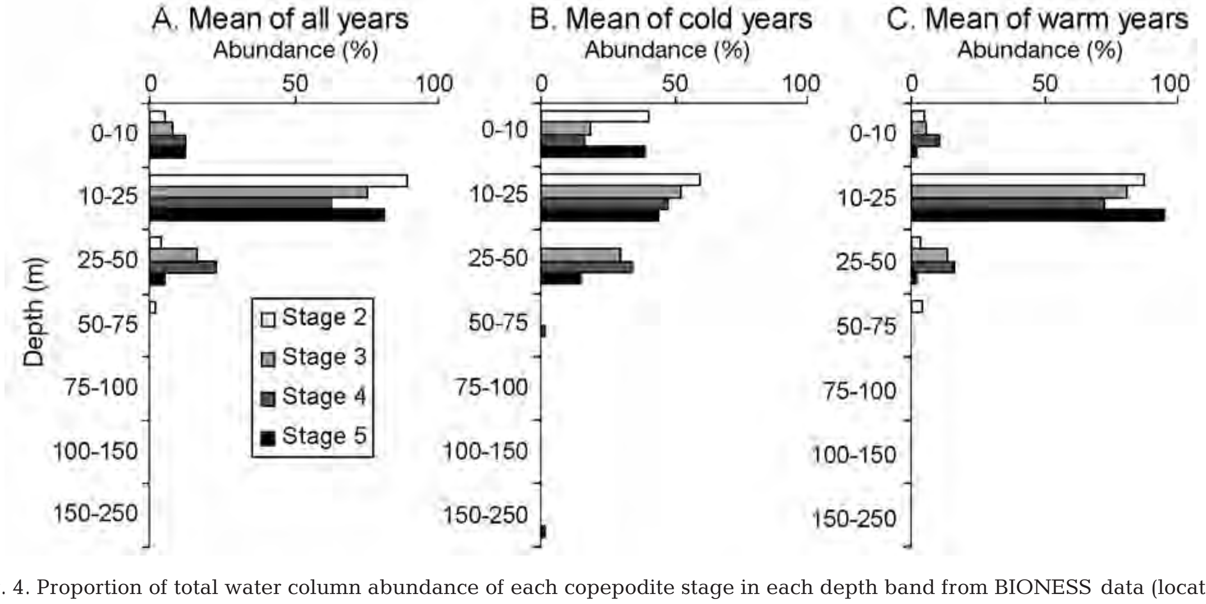

Fig. 4. Proportion of total water column abundance of each copepodite stage in each depth band from BIONESS data (locations shown in Fig. 1). (A) mean of all years, (B) mean for cold years (2000, 2001, and 2002), and (C) mean for warm years (1986, 1987, 1993, 2003, and 2004)

scarce in late spring), and the mean proportion of C5 in the surface layer for these 3 yr was 39% compared to 2% for the remaining years. Although we have not included environmental data from the B sample locations in this study, the years 2000, 2001, and 2002 were the coldest years of the sampling period according to data from the Amphitrite Point lighthouse on the southwest coast of Vancouver Island (Table 2, data available at: www-sci.pac.dfo-mpo.gc.ca/osap/data/lighthouse/amphitrt.txt). We have thus designated 2 groups of years, warm (1986, 1987, 1993, 2003, 2004) and cold (2000, 2001, 2002), and show the depth distributions separately Fig. 4B,C. When the depth distributions of each copepodite stage were compared to the distributions of the other stages (C2 to C5) within each group of warm or cold years, they were also significantly correlated ($p < 0.01$ in most cases), the only exception being C2 versus C4 in cold years, where $p = 0.07$.

Notwithstanding the change in distribution of total abundance versus depth between warm and cold years, these analyses show that the fraction of the total contributed by each developmental stage is approximately homogeneous across all upper depth strata. The CPR samples at about 7 m, and we cannot know with any certainty the degree of mixing behind the fast-moving, large vessels used to tow it, but it is likely that the samples contain plankton from well-mixed surface 10–15 m waters, perhaps deeper. Although the CPR will only be sampling a fraction of the total water column copepodites, it should be sampling each stage equally efficiently, and there is likely no bias caused by sampling to account for the discrepancy in peak biomass timing estimates.

Three time series of cohort width from OSP, the Strait of Georgia, and the CPR data in Fig. 1 are compared in Fig. 5; note that periods of overlap are minimal. The Strait of Georgia populations have a narrower cohort than the oceanic populations, which would be expected from the shorter duration of biomass described there by Fulton (1973) and compared by Miller (1993).

Table 2. Mean annual sea surface temperature (SST) from Amphitrite Point lighthouse for the years in which BIONESS data are available

Year	Mean annual SST (°C)
1986	10.575
1987	10.925
1993	10.592
2000	10.183
2001	9.875
2002	10.233
2003	10.750
2004	10.958

DISCUSSION

As high-frequency sampling of *Neocalanus plumchrus* in the NE Pacific is rare, and oceanic sampling is even less common, the CPR program has provided the greatest temporal resolution for this area (approximately monthly) since its inception in 2000. However, even this is inadequate for determining peak biomass timing without extrapolation. A few detailed surveys occurred prior to 2000, although in many cases separate stages were not counted. Two studies that do offer the opportunity to examine whether peak biomass has been found to occur when C5 copepodites comprise ~50% of the population are TT data from May 1996

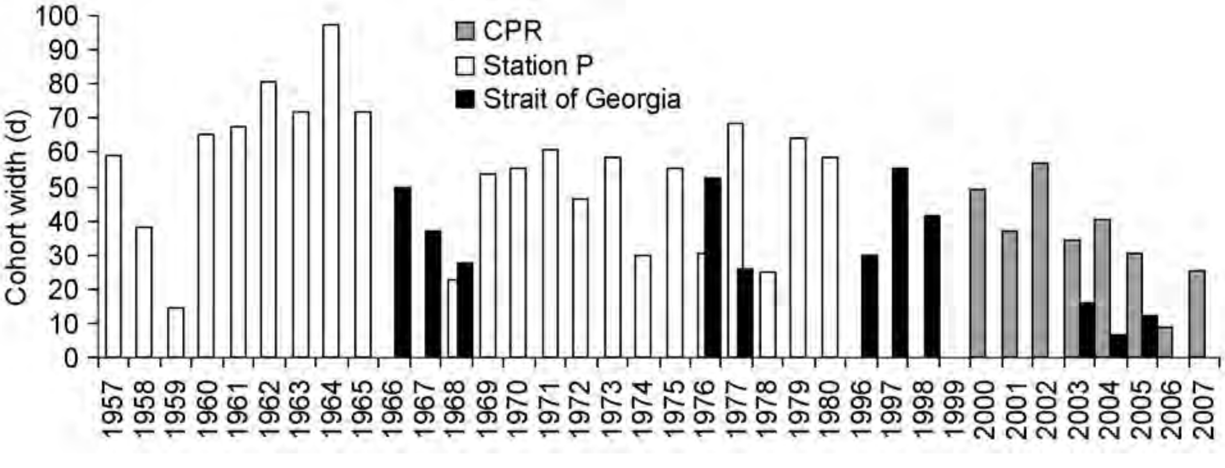

Fig 5. *Neocalanus plumchrus*. Index of cohort width in populations in the Strait of Georgia (from bongo net samples) and the oceanic NE Pacific (Ocean Station P net data, 1957 to 1980, and CPR data, 2000 to 2007, from the region shown in Fig. 1). No sampling occurred between 1981 and 1995

(Goldblatt et al. 1999) and SUPER Program data from May 1988 (Miller 1993), although the timing of this latter survey was such that only *N. flemingeri* copepodites were sufficiently abundant. TTs also took place in June 1997, but by this later time, C5 copepodites already made up more than 50 % of the population, as did *N. flemingeri* copepodites in both years. The 1988 *N. flemingeri* data and the 1996 *N. plumchrus* data are shown in Fig. 6 and support the idea that peak biomass occurs when C5 copepodites make up approximately half of the population, since both graphs have a peak at about 60 % C5, within the range suggested by Mackas et al. (1998) of 35 to 65 %. They also both show a decline in total abundance as the population approaches 100 % C5, expected if older C5 are migrating out of the surface layer to enter dormancy, but not evident in the CPR data in Fig. 3 (a conversion of these abundance data to biomass in the same manner as the CPR data in Fig. 3 did not change the shape of the graphs in Fig. 6). Although *N. flemingeri* is a different species with somewhat different behaviors to *N. plumchrus*, we have included the data in Fig. 6 for 2 reasons: (1) because so few suitable data exist for comparison, and (2) because *N. flemingeri* diapauses as an adult, we might expect the peak in *N. flemingeri* biomass to occur farther to the right of the graph than for *N. plumchrus*, i.e. when a higher proportion of the population is at C5, yet it does not. The fact that it is comparable to the *N. plumchrus* TT data reinforces the past utility of the 50 % C5 peak biomass index, while suggesting that the post-2000 CPR data show something quite different.

Figs. 2 & 3 suggest that the peak in biomass of *Neocalanus plumchrus* in the subarctic NE Pacific is now occurring when the population is mostly at the premigrant stage. This seems to have been true in each year since the CPR survey began in 2000. We suggest that this must indicate a recent change in developmental chronology, compared to the period prior to 1998, since a depth-dependent sampling bias is unlikely. One possible change could be that C5 are taking longer to store the lipid necessary for them to successfully diapause. If the pre-dormant duration of C5 has increased to provide additional time for lipid accumulation, our model (Fig. 7B) shows that this change causes an increase in the overall fractional abundance of C5, and also shifts the stage ratio at the date of peak biomass to a higher percentage of C5 (more similar to the graphs in Fig. 3). However, this explanation would also imply a prolongation of the total developmental sequence, such that significant numbers of C5 would continue to be caught later in the year, or over a longer period. This has not been seen from CPR data collected through the summer. The graphs in Fig. 2 suggest instead that the decline in numbers has become more rapid, with few individuals found after mid-June. This contrasts with OSP data from the 1970's when peak biomass often did not occur until July (Mackas et al. 2007).

An alternative explanation is that the cohort width has narrowed. Spawning occurs over an extended period beginning in the autumn (Miller et al. 1984, Miller & Clemons 1988), but nauplii presumably only develop and migrate to the surface when conditions are suitable, i.e. in early spring. Mackas et al. (1998) concluded that differential survival of early versus late-arriving copepodites was responsible for the earlier peak in biomass in warm conditions. If the correct conditions for advancement occur for a shorter period of time, then the cohort will be more synchronized. Increased synchronization (a narrower cohort) will also strongly push the timing of peak biomass to a higher percentage of C5 (Fig. 7C). In the extreme case of complete synchronization of the cohort (all individuals exactly the same age in days), the peak biomass will occur when the entire population is at the C5 stage, and very close to the date when all individuals simultaneously enter diapause.

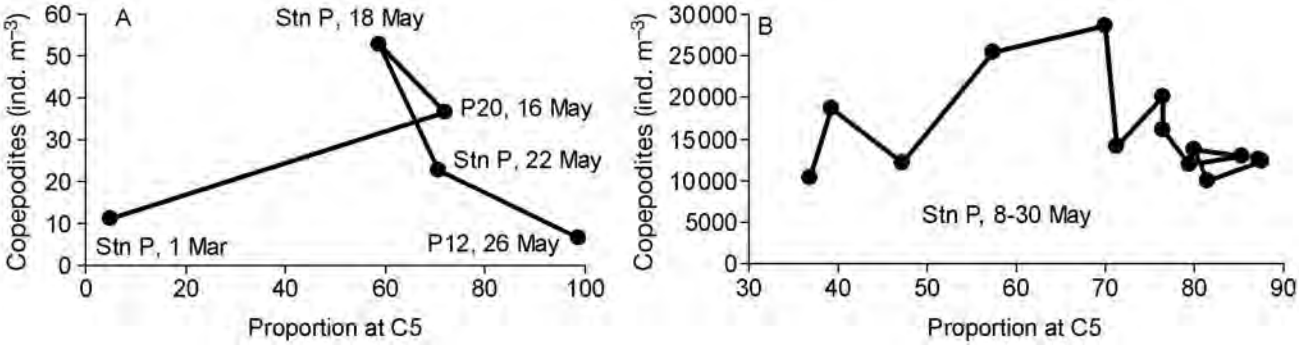

Fig 6. *Neocalanus plumchrus* and *N. flemingeri*. (A) Proportion of the *N. plumchrus* C2–C5 community at C5 against the mean C2–C5 density (to 150 m) of copepodites collected by Tucker trawls in 1996. Station name (Ocean Station P, P20, or P12, see Fig. 1 for location) and date of sampling are shown alongside each data point. (B) *N. flemingeri* data from Ocean Station P, May 1988

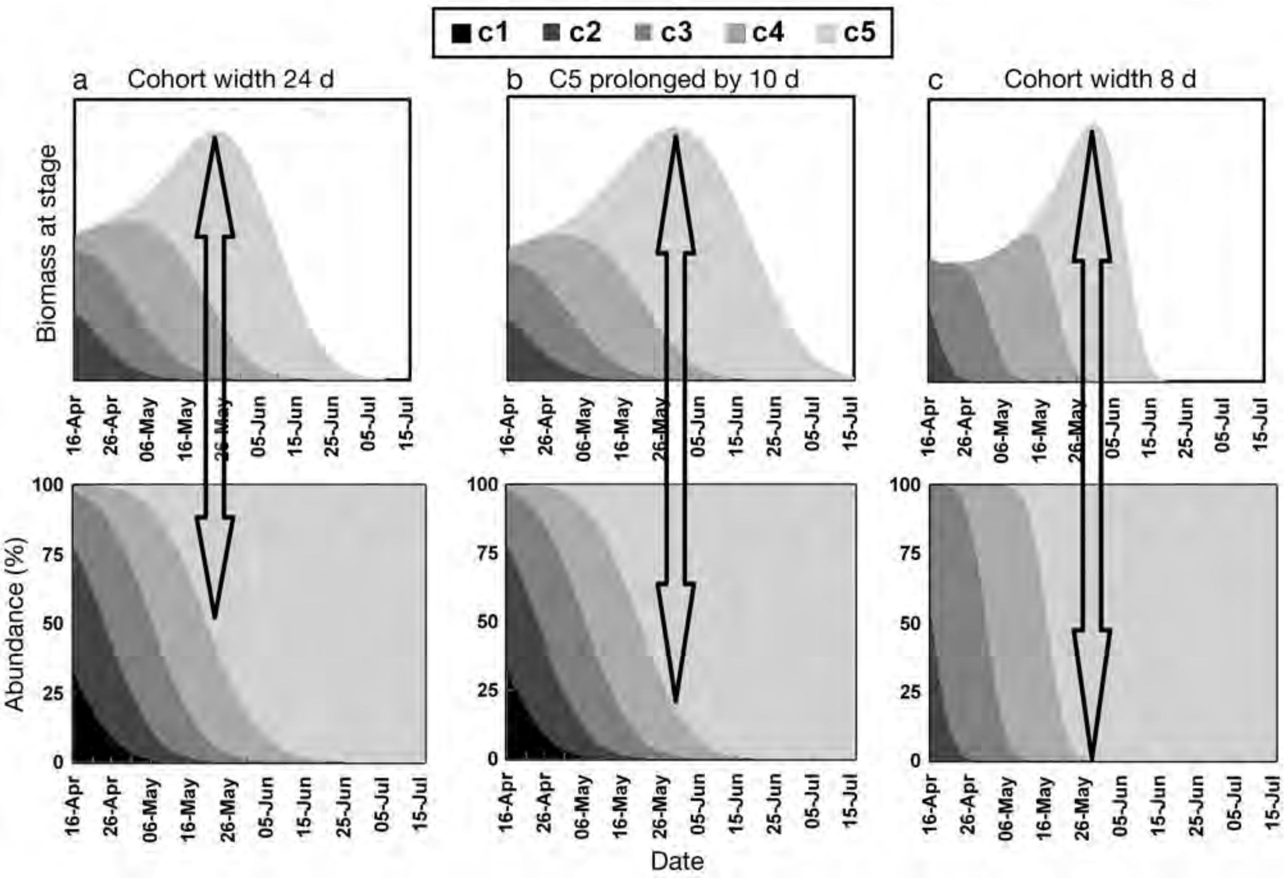

Fig 7. Model output showing stage-composition of total upper-ocean population biomass (top) and of percentage numeric abundance (bottom) vs. sampling date. (a) Base model as used in Mackas et al. (1998), biomass maximum occurs at about 50 % C5; (b) Persistence/prolongation of the pre-dormant duration of C5 (to allow accumulation of sufficient lipid to support subsequent dormancy), biomass maximum occurs at about 80 % C5; (c) Narrowing of the overall cohort age structure by a factor of 3 (due to a narrower spawning or survival/developmental window), biomass maximum occurs at nearly 100 % C5. Recent CPR time series are most similar to the pattern shown in (C)

All cohort widths post-2000 in the Strait of Georgia were narrower than the narrowest cohort there pre-2000, lending some support to the idea that cohort width in this region has also narrowed since 2000 (Fig. 5). An analysis of variance (ANOVA) of the cohort widths found in 3 time periods (1966–1977, 1996–1998, and 2003–2005) shows that the cohort widths are significantly narrower ($F = 8.28$, $p < 0.05$) between the latter time period and both previous periods. The narrowest cohort in the oceanic NE Pacific was also found post-2000, in 2006 CPR data, although narrow cohorts also occurred at OSP in 1959, 1968, and 1978 (Fig. 5). The widest cohorts occurred in OSP data, and in fact 12 of the 21 years of OSP data had wider cohorts than the widest cohort in the CPR data (2002). We can consider the CPR data to be a continuation of the OSP time series, with the caveats that the CPR also sampled east of OSP (Fig. 1), and the OSP data were collected much more frequently. The time series can then be divided into 3 time periods, 1957–1965, 1968–1980, and 2000–2007. An ANOVA of cohort widths in each period shows that the most recent time period has significantly shorter cohorts than the earliest time period ($F = 4.71$, $p < 0.02$) but that adjacent time periods are not significantly different. The method of data collection and its frequency have changed in the Strait of Georgia time series. Prior to 2000, *Neocalanus plumchrus* biomass was calculated by converting from total zooplankton biomass (R. El-Sabaawi pers. comm.), whereas post-2000, *N. plumchrus* has been counted separately. It is not clear whether this would lead to a change in the cohort width, but the result remains somewhat speculative.

Thus, although the lack of consistently collected and fully comparable data means that the results must be treated with some caution, the evidence suggests that spring cohorts of *Neocalanus plumchrus* in both the Strait of Georgia and the oceanic NE Pacific have narrowed over the preceding decades and are now at their narrowest.

The mechanism behind the advancement of peak biomass in warm years was considered by Mackas et al. (1998). The timing of the onset of thermal stratification was consistent with the earlier peak in biomass in the coastal Strait of Georgia populations compared to those at OSP, but no significant relationship was found between 3 indices of thermal stratification timing and the interannual variability in developmental timing. We have also considered temperature indices in relation to cohort narrowing. Mean monthly sea surface temperature is available from Amphitrite Point lighthouse, and winter (December to February), spring (March to May), and annual mean temperatures were correlated with the cohort width time series. In all cases, the correlations were negative (warmer temperatures were correlated with narrower cohorts), but only significantly so for the CPR time series and mean annual temperature of the previous year. Similarly, mean annual values of the Pacific Decadal Oscillation index were also negatively correlated with the time series, but only significantly so for the combined CPR and OSP, NE Pacific time series. It is likely that temperature is having some effect on both the timing of the peak biomass and the width of the cohort, but whether this is supplemented by other mechanisms or is in fact a proxy for another mechanism is not yet resolved.

There was also insufficient evidence to show whether the microzooplankton prey that make up the bulk of the *Neocalanus* diet at OSP (Gifford 1993) were even partially responsible for the advancement of peak biomass. Modeling results indicated that the copepods were more likely to influence the dynamics of their prey than vice versa. Dagg et al. (2006) also showed that mesoscale variations in food environment did not affect the final size before diapause of *N. plumchrus* and *N. flemingeri* in shelf waters of the Gulf of Alaska. Populations of *N. plumchrus* in the western Pacific have shown interdecadal variability in developmental timing of a similar magnitude. However, since the 1970s the pre-dormant surface-layer populations in the NW Pacific have not reached 50 % C5, suggesting that the cohort width may be increasing in the NW Pacific rather than narrowing (Chiba et al. 2006, K. Tadokoro unpubl. data). A significant correlation between phosphate concentrations and timing of peak biomass of C5 was found, suggesting that high nutrient conditions may prolong the period when suitable prey was available. It is possible that declining nutrient concentrations or other factors that limit prey availability are operating in the NE Pacific.

Whatever the cause, the results of our study suggest that not only is the period of plenty for *Neocalanus* predators occurring earlier in the year, but it is getting narrower. This has severe implications for the trophic functioning of the NE Pacific if the cause persists.

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Seabird nestling diets reflect latitudinal temperature-dependent variation in availability of key zooplankton prey populations

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ABSTRACT: We report on historical (1978 to 1982) and more recent (1996 to 2000) variation in the nestling diet of Cassin's auklet *Ptychoramphus aleuticus* breeding at Triangle Island (southern) and Frederick Island (northern), British Columbia, Canada; these islands are influenced by the California and the Alaska Current ecosystems, respectively. Ocean climate conditions off the British Columbia coast varied tremendously between 1978 and 2000. At both colonies, the nestling diet was composed largely of copepods and euphausiids, with fish contributing substantially in some of the warmer years at Triangle Island. The copepod *Neocalanus cristatus* was the single most important prey item at both colonies, and Stage V copepodites dominated in all sampling periods. We used a recently published temperature-dependent phenology equation to estimate the timing of peak biomass of *Neocalanus* near Triangle and Frederick Islands. During warm water years (such as 1996 and the El Niño of 1998), the timing and duration of *N. cristatus* availability in surface waters near Triangle Island was early and limited (mismatched) in contrast to cooler years (such as 1999 and 2000), when this prey was available to birds throughout the breeding season (matched). We argue that Cassin's auklet nestling diet data reflect the temperature-related timing of *Neocalanus* prey availability to seabirds in surface waters. Our results support the argument that inadequate overlap of prey availability and predator breeding (i.e. temporal trophic mismatch) is more likely on Triangle Island, where zooplankton peaks often occur earlier and are narrower, than on Frederick Island, where prey peaks are later and more protracted. Poor reproductive performance is the biological consequence of such trophic mismatch for Cassin's auklet. If the frequency of El Niño-like events increases and if ocean temperatures rise in the future, we predict an increase in the frequency of trophic mismatch events in the northeast Pacific Ocean.

KEY WORDS: Copepod availability · Ocean temperature · Match-mismatch · Seabirds · Cassin's auklet

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INTRODUCTION

Reports of ocean climate change on upper trophic level predator (e.g. seabirds) populations are becoming more frequent throughout the Northern Hemisphere as sea surface temperature (SST) variability increases and extremes are recorded (e.g. North Sea: Proffitt 2004; North Atlantic: Sandvik et al. 2008; Norway: Durant et al. 2003; Canadian Arctic: Gaston et al. 2005; Newfoundland: Montevecchi & Myers 1997; California: Sydeman et al. 2006, Lee et al. 2007; British Columbia: Gjerdrum et al. 2003, Hedd et al. 2006;

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Alaska: Anderson & Piatt 1999, Springer et al. 2007). In several cases, authors have sought to explain climate-related variation in reproductive performance of marine birds by examining phenology of breeding and prey availability and the possibility of matches and mismatches in seasonal timing (e.g. Bertram et al. 2001, Hedd et al. 2002, Durant et al. 2005, 2007, Suryan et al. 2006, Hipfner 2008, Gaston et al. 2009).

In the northeast Pacific Ocean, researchers invoked the match-mismatch hypothesis to explain failed reproduction in warm ocean years (1996 and 1998) for Cassin's auklets *Ptychoramphus aleuticus* on Triangle Island, British Columbia, Canada (Bertram et al. 2001, Hedd et al. 2002). They argued that in warm years there was less temporal overlap between the parental provisioning period and availability of a key prey species, *Neocalanus cristatus*, in surface waters. Hipfner (2008) tested the predictions of the match-mismatch hypothesis and found strong support for the explanation of Bertram et al. (2001) using a more recent and extensive time series (1996 to 2006) for Cassin's auklet on Triangle Island. Hipfner (2008) further demonstrated that it was the timing of prey availability, rather than prey abundance, which was the key factor determining the seasonal prevalence of *N. cristatus* in the nestling diet and concluded that seasonal timing mismatches could have significant demographic consequences for the world's largest Cassin's auklet population on Triangle Island.

The strong mismatches between *Neocalanus* prey availability and the timing of Cassin's auklet reproduction at Triangle Island reflect the geographic range of the prey, the highly seasonal life cycle of the prey, and the temperature-dependent nature of the seasonal peak and duration of prey availability. *N. cristatus* is a 'subartic copepod' and is not found as prey on Cassin's auklet colonies in California and Mexico because those colonies lie well below the southern limit to the geographic extent of *Neocalanus* spp. (Batten et al. 2003). The copepod prey are highly seasonal in surface waters (where they are available to Cassin's auklet to a depth of 40 m [mode]; Burger & Powell 1990) because of their distinctive life history strategy and annual life cycle. The copepod nauplii migrate from mesopelagic depths (400 to 2000 m) to feed and grow and then disappear from surface waters when they reach the final copepodite stage (cV) to migrate back to the deep sea zones and a prolonged dormancy (Mackas et al. 1998, 2004, 2007). In the northeast Pacific, total mesozooplankton biomass and productivity are strongly dominated by the large-bodied calanoid copepods of the genus *Neocalanus* (Mackas et al. 2007). As a consequence of their life history strategy as 'interzonal migrants' combined with their dominance of the regional mesozooplankton biomass, the annual peak of total mesozooplankton biomass in the upper layers of the subarctic Pacific is intense and may be very narrow in duration (Mackas & Tsuda 1999).

Latitudinal differences in the timing of *Neocalanus* copepod prey biomass peaks are expected based on regional temperature differences in the northeast Pacific. For *N. plumchrus*, monthly sampling using a continuous plankton recorder revealed that the timing of peak biomass (when 50 % of the population consists of copepodites at Stage cV) occurs about 5 wk earlier at the southernmost (40° N) part of the range than at the northernmost part (Bering Sea), with intermediate areas having intermediate timing (Batten et al. 2003). Mackas et al. (2007) further observed that the latitudinal range of developmental timing is at least as large, and probably larger, than was originally reported by Batten et al. (2003) and developed a new predictive temperature-dependent phenology equation for the northeast Pacific. The phenology equation demonstrates that

> 'variability of *N. plumchrus* life cycle timing is associated very strongly, and approximately linearly, with cumulative anomalies of upper-ocean temperature during the season in which the copepods are feeding and growing in the near-surface layer' (Mackas et al. 2007, p. 238, Fig. 8b).

Within the northeast Pacific Ocean, British Columbia, Canada, occupies a pivotal position from an oceanographic perspective, because the North Pacific Current bifurcates off its coast forming the Alaska Current to the north and the California Current to the south. Associated with these major currents are 3 oceanographic domains, the downwelling domain in the north, the upwelling domain in the south, and the transitional domain in the central coast (Ware & McFarlane 1989; Fig. 1). The Queen Charlotte Sound, in the transitional domain, also provides an obstacle to poleward transport of warm southern waters by disrupting the effectively continuous coastline that extends from central California to the northern tip of Vancouver Island (but see Zamon & Welch 2005).

Higher local adult annual survival of Cassin's auklets at Frederick Island, in the northern downwelling domain, than at Triangle Island, at the northern boundary of the California Current Ecosystem in the upwelling domain, indicates that British Columbia is a key location for the detection and investigation of latitudinal variation in oceanographic influences on upper trophic level predator demographics in the northeast Pacific (Bertram et al. 2005). Moreover, in striking contrast to Triangle Island, there have been no reports of reproductive failures on Frederick Island from historical reports (Vermeer 1985) or more recent comparisons (1994 to 1998, 2000 cited in Bertram et al. 2005).

In the present study we contrast inter- and intra-year nestling diets of Cassin's auklets on Triangle and Fred-

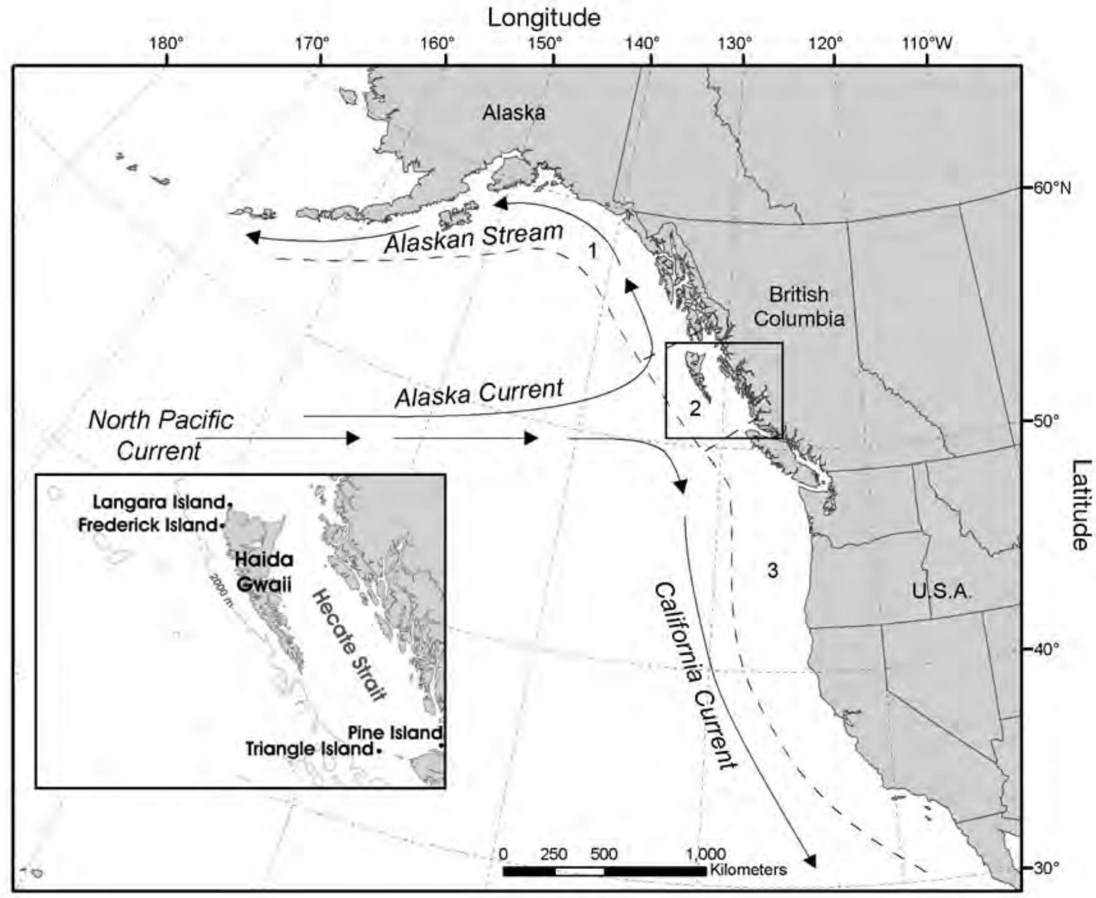

Fig. 1. Study sites, major currents, and oceanographic domains (adapted from Ware & McFarlane 1989). (1) Coastal downwelling domain; (2) transition zone; (3) coastal upwelling domain. Note that the north-south location of the bifurcation of the North Pacific Current varies between years (see Freeland & Cummins 2005 and also Batten & Freeland 2007). The 2000 m isobath and locations of Langara Island and Pine Island light stations are also shown in the inset

erick Islands and look for evidence of trophic mismatches at both colonies to explore contributions of diet composition to the observed inter-colony variation in vital rates. We investigate mismatch events of *Neocalanus cristatus* using the new equation of Mackas et al. (2007) to estimate the timing of peak biomass in relation to the amount of *N. cristatus* in the nestling diet in the late chick-rearing period. The study period encompasses a natural experiment before, during, and after the large 1997-1998 El Niño Southern Oscillation (ENSO; Wolter & Timlin 1998) and subsequent La Niña events, enabling us to examine their influences on the diets of upper trophic level seabirds in the oceanographically distinct domains in northern and southern coastal British Columbia. Our results show how mismatches have not been observed on Frederick Island and how the geographic distribution and temperature-dependent life cycle of the prey predispose the Triangle seabird colony to trophic mismatches in warm years.

MATERIALS AND METHODS

SST records. We obtained monthly SST records from Pine Island (50° 35′ N, 127° 26′ W, in keeping with previous work by Bertram et al. 2001 and Hedd et al. 2002) and Langara Island (54° 09′ N, 133° 02′ W) light stations (www.pac.dfo-mpo.gc.ca/sci/OSAP/data/SearchTools/Searchlighthouse_e.htm). Consistent with previous work on Cassin's auklet diet in British Columbia (e.g. Bertram et al. 2001, Hedd et al. 2002), we plotted average SST for the month of April to reflect ocean conditions that affect prey availability.

Study sites. While both study sites are among the outermost western islands on the coast of British Columbia and are located near the continental shelf break (200 m), they are influenced by different oceanographic domains (Fig. 1). Triangle Island (51° 52′ N; 129° 05′ W), at the northern end of the California Current Ecosystem, is in the coastal upwelling domain. It is the largest seabird colony in British

Columbia and contains the largest Cassin's auklet breeding colony in the world (540 000 pairs in 1989; Rodway et al. 1990). This windswept and effectively treeless island is the outermost island of the Scott Island chain, 45 km WNW of Cape Scott at the northern tip of Vancouver Island. It has been protected since 1971 as an ecological reserve by the province of British Columbia and is closed to the public (Anne Vallée Triangle Island Ecological Reserve, www.env.gov.bc.ca/bcparks/eco_reserve/anne_er.html).

Frederick Island (53° 56′ N, 133° 11′ W) lies approximately 2 km off the northwest coast of Haida Gwaii (Queen Charlotte Islands). The colony had approximately 90 000 pairs of nesting Cassin's auklets in 1980 (Rodway 1991, Rodway et al. 1994). Frederick Island is largely forested, and the vegetation is described by Rodway et al. (1994). The island is part of Duu Guusd Tribal Park and is protected as a Wildlife Habitat Area (Frederick Island, 6-037) for ancient murrelets *Synthliboramphus antiquus* and Cassin's auklet by the province of British Columbia (http://www.env.gov.bc.ca/cgi-bin/apps/faw/wharesult.cgi?search=number&select=6&number=037&submit=Search)

Nestling diet data. We used historical published records (Vermeer 1985) and available raw data files to reconstruct prey sampling from Triangle Island (1978, 1979, 1980, 1981, 1982) and Frederick Island (1980, 1981). More recent prey sampling was conducted from 1996 to 2000 in West Bay on Triangle Island (see Bertram et al. 2001) and also on Frederick Island from 1996 to 1998 and in 2000 (Table 1). Diet samples were collected by capturing incoming parents using a barrier net ('pheasant net'). We assisted adult birds to regurgitate the meals intended for nestlings by massaging the gular pouch while the beak was suspended over a pre-weighed sample container. The wet mass of sample was determined. We then added 10 % formalin (buffered with borax to prevent degradation of invertebrate body parts) in sea water to each container to preserve the meal for identification and enumeration. Approximately 10 samples were collected every 10 d during a fixed time frame during the chick-rearing period at each colony. Timing of hatching is positively correlated on the 2 colonies ($\rho = 0.9$, $p = 0.004$, $n = 7$, A. Harfenist unpubl.) and occurs about 1 wk earlier on Triangle than on Frederick Island, so diet sampling began on 18 to 19 May (Period 1) on Triangle and on 27 May to 3 June (Period 2) on Frederick Island.

Diet analyses: assumptions and corrections. Species composition is reported as % wet mass in order to compare more recent samples with historical data (Vermeer 1985). For both the general and specific diet composition, % mass was expressed as a % of identified prey. We assumed that the proportions of identifiable and unidentifiable items were distributed similarly for all major prey species. The mass of euphausiids in the historical samples (1978 to 1982) was corrected because of the digested euphausiid category, which did not exist for the more recent samples. The mass of digested euphausiids was added, by species, according to the proportion of euphausiids identified in the corresponding sampling period. The euphausiid *Thysanoesa longipes* in the historical samples (1978 to 1982) is the same species as identified as *T. inspinata* in the more recent samples. Finally, the inter-annual comparisons were limited to samples collected between mid-May and the end of June (Periods 1 to 5), as these data were available for both colonies in most years.

Is *Neocalanus* prey phenology reflected in nestling diets? We investigated the relationship between the percentage of *N. cristatus* in Period 5 (26 June to 4 July, when the most data were available for comparison in the late chick-rearing stage), and the timing of peak biomass of *N. plumchrus* near Triangle and Frederick Islands using a newly available temperature-dependent phenology equation for the British Columbia continental margin (date of max biomass = $-0.16x + 169$, where x is degree-days relative to a 6 degree baseline, i.e. sum $[x-6]$ from Days 1 to 92 between 1 March and 31 May; Mackas et al. 2007, D. Mackas pers. comm.). Although no similar equation is available for *N. cristatus*, it is known that *N. cristatus* is available in surface waters longer and has a broader stage/age at any given date later and for longer in the season than *N. plumchrus* (D. Mackas pers. comm.) and thus can potentially overlap more extensively with Cassin's auklets during the incubation and chick-rearing periods. It is reasonable that both *Neocalanus* species demonstrate latitudinal variation in the timing of peak biomass and that differences in the peak timing of *N. cristatus* between colonies and years would be similar for *N. plumchrus* but with a greater potential capacity for temporal persistence. We used SYSTAT 10.2 for all analyses.

RESULTS

April SSTs

Within each year, the average April SST was always higher near Triangle Island (Pine Island light station) than near Frederick Island (Langara Island light station; Fig. 2). There was large inter-annual variation in the average April SSTs; however, temperatures rose and fell in unison on Langara and Pine Islands. The 1990s were generally warm, and 1998 was one of the warmest years on record near both colonies. SSTs dropped precipitously in 1999 and 2000 near both colonies.

Nestling diet composition

Overall, the diet of Cassin's auklet at both Triangle and Frederick Islands was dominated by 2 types of crustacean prey (copepods and euphausiids) and fish (Fig. 3). During Periods 1 to 5 in all years, these prey together contributed 89 to 99 % by overall mass (Fig. 3). Three other types of crustaceans including carideans, brachyurans, and amphipods occurred frequently in the diet (Fig. 3 and Tables S1 & S2 in the Supplement, available at www.int-res.com/articles/suppl/m393p199_app.xls), but in general they contributed little by mass.

Annual-level variation

While copepods, euphausiids, and fish comprised the bulk of the diet of Cassin's auklet, the relative contribution of these prey groups varied widely between sites and among years (Fig. 3). Overall, however, copepods were the predominant prey. At both sites and in all years, a single species, *Neocalanus cristatus*, in particular Stage cV, contributed > 99 % to biomass of copepods in the diet.

Triangle Island

At Triangle Island, copepods predominated the diet in both 1997 (63 %) and 1999 (56 %), euphausiids predominated in 1980 (49 %), 1981 (53 %), 1996 (62 %), and 2000 (57 %), and fish were the most important prey consumed in 1998 (46 %). Three species of euphausiids (*Euphausia pacifica*, *Thysanoessa spinifera*, and *T. inspinata* [earlier identified as *T. longipes*]) were taken by Cassin's auklets, with both adult and juvenile age classes identified for the *Thysanoessa* spp. Adult *T. spinifera* comprised >25 % of the diet at Triangle in 1980, 1981, and 2000, while in 1996, *E. pacifica* contributed 24 % by mass. In 1996, adult *T. spinifera* and juvenile *T. inspinata* also contributed >10 % to the diet, while in 2000, *E. pacifica* and adult *T. inspinata* also each contributed >10 % by mass.

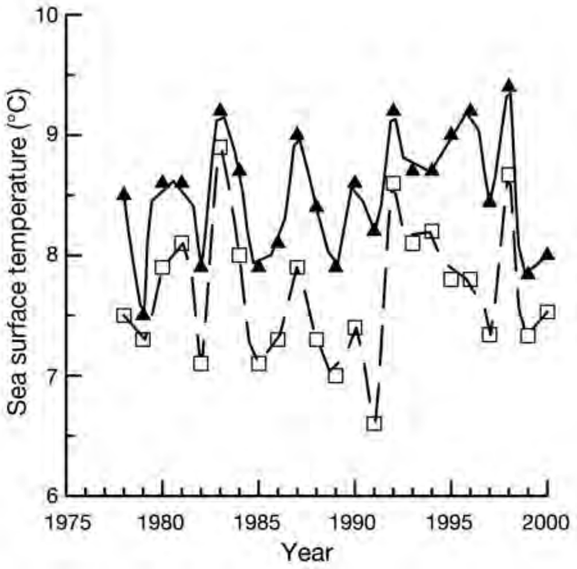

Fig. 2. Average April sea surface temperatures for Pine Island (▲) and Langara Island (☐) during the study period. Note that temperatures vary over time in unison and are always warmer on Pine Island in the south than on Langara Island in the north of coastal British Columbia. Data are from www.pac.dfo-mpo.gc.ca/sci/OSAP/data/SearchTools/Searchlighthouse_ e.htm

Fish were the predominant prey at Triangle only in 1998, but they also contributed 30 % to the diet in 1997. Fish were highly digested at both sites and, in general, this component of the diet has been poorly documented (Tables S1 & S2). In all, 5 fish families were identified at Triangle. By mass, the rockfishes *Sebastes* spp. were the most important of the fish prey, with flatfishes Pleuronectidae and Irish lords *Hemilepidotus* spp. contributing significantly in some years. Rockfishes accounted for all fish identified at Triangle in 1997 and 50 % of those identified in 1998. The flatfishes and Irish lords each comprised an additional 10 % of the diet in 1998. Fish from the family Cottidae were identified in the diet at Triangle only in 1999, when they occurred in 26 % of samples.

Carideans, amphipods, and brachyurans often occurred frequently, and sometimes in large numbers, at Triangle (Fig. 3, Table S1), but these groups generally made minor contributions. Exceptional were 1996 when unidentified brachyuran (crab) megalops contributed 4 % to the diet, and 1998, when 7 % of the diet consisted of amphipods, largely *Vibilia propinqua*.

Frederick Island

The diet of Cassin's auklet at Frederick Island was also highly variable among years (Fig. 3, Table S2). Copepods were again the most important prey overall, dominating the diet in 1980 (48 %), 1981 (48 %), and 1998 (51 %).

Euphausiids were the most important prey at Frederick in 1996 (59 %) and 2000 (52 %), while in 1997, copepods (46 %) and euphausiids (44 %) contributed similarly to the diet. In years when euphausiids were important, it was largely adult *Thysanoessa spinifera* that were consumed. They contributed 46 % to the overall diet in 1996, 30 % in 1997, and 35 % in 2000. *Euphausia pacifica* was important in 2000 only, when it contributed 10 % by mass.

Unlike at Triangle, fish was never the annually predominant prey group at Frederick, but were significant

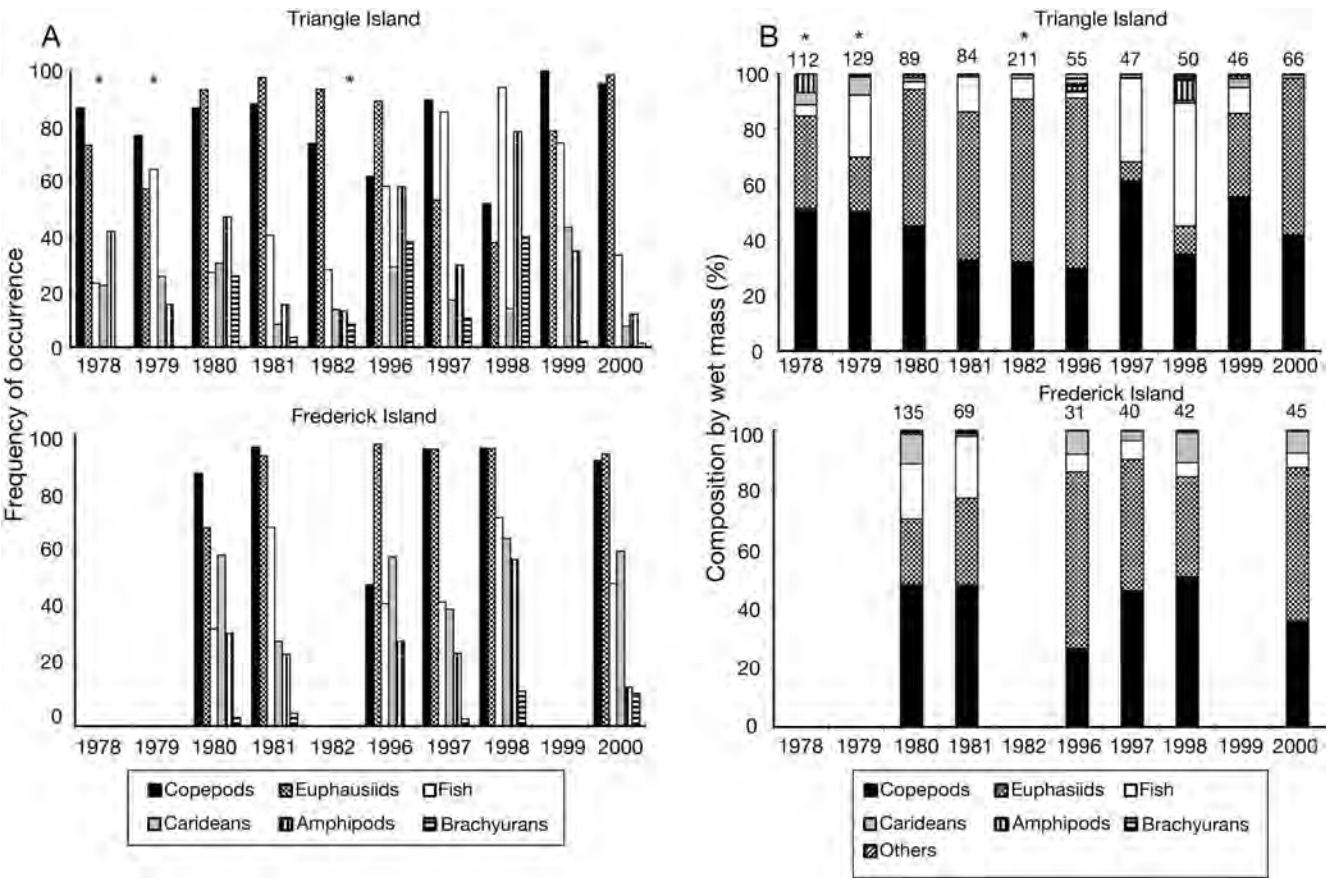

Fig. 3. *Ptychoramphus aleuticus.* Annual trends in the general composition of Cassin's auklet diet at Triangle and Frederick Islands between mid-May and the end of June expressed as (A) percent frequency of occurrence, and (B) percent by wet mass for the 6 major prey classes. Years indicated with an asterisk (1978, 1979, and 1982 at Triangle Island) are from Vermeer (1985) and include data from late May to the end of July. The number of samples examined each year is indicated above the bar

during the 1980s, contributing 19% by mass in 1980 and 21% in 1981. The species consumed in these years, however, were unidentified. Since 1996, fish have contributed only ~5% yr^{-1} to the diet at Frederick Island, and in 1998 and 2000, largely rockfishes (>4% in 1998, 3.5% in 2000) and Irish lords (1% in 2000) were consumed (Table S2).

Unlike at Triangle, carideans (shrimps and mysids) were important to the nestling diet at Frederick, where they contributed >7% by mass in 4 of 6 yr. The bulk of the carideans were *Pandalopsis dispar*, and *Pandalus* spp. At Frederick, amphipods and brachyurans occurred frequently, but they never contributed >1% by mass (Table S2).

Within-year variation

Apart from high dietary variation among years, at both sites there were substantial within-year changes in diet composition (Fig. 4) that appeared to be driven by availability of copepods. At Triangle, copepod occurrence in the diet generally peaked early in the breeding season (mid-May to early June, Periods 1 to 3), and its importance then declined through to fledging. The seasonal persistence of copepods, however, showed substantial variation among years (Fig. 4). In 1996 and 1998, for example, copepods had almost or completely disappeared from the diet at Triangle by late June (Period 5), while in 1980, 1981, and 1999, copepods were delivered to chicks until mid-July. Late-season sampling in 1980, 1981, and 1999 was particularly instructive, demonstrating that regardless of the level of seasonal dominance, copepods do eventually disappear from the diet, presumably coincident with cV migration to depth (Bertram et al. 2001). The temporal window of copepod availability to Cassin's auklets therefore varies among years, and also presumably between the breeding sites. At Frederick, the timing of copepod availability either begins later and/or it extends through the season as in 1980, 1981, and 1998 when copepods persisted in the diet at

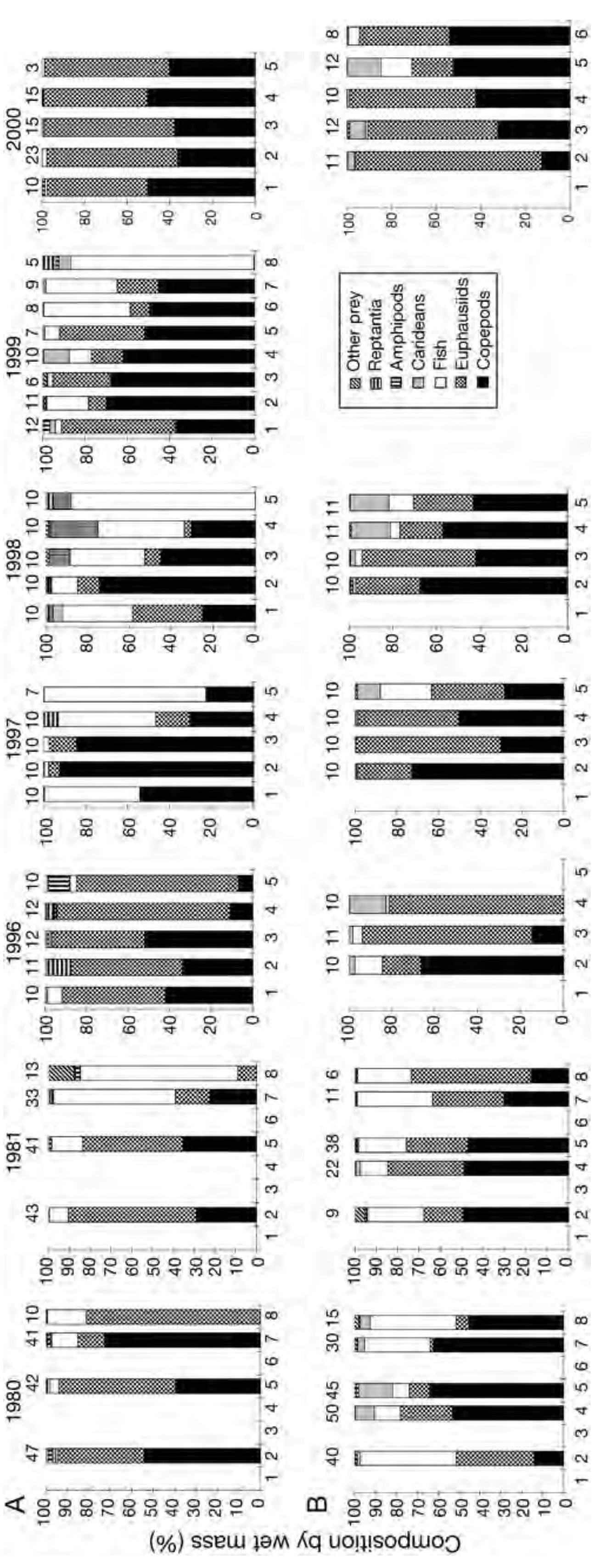

Fig. 4. *Ptychoramphus aleuticus*. Within-year trends in the general composition of Cassin's auklet diet at (A) Triangle and (B) Frederick Island expressed as percent composition by wet mass. Data are summarized and blocked by period within each year as follows: Period 1 = 18–19 May; 2 = 27 May–03 June; 3 = 7–10 June; 4 = 12–19 June; 5 = 26 June–4 July; 6 = 8 July; 7 = 13–20 July; 8 = 21–30 July. The number of samples examined in each period is indicated above the bar

Frederick after they had disappeared on Triangle. In 2000, a cooler year in the time series, occurrence of *Neocalanus cristatus* increased during Periods 1 to 5 on Frederick Island while remaining stable on Triangle Island.

Latitudinal differences in the effects of prey phenology on nestling diet are evident from the relationship between peak biomass timing of *Neocalanus* near Triangle and Frederick Islands and the representation in the nestling diet in the late chick-rearing period (Fig. 5). A significant positive relationship between percentage *Neocalanus* in the nestling diet and the timing of peak biomass exists on the southern island (Triangle Island: $y = 2.23x - 260.73$, $R^2 = 0.919$; $F_{1,5} = 56.78$, $p < 0.01$), but was not detected on the northern island (Frederick Island: $y = -0.22x + 76.99$, $R^2 = 0.02$; $F_{1,3} = 0.06$; $p > 0.8$). The paucity of *Neocalanus* late in the nestling diet period on Triangle Island in the years of 1996 and 1998 indicates a mismatch with the prey phenology in those warm spring years.

As copepods are a preferred prey item for Cassin's auklet in British Columbia, both the overall importance and seasonal timing of other prey presumably vary in accordance with copepod availability. At Triangle, either fish or euphausiids became generally more important in the diet through the season as copepods disappeared (Fig. 4). Euphausiids supplemented the diet in 1996 and 2000, but the species involved in each year were different (Fig. 6). In 1996, *Euphausia pacifica* was consumed early followed by a mix of adult and juvenile *Thysanoessa spinifera* and juvenile *T. inspinata* as the season progressed. In 2000, *E. pacifica* was less important, and adult *T. spinifera* and both adult and juvenile *T. inspinata* figured prominently. In the absence of copepods at Frederick, the diet consisted largely of euphausiids and fish in the 1980s, and mainly euphausiids from 1996 to 2000 (Fig. 6). Carideans were also important late in the breeding season during some years in the 1990s (Fig. 4). *T. spinifera* was the dominant euphausiid delivered to chicks at Frederick Island; adult *T. spinifera* early in the season were replaced later in some years by juveniles (Fig. 6). 1981 was notably different, when largely juvenile *T. inspinata* were delivered to chicks from the end of June.

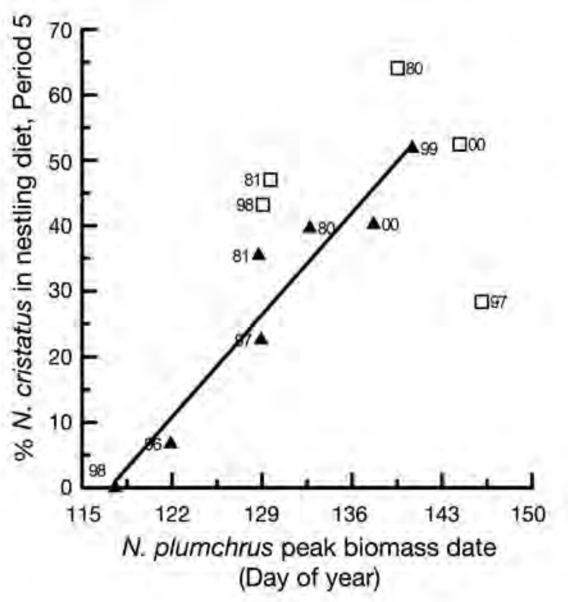

Fig. 5. *Neocalanus cristatus* and *N. plumchrus*. Prey phenology effects on predator diet show latitudinal differences related to variation in SST. The percentage of *N. cristatus* in Cassin's auklet nestling diet in Period 5 (26 June to 4 July, y) versus the predicted date of peak biomass of *N. plumchrus* based upon the temperature-dependent phenology equation of Mackas et al. (2007, see 'Materials and methods'). We drove the phenology equation using SST data from Pine Island light station (for Triangle Island) and from Langara light station (for Frederick Island). A significant positive relationship exists on the southern island (Triangle Island; (▲): $y = 2.23x - 260.73$, $R^2 = 0.919$; $F_{1,5} = 56.78$, $p < 0.01$), but was not detected on the northern island (Frederick Island; (☐): $y = -0.22x + 76.99$, $R^2 = 0.02$; $F_{1,3} = 0.06$; $p > 0.8$). The figure highlights the fact that Cassin's auklet nestling diet on Triangle Island is mismatched with the phenology of *Neocalanus* copepod prey in the early sprin years of 1996 and 1998 in our time series

Copepod variety

While *Neocalanus cristatus* dominated the copepod portion of the diet, 24 copepod species were identified in the diet of Cassin's auklet in British Columbia; 21 species at Triangle Island and 12 species at Frederick Island (Tables S1 & S2). Other copepods occurred frequently in some years, and sometimes in relatively large numbers, but they always contributed little by mass (Tables S1 & S2). In general, copepod diversity was high at both sites during the 1998 El Niño; occurrence of *Calanus marshallae* (Stage cV) and *Pseudocalanus mimus* was >10 % at Triangle Island and *N. plumchrus* (Stage cV), *Paracalanus parvus, Pseudocalanus* spp., *Oithona similis*, and *Cyclopoid* spp. each occurred in >10 % of samples at Frederick Island (Tables S1 & S2). Copepod diversity was also relatively high at Triangle Island in 1999, when *Pseudocalanus* spp. occurred in 22 % of samples.

Other prey species

Seventeen species or groups of amphipods were identified: 16 at Triangle Island and 11 at Frederick Island (Tables S1 & S2). Amphipods occurred frequently and often in large numbers, but they always contributed negligibly by mass. Three species, *Themisto pacifica*, *Brachycelus crusculum*, and *Vibilia propinqua*, occurred frequently (i.e. in >15 % of samples in at least 1 year) at both sites while *Brachycelus* spp., *Hyperoche medusarum*, and *Primno abbysallis* also occurred frequently in the diet during some years at Triangle Island.

DISCUSSION

Peak timing and duration of availability of *Neocalanus*

Together, copepods and euphausiids contributed >89 % to the diet of Cassin's auklet nestlings on both Triangle and Frederick Islands in all years of the study. Our findings confirm and extend historical observations from 1978 to 1982 (Vermeer 1981, 1985, Vermeer et al. 1985) and also offer new insights into latitudinal patterns of temporal variation in the timing of *Neocalanus* prey availability in surface waters and its association with ocean climate variability.

Our results are consistent with the idea that the diet of nestling Cassin's auklets in British Columbia reflects the temporal availability of *Neocalanus cristatus* prey within the foraging range of the colony (10 to 90 km on Triangle, Boyd et al. 2008). *N. cristatus* is a highly profitable prey item that is linked to rapid nestling growth (Bertram et al. 2001, Hedd et al. 2002, Hipfner 2008), and thus its dietary occurrence should reflect regional availability of Stage cV copepodites in surface waters.

We argue that the opportunity for a temporal mismatch between Cassin's auklet provisioning and *Neocalanus* prey timing has a latitudinal component and is greater on Triangle Island than on Frederick Island in warm years such as 1996 and the El Niño event of 1998 (which are both known years of reproductive failure on Triangle Island but not on Frederick Island; Bertram et al. 2001, 2005). Note that it is not only the timing of the peak of, but also the duration of, the *Neocalanus* availability in surface waters that affects foraging Cassin's auklet parents. In warm years, the biomass peak of *Neocalanus* is early and narrow in duration, whereas in cooler years, the biomass peak is later and broader in duration (Mackas & Galbraith 2002, Batten & Mackas 2009, this Theme Section). We argue that within a warm year, the peak will be early and narrow on Triangle Island, but farther north around Frederick

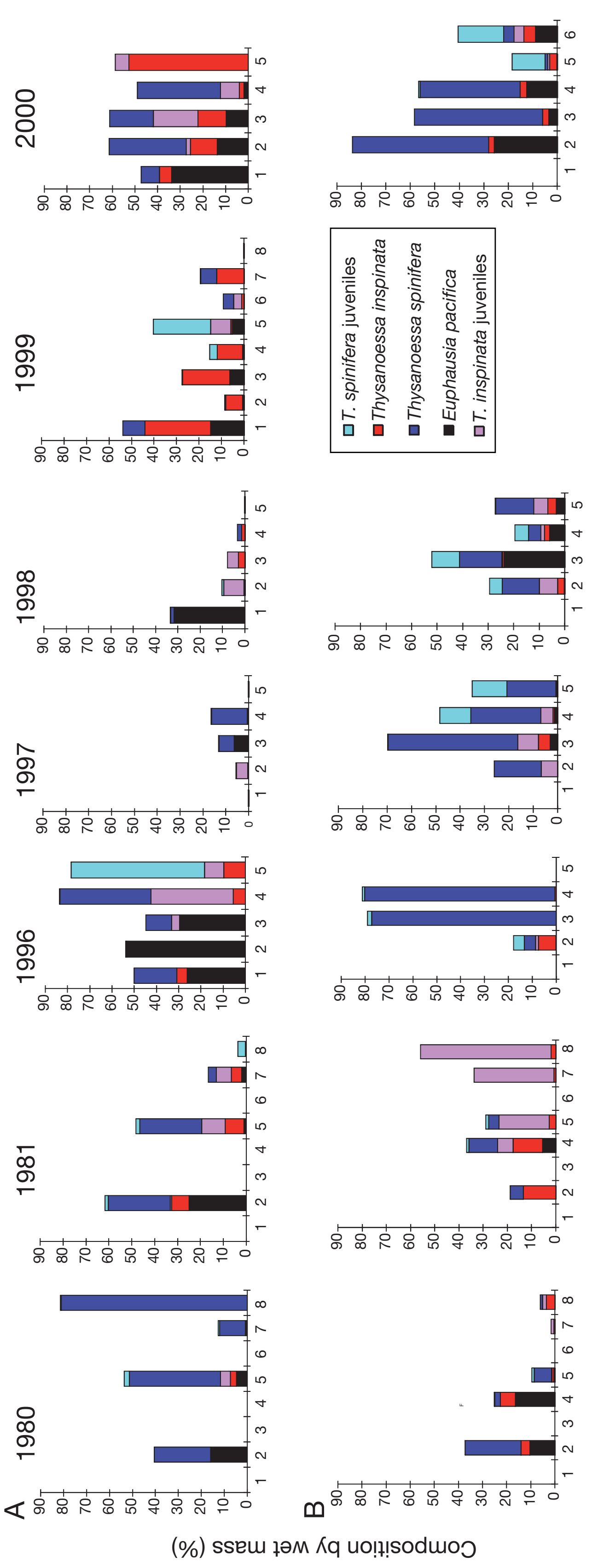

Fig. 6. *Ptychoramphus aleuticus*. Annual trends in the species composition of the euphausiid portion of the diet at (A) Triangle and (B) Frederick Islands, expressed as percent composition by wet mass. Note that the maximum *y*-scale value is 80%. Data are blocked by period as in Fig. 4

Island, the peak will be later and more protracted. Poor reproductive performance is the biological consequence of a trophic mismatch for Cassin's auklet.

Our data and analyses show that in the warm El Niño year of 1998, the peak of *Neocalanus* at Triangle Island was earlier (28 April) and diminished progressively to 0 during the chick-rearing period (mismatched) in marked contrast to Frederick Island where the peak occurred later (9 May) and persisted in the nestling diet at over 40% wet mass throughout the nestling period (matched). In contrast to warm years, mismatches were not observed at either colony in cool years. During the cool ocean year of 2000, the peak dates were relatively late and close in time (18 May on Triangle and 24 May on Frederick), and *Neocalanus* copepods were available on both colonies throughout chick rearing. Note, too, that on Frederick Island in 2000, *N. cristatus* increased steadily in the nestling diet from 10% in Period 1 to roughly 50% in Period 5 of chick rearing. The gradual increase in *N. cristatus* in the nestling diet over time in 2000 likely reflects the growing availability of fully grown, oil-laden Stage cV copepodites in surface waters in this cool year.

Independent evidence from 2005 supports our conclusion that mismatches are more likely to occur on Triangle than on Frederick Island. In general, for British Columbia in 2005, SSTs were warmer than normal (DFO 2006). The seasonal timing of the peak copepod biomass was anomalously early off North Vancouver Island in 2005, and as in 1998, the *Neocalanus* copepods left the surface layer early in the season (Mackas et al. 2006). On Triangle Island in 2005, *N. cristatus* were scarce in the nestling diet (DFO 2006, Hipfner 2008, M. Hipfner pers. comm.), indicating a trophic mismatch.

As a result of the mismatch, only 8% of nesting pairs were successful (Sydeman et al. 2006), and nestlings showed retarded development and overall poor production in 2005 on Triangle Island (DFO 2006, Hipfner 2008). In marked contrast, nestlings on Frederick Island in 2005 were developmentally robust (M. Hipfner pers. comm.), an indication that no trophic mismatch occurred in the northern region and that food web effects of the 2005 warm event were largely limited to the California Current Ecosystem (see Mackas et al. 2006, Sydeman et al. 2006).

Coho salmon growth and survival mirror the seabird patterns

Upper trophic level predators other than seabirds also show strong responses in production in relation

Table 1. *Ptychoramphus aleuticus.* Details of the sampling dates and the number of nestling diet samples collected from Cassin's auklet parents at Triangle and Frederick Islands, 1978 to 2000

Year	N	Sampling period
Triangle Island		
1978	112[a]	27 May – 25 July
1979	129[a]	27 May – 25 July
1980	140	27 May – 27 July
1981	130	28 May – 25 July
1982	211[a]	30 May – 28 July
1996	55	19 May – 28 June
1997	47	18 May – 28 June
1998	50	18 May – 28 June
1999	68	18 May – 27 July
2000	66	19 May – 29 June
Frederick Island		
1980	180	28 May – 23 July
1981	86	1 June – 30 July
1996	31	28 May – 18 June
1997	40	28 May – 28 June
1998	42	28 May – 28 June
2000	53	28 May – 8 July
	988	

[a] Raw data were unavailable for these years, but the annual values are included in Fig. 3 for completeness based upon Vermeer (1985)

to changes in zooplankton that are related to ocean climate (e.g. Mackas et al. 2007). Additional independent information on juvenile coho salmon *Oncorhynchus kisutch* growth rates also mirror the dichotomy of seabird responses to warm ocean years in northern and southern British Columbia. Growth rates of salmon in SE Alaska have been largely uniform ranging from 1.4 to 1.5 mm d^{-1} from 1998 to 2005. In contrast, on the west coast of Vancouver Island, growth rates were well below average in 1998 and were the lowest on record (<0.8 mm d^{-1}) in 2005 (Trudel et al. 2007). The variation in growth rates has also been positively linked to variation in survival and hence production (Trudel et al. 2003, 2007, Mackas et al. 2007). While juvenile coho salmon are largely piscivorous, the strong and similar pattern to Cassin's auklet suggests that bottom-up processes (cf. Ware & Thomson 2005, Frederiksen et al. 2006) influence production at higher trophic levels for both seabirds (see also Ware & McQueen 2006a,b) and salmonids (see also Roth et al. 2007, Sydeman et al. 2008). Poor availability of *Neocalanus* prey may indeed contribute to the observed poor year classes of Pacific sand lance *Ammodytes hexapterus* in warm years around Triangle Island (Hedd et al. 2006), and the poor recruitment could contribute to the poor growth of coho salmon, which are known to prey heavily upon sand lance (Brodeur & Pearcy 1990).

CONCLUSION

Rising global terrestrial and marine temperatures are forecasted based on global temperatures from 1850 to 2007 (www.metoffice.gov.uk/corporate/pressoffice/myths/2.html).

If warming continues and if predictions of more frequent ENSO events (e.g. Herbert & Dixon 2002) are realized, then we would expect to have more trophic mismatch events on Triangle Island, which is influenced by the California Current Ecosystem, than on Frederick Island in the cooler Alaska Current Ecosystem. Finally, recent work demonstrates that the average cohort widths of *Neocalanus plumchrus* in the northeast Pacific were significantly narrower in 2000–2007 than 1957–1965 (Batten & Mackas 2009). Narrowing of the duration of prey availability in surface waters, coupled with our diet observations, further supports the idea that the frequency of mismatches could increase on Triangle Island and possibly even occur for the first time on Frederick Island if prey cohort width becomes narrower in the future.

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Winter pre-conditioning of seabird phenology in the California Current

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ABSTRACT: Climate change is predicted to affect the phasing and amplitude of upwelling in eastern boundary current marine ecosystems. Effects may be strongest during the spring or summer 'upwelling season,' but may also be influential during winter before the spring transition. We tested the hypothesis that wintertime environmental forcing 'pre-conditions' the ecosystem and affects the timing and success of breeding in 2 species of seabird, Cassin's auklet *Ptychoramphus aleuticus* and common murre *Uria aalge*, reproducing in the central California Current. Time series of the mean and variance of egg-laying dates were correlated with regional winds and sea surface temperature, which were used as proxies for the forcing and oceanic response of coastal upwelling, respectively. Winter proxies of upwelling were the most significant determinants of seabird reproductive phenology, with anomalously strong upwelling in January to March leading to earlier dates of egg-laying in both species. We hypothesized that anomalous (early) winter upwelling, even of weak magnitude or short duration, could seed the region with sufficient nutrients to enhance productivity and prey availability, leading to a healthier adult breeding population and an earlier start to the breeding season. The magnitude of the previous year's November winds were also positively correlated with the variance of egg-laying dates for the common murre, with upwelling-favorable winds leading to greater synchrony in egg-laying. We conclude that winter environmental conditions are important determinants of ecosystem dynamics in the California Current, and that seabird phenology is a particularly useful ecosystem indicator.

KEY WORDS: Cassin's auklet · Common murre · California current · Phenology · Upwelling · Winter · Ecosystem indicator

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INTRODUCTION

Global climate change is expected to alter both the mean and variance of many meteorological and oceanographic parameters (Trenberth 2001, IPCC 2007), including the phasing and intensity of upwelling in eastern boundary current marine ecosystems. Changes in the phasing of upwelling may influence habitat suitability, primary productivity, and various mid-level ecological interactions (Stenseth et al. 2002, Parmesan 2006), with ascending effects to the upper trophic levels. The effects of changes in upwelling on ecosystem dynamics may be greatest during the spring-summer upwelling season, but may also be influential during winter before the spring transition.

As an apparent consequence of climate change, a variety of plant and animal parameters, including life history characteristics and demographic attributes, have shifted in a manner consistent with expectations under global climate warming. However, the vast majority (>90 %) of changes documented to date come from terrestrial ecosystems and species (Richardson & Poloczanska 2008). Very few of these studies examined changes in biological time series, other than variability

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in the average parameter state, and whether mean values have shifted systematically through time. Phenology is defined as the timing of key events in plant or animal life histories, for example, the average dates of egg-laying in birds or bud burst in trees. Phenology is a very sensitive indicator of climate-driven ecosystem changes (Beebee 1995, Forchhammer et al. 1998, Stenseth & Mysterud 2002, Parmesan & Yohe 2003, Root et al. 2003, Parmesan 2006). In marine ecosystems, phenological changes have been related to climate variability and change for both lower (Mackas et al. 2001) and upper trophic level species (Abraham & Sydeman 2004).

A substantial component of the climate change literature for marine ecosystems concerns marine birds (Durant et al. 2004). Studies from the northern and southern hemispheres have related seabird phenology to oceanographic and atmospheric variability (Sydeman et al. 1991, 2006, Bertram et al. 2001, Abraham & Sydeman 2004, Frederiksen et al. 2004, Barbraud & Weimerskirch 2006, Reed et al. 2006, 2009, Byrd et al. 2008, Wolf et al. 2009), but none of these studies examined anything other than mean or median dates of reproduction, and most studies have looked at 'oceanographic climate' during the spring/summer breeding periods for the birds. Indeed, investigating within-season variability in winter, spring, and summer, and in relation to the distribution of dates of reproduction and reproductive success may be revealing. Moreover, few studies, with the exception of Abraham & Sydeman (2004), examined early oceanographic or climatic parameters that may 'pre-condition' ecosystems and influence the developing food webs upon which seabirds depend to obtain the resources for reproduction.

Seabirds have been proposed to be among the best environmental and ecological indicators for coastal marine ecosystems (Cairns 1987). Phenological attributes of seabirds are clearly relevant to evaluating the role of seabirds as indicators of marine ecosystem and food web dynamics. In particular, it has been argued that seabirds are reliable indicators because as top predators they 'integrate' and 'amplify' environmental variability to produce interpretable signals in their time series. This assumption has rarely been tested comprehensively (but see Wells et al. 2008).

In the present study, we evaluated the hypothesis that seabirds integrate environmental variability, and, as a result, demonstrate interpretable signals in their phenology that are significant in a climate change-ecosystem change context. We tested this hypothesis by correlating wind and sea surface temperature (SST) time series over a wide geographic area with egg-laying dates of 2 species of seabird in the California Current large marine ecosystem along the US west coast. Winds and SST were used as proxies for the forcing and oceanic response for coastal upwelling, respectively (Huyer 1983, Hickey 1998). We selected 2 species of birds, a planktivore (Cassin's auklet) and a piscivore (common murre), to examine differential responses to variation in the duration and phasing of upwelling. We investigated ecosystem pre-conditioning and how seabirds integrate environmental variation by considering how wind and SST influence phenology up to 6 to 8 mo before the initiation of reproduction each year.

MATERIALS AND METHODS

Egg laying data for Cassin's auklet *Ptychoramphus aleuticus* and common murre *Uria aalge*, herein referred to as auklet and murre, have been collected by biologists of the Point Reyes Bird Observatory (PRBO) under contract with the US Fish and Wildlife Service (USFWS) at Southeast Farallon Island (SEFI; 37° 41′ 53.88″ N, 123° 0′ 5.76″ W; Fig. 1) since the early 1970s. The Farallon National Wildlife Refuge, including SEFI and the North Farallon Islands, hosts one of the richest marine bird nesting colonies in the world, with at least 12 regularly breeding species (Sydeman et al. 2001). Auklets are planktivorous, feeding primarily on euphausiid crustaceans (Ainley et al. 1996, Abraham & Sydeman 2004, 2006) and have a foraging radius of ~60 km from the colony (Mills et al. 2007); they do not generally forage on inner shelf habitats (<50 m depth; Yen et al. 2005). In contrast, murres are omnivores and generally range within the 3000 m isobath, and ~100 km from the colony (Mills et al. 2007). Once murres finish molting they occupy nest sites on the Farallones in October and November (Ainley & Boekelheide 1990). Auklets inhabit the Farallones throughout the year, but in September and October they tend to molt at sea (Manuwal 1974). Each year, a variable number of birds is profiled, and the dates when eggs are laid and hatched are recorded and fledgling survival is observed (see Appendix 1 for summary statistics on reproductive timing). For both species, only the first egg-laying dates are considered in the calculation of the mean and variance time series. Thus, we have a 35 yr time series of the mean and variance of egg-laying dates for both auklets and murres. Hatching dates were not used, as the results were quantitatively similar to that of egg-laying dates, and we were most interested in the climate-oceanographic correlates of the initiation of breeding dates, which is best studied using egg-laying dates.

The environmental variables compared to the seabird phenology are based on satellite-derived SST and meridional wind data, available from the National Oceanic and Atmospheric Administration (NOAA)

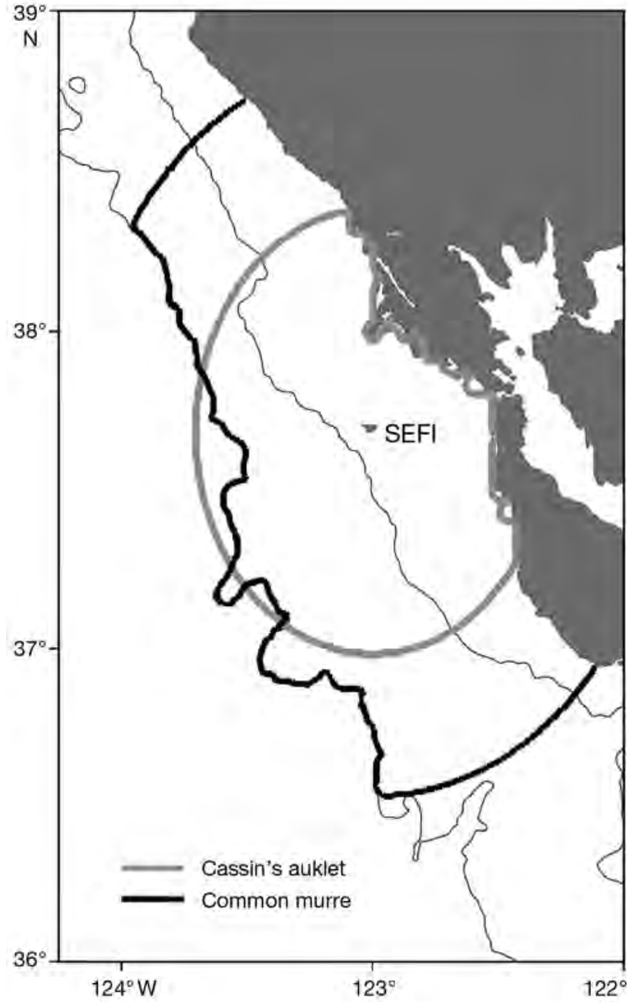

Fig. 1. Southeast Farallon Islands (SEFI), showing the estimated foraging ranges for common murre and Cassin's auklet. The 300 m and 3000 m isobath are contoured

Coastwatch Program (http://coastwatch.pfel.noaa.gov/data.html). The SST data come from Pathfinder version 5.0 day and night monthly composites, available from January 1985 to the present at a spatial resolution of 4.4 km (Kilpatrick et al. 2001). The wind data are from NOAA/NCDC blended monthly mean sea surface winds at 0.25° (~25 km) resolution (Zhang et al. 2006). The west coast of North America in the vicinity of the Farallon Islands is oriented in the north-south direction, thus the 'v' component of the wind is aligned along the north-south (meridional) direction and drives coastal upwelling. Southward winds (–v) are upwelling favorable, whereas northward winds (+v) cause downwelling.

Analyses have been performed over the time period common to the biological and physical time series (1988 to 2006). Gaps in the SST data were filled by a linear interpolation on the monthly mean time series at a particular grid location; for the months of January through March, only 8 % of the total time series had >3 missing monthly values. Over 80 % of the total time series had <5 missing months. Most gaps in the time series were only 1 mo in length, but some were up to 5 mo, especially in the coastal area around Point Conception, California (34.5° N, 121° W). There were no gaps in the meridional wind time series.

Statistical analyses. Spearman's rank correlation method (Kendall & Gibbons 1990) was used to relate the physical and biological series, as this technique does not assume normal distributions for the time series. The method calculates a correlation coefficient, C, and a probability, p, that the correlation is due to chance. The relationship between any 2 time series may be simultaneous (lag 0), or one may lead or lag the other. We derived spatial correlation maps between the monthly mean gridded satellite data for a particular month (winds and SST) and the annual mean and variance of egg-laying dates for each species. To examine the cumulative effect of upwelling, averages of consecutive months were also considered. Only spatial correlation maps with large areas of significant correlations were used in the final interpretation of the birds' response to the physical oceanic conditions. Given the large number of tests performed, correlations with $p < 0.01$ were assumed to be significant.

RESULTS

Variability in egg-laying dates

The mean and variance of egg-laying dates for both auklets and murres were related to annual reproductive success (number of chicks fledged per breeding pair). For both species, egg-laying dates were inversely related to breeding success ($C = -0.33$, $p < 0.06$ for auklets and $C = -0.39$, $p < 0.02$ for murres). That is, an early mean egg-laying date resulted in a larger number of viable fledglings per breeding pair. However, the 2 species show different relationships between egg-laying variances and reproductive success, especially since ~1990. Auklets were lower in trophic level, generally breeding earlier in the year, and having more variability in timing of egg-laying than murres. For auklets, variance in egg-laying corresponding to a longer breeding season, with younger birds typically breeding later in the season; this could result in a positive relationship with breeding success if the birds raise more than 1 clutch ('double-brood') in years of extended reproduction (Abraham & Sydeman 2004). In contrast, reproductive success of murres was enhanced when breeding synchrony was greatest (Birkhead 1977, Sydeman et al. 1991), with synchrony reflected by small variance in egg-laying dates (C = –0.51; p < 0.01).

The mean egg-laying dates for auklets and murres between 1972 and 2006 reveal substantial interannual variability (Fig. 2a). From 1972 to 2006, there was a positive trend in the auklet mean egg-laying dates (slope = 0.40 d yr^{-1}, p = 0.14) and a negative trend in the murre mean egg-laying dates (slope = –0.24 d yr^{-1}, p = .07). The planktivorous auklets initiated reproduction before murres in all years except 1992. In strong El Niño years (1983, 1992, 1998), the mean egg-laying dates for both species were significantly delayed; for auklets, the delay was upwards of 60 d, whereas for murres it was ~20 d. The mean egg-laying dates of the species were correlated (C = 0.55, p < 0.01). The variance in egg-laying dates (Fig. 2b) changed over the observation period. Until 1990, the variances of egg-laying dates for both species co-varied (C = 0.46, p < 0.05), but the correlation was negative (C = –0.51, p < 0.05) after 1990. During El Niño years, variance in egg-laying dates of auklets decreased, whereas for murres the variance increased. The mean and variance of egg-laying dates for auklets were inversely correlated (C = –0.47, p < 0.01) — when breeding early the population showed greater variability. For murres, there was no meaningful correlation between the mean and variance.

Correlation maps between meridional winds and egg-laying dates

Correlation maps constructed from correlations between meridional winds and mean egg-laying dates showed significant correlations only for the months of January, February, and January-February combined (other months are not shown). The correlations were positive and hold for both auklets (Fig. 3a) and murres (Fig. 3b), indicating that wintertime upwelling-favorable winds correspond to earlier mean egg-laying dates for both species. The January correlations for both species ranged between 0.58 and 0.76 for most of the region between 32°–44° N and 120°–128° W, encompassing almost the entire US West Coast. For auklets, the spatial correlations break down north of 41° N and in the area south of 36° N, shoreward of 123° W. For murres, the correlations break down primarily in the southern part of the domain. In February, the regions of high correlation for both auklets and murres lie south of the Farallon Islands, having values between 0.58 and 0.70.

The correlation map with the largest area of significant correlations was for the time series constructed by averaging the January and February meridional winds. The spatial extent of the correlation was similar for both auklets and murres, with high correla-

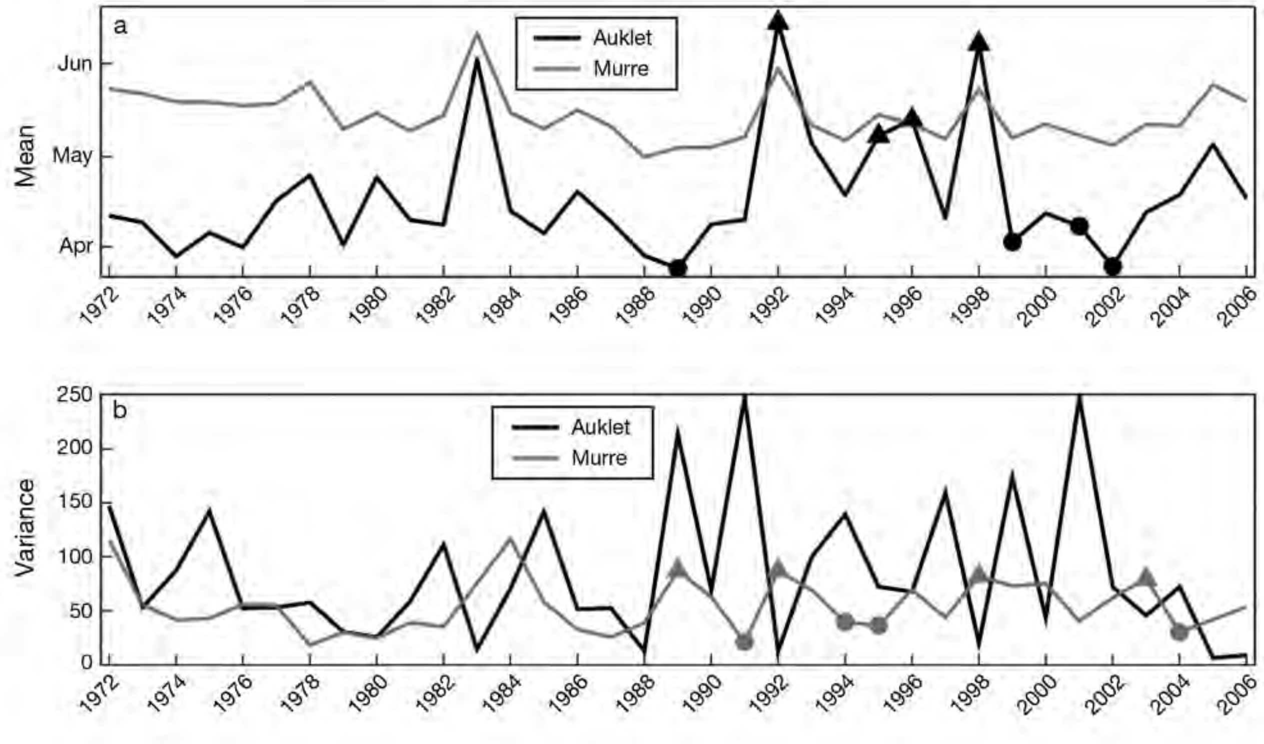

Fig. 2. *Ptychoramphus aleuticus* and *Uria aalge*. Time series of (a) mean of egg-laying dates and (b) variances of egg-laying dates. For the time period 1988 to 2006 (years of available wind and sea surface temperature (SST) data), the 4 years of the smallest (largest) values of auklet means and murre variances are marked with circles (triangles)

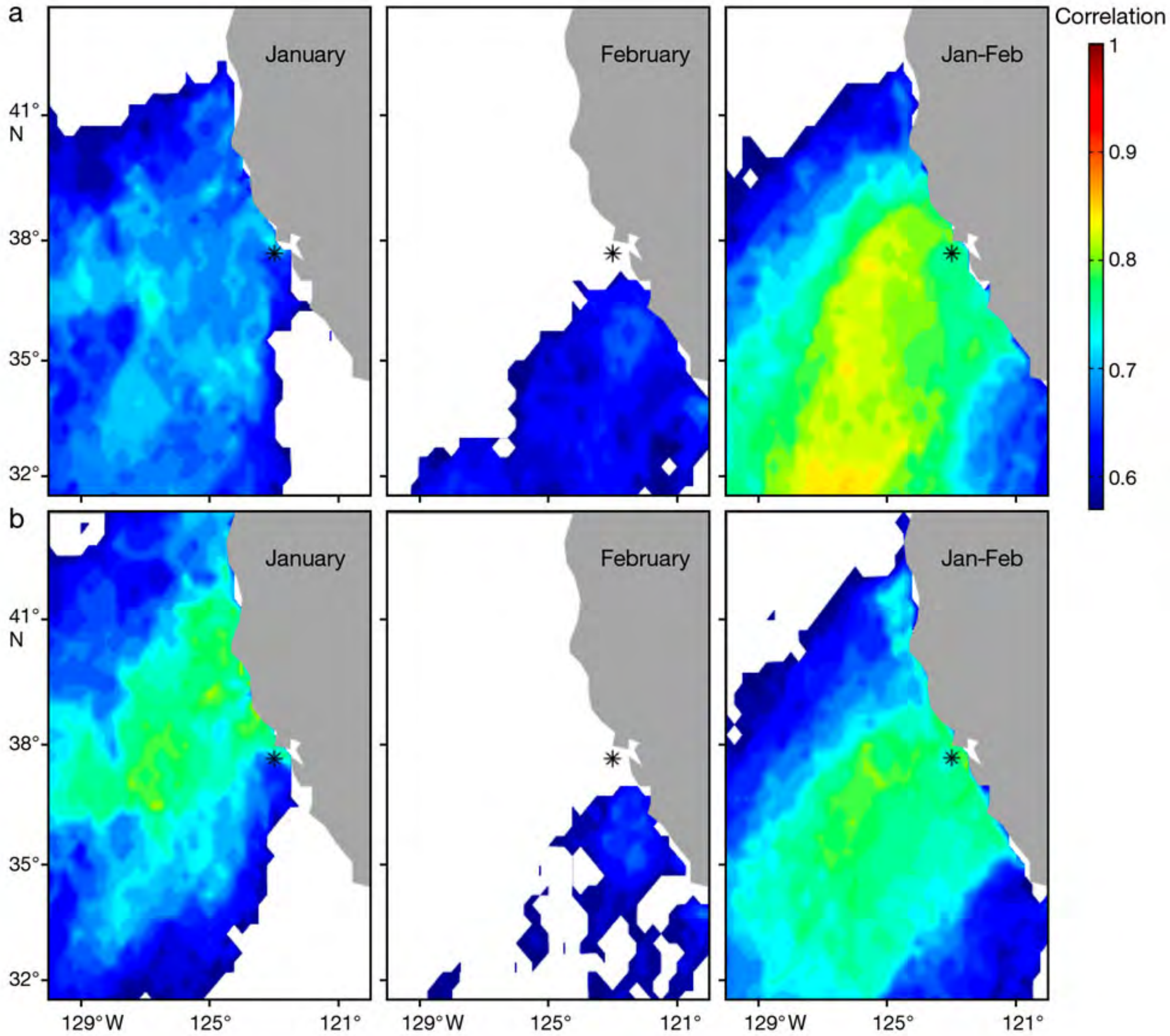

Fig. 3. *Ptychoramphus aleuticus* and *Uria aalge*. Correlations between meridional wind and mean egg-laying dates for (a) auklets and (b) murres. The spatial meridional wind data are the monthly means for January, February, and the average of January and February. For this and all subsequent correlation maps, a black asterisk marks the location of southeast Farallon Islands (SEFI). Only correlations with $p < 0.01$ are shown; areas in white are for non-significant correlations ($p > 0.01$)

tions throughout the domain, except for an increasing area of low or non-significant correlations north of approximately 40° N. It is interesting to note that while correlation values were highest for auklets in the composite of January-February winds, the January winds alone provided the highest correlations for murres. The relationships for both species are slightly non-linear; a quadratic regression of wintertime January-February winds explained 60.61% of the variance in mean egg-laying dates of auklets (Fig. 4a) and 44.87% of the variance in egg-laying dates of murres (Fig. 4b).

A strong positive relationship occured between meridional winds and variance of murre egg-laying dates (Fig. 5), but no such relationship existed for auklets. A positive correlation indicates that northward (downwelling favorable) winds are related to higher variance in murre egg-laying dates. Notably, the correlation was strongest in November of the previous year (e.g. the 1983 egg-laying variance was correlated to the November 1982 meridional winds), with a maximum correlation value of $C = 0.94$, centered at 42° N, 132° W, which decreases offshore to $C = 0.59$. This region of high positive correlation is located well to the northwest of the Farallon Islands, but corresponds to the center of the North Pacific (subtropical) High, which modulates coastal upwelling in the California Current (Schwing et al. 2002).

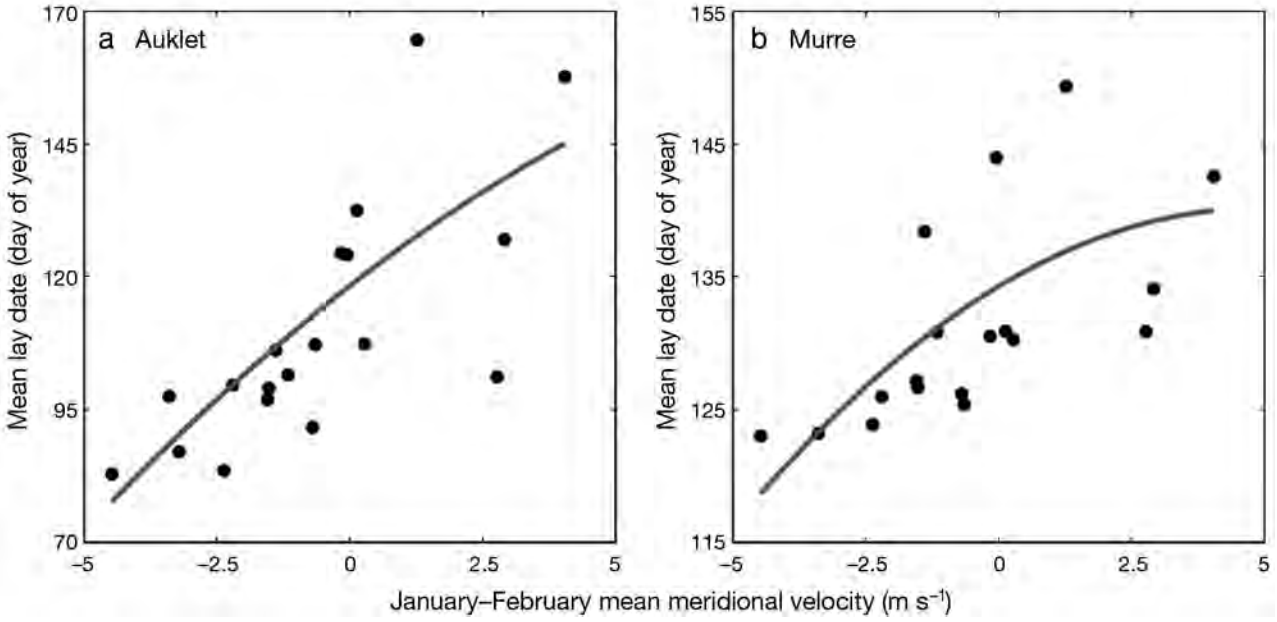

Fig. 4. *Ptychoramphus aleuticus* and *Uria aalge*. Bivariate plot between meridional wind and mean egg-laying dates for (a) auklet and (b) murre. Location of the January-February mean meridional wind data is 37.5° N, 125.5° W

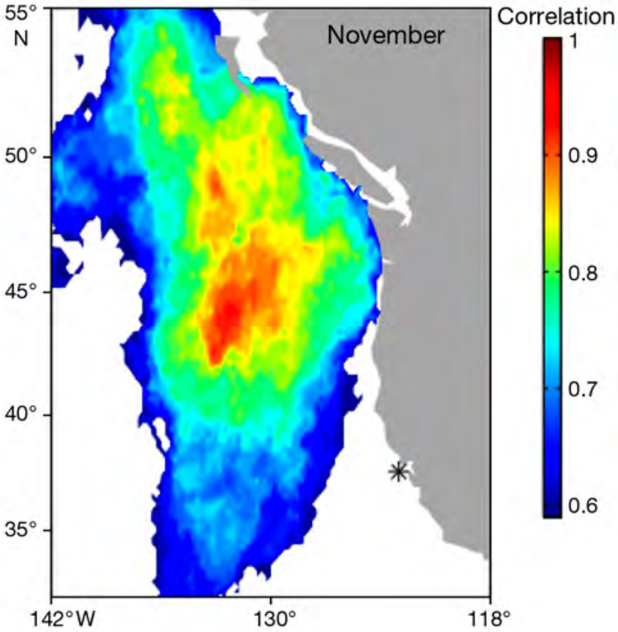

Fig. 5. *Uria aalge*. Correlations between meridional winds and variances of egg-laying dates for murres. Wind data are monthly means for November of the previous year

Correlation between SST and egg-laying dates

Correlation maps of SST and mean egg-laying dates for February, March, and February-March showed the greatest extent of significant positive correlations for both auklets (Fig. 6a) and murres (Fig. 6b). Positive correlations imply that both species lay their eggs earlier (later) when the regional SST is cool (warm). The correlation maps of SST have a much higher spatial resolution (4.4 km) than the wind correlation maps (approximately 25 km), and consequently appear grainier. Both auklets and murres had similar spatial correlation patterns, with higher correlations along the coast and decreasing correlations with increasing distance offshore. However, the offshore extent, as well as the magnitude, of the correlation coefficients was much higher for auklets than murres in all 3 temporal averages (February, March, and February-March).

In February, auklet correlation values were highest (C = 0.94) southward of the Farallon Islands, on the continental shelf. In March, the area of highest correlation (C = 0.97) was in the northern shelf area, around 42° N. The SST averaged over February and March had the highest spatial extent of significant correlation. The same spatial patterns were evident in the murre–SST correlation maps, though with generally lower correlations everywhere.

There were also significant correlations between SST and the variance of auklet egg-laying dates in February (Fig. 7). These correlations were negative, ranging from −0.79 to −0.58, implying that colder SSTs are associated with longer time spans of egg-laying periods. However, the spatial extent of the significant correlations was rather limited. No significant correlations were found between SST time series and variance of murre egg-laying dates.

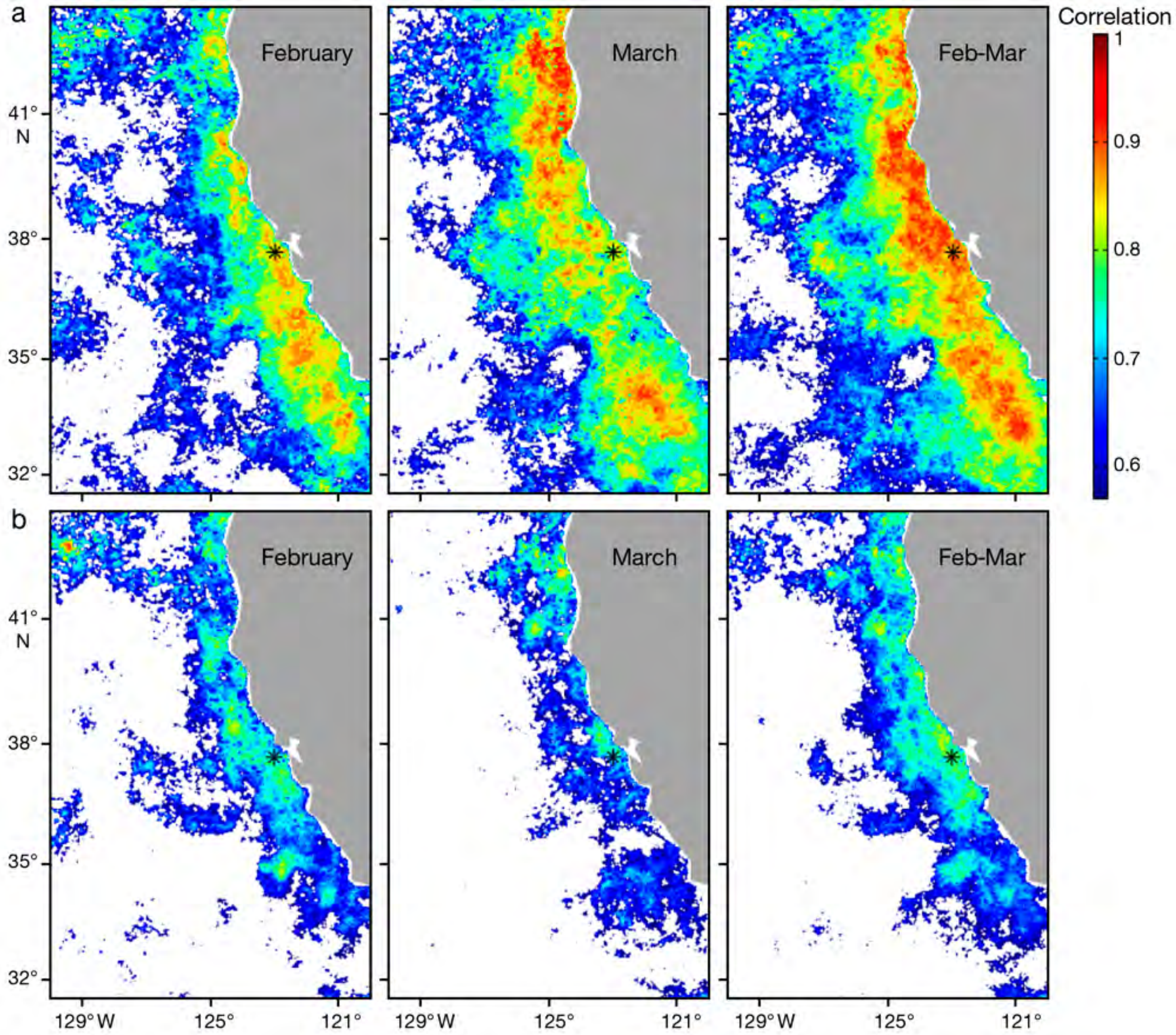

Fig. 6. *Ptychoramphus aleuticus* and *Uria aalge*. Correlations between sea surface temperature (SST) and mean egg-laying dates for (a) auklets and (b) murres. SST data are monthly means for February, March, and the average of February and March

DISCUSSION

We have evaluated the hypotheses that wintertime environmental forcing 'pre-conditions' the ecosystem and that seabirds 'integrate' environmental variability as demonstrated by interpretable signals in their timing of breeding (i.e. phenology). We tested these hypotheses by creating monthly estimates of winds and SSTs over the Northeast Pacific and producing spatial correlation maps to investigate the overall scales of integration. Upwelling in the central-northern California Current is most intense during the months of May to July each year (Bograd et al. 2009), but we found wintertime (November, January to March) proxies of upwelling to be the most significant determinants of seabird phenology. Upwelling in the California Current is the primary driver for primary and secondary productivity (Largier et al. 2006), so undoubtedly the relationships we have established are indirect, mediated by changes in prey resource availability. Herein, we compare the responses of these 2 species of seabird, an obligate planktivore (auklet) and an omnivore (murre), to winter environmental conditions, as indexed by surface winds (atmospheric forcing) and SSTs (oceanic response). We touch upon the specifics of prey resource availability later in this discussion. To our knowledge, this is one of the first attempts at a spatio-temporal integration of climate-oceanographic and

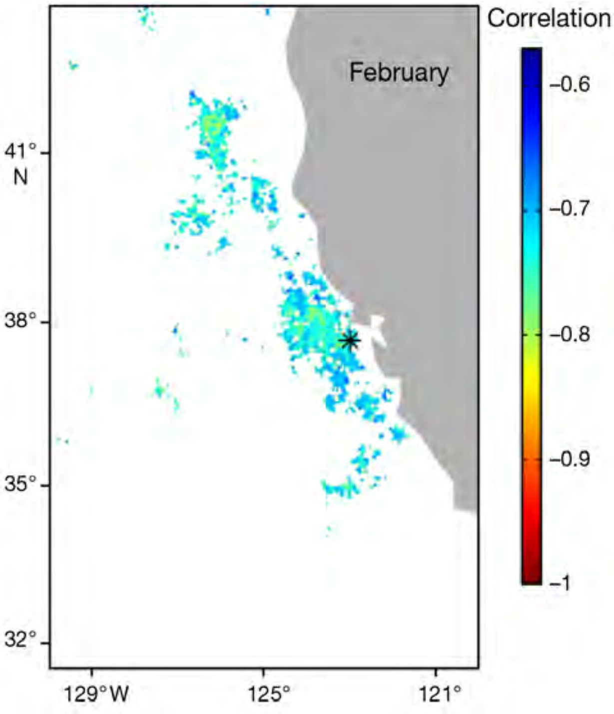

Fig. 7. *Ptychoramphus aleuticus*. Correlations between sea surface temperature (SST) and variances of egg-laying dates for auklets. SST data are monthly means for February

phenological variables. Clearly such information is critical to assessing the role of seabird phenology as an indicator of ecosystem dynamics, as has been recently proposed (Sydeman et al. 2008).

Ecosystem pre-conditioning

Previous studies have found relationships between wintertime oceanographic conditions and seabird ecology in the region (Abraham & Sydeman 2004, Miller & Sydeman 2004), but the temporal pattern of ecosystem 'pre-conditioning' revealed by the present study is considerably earlier than expected. The cumulative effect of meridional winds on the mean egg-laying dates for both species was strongest in winter (January and February). The spatial correlation maps revealed the strongest correlations to the north and southwest of the Farallones, presumably reflective of atmospheric forcing conducive to upwelling (Fig. 3). From an ornithological perspective, auklets and murres can produce eggs within ~10 to 15 d after fertilization (Astheimer 1986). The fast egg production and the spring timing of the average egg-laying (29 March to 7 May for auklets and 6 to 22 May for murres; Fig. 2a; Appendix 1) would suggest March/April environmen-

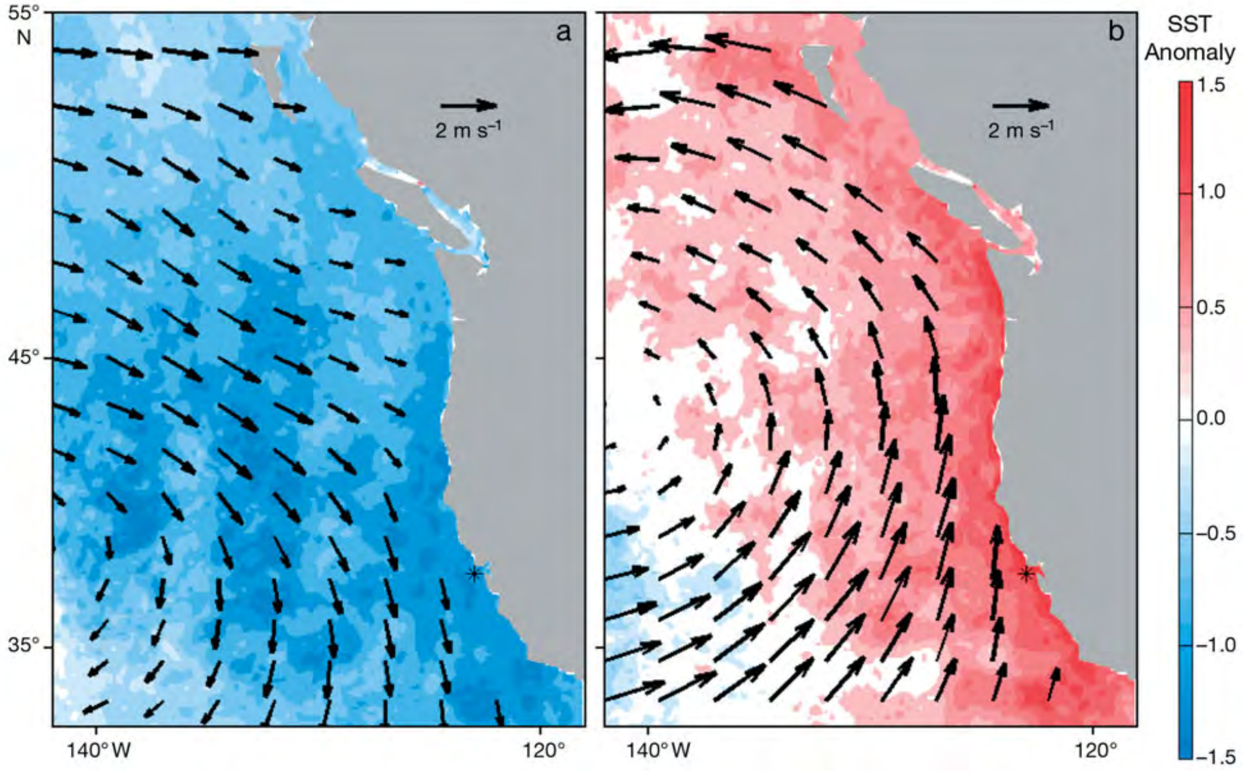

Fig. 8. *Ptychoramphus aleuticus*. Anomalies of January-February winds and February-March sea surface temperatures (SSTs) for (a) the 4 years of the earliest auklet egg-laying means and (b) mean of the 4 years of latest auklet egg-laying means. For clarity, arrows are plotted every 2.5°

tal signals being the most influential to the timing of breeding. However, from an ecosystem and food web development perspective, the winter relationships make sense. In the Point Arena region, upwelling is strongly intermittent in winter (Bograd et al. 2009). However, it is this intermittent upwelling that appears most significant to the timing of seabird egg-laying.

We hypothesize that intermittent upwelling in winter stimulates and fuels food web development, which ultimately affects seabird body condition and egg-laying dates. Estimates of the timing between upwelling and primary and secondary productivity are important in this regard. In the California Current system near Bodega Bay, upwelling followed by a relaxation of 3 to 7 d is most favorable for phytoplankton blooms (primary productivity; Wilkerson et al. 2006). For secondary production, the results are highly species dependent and also variable by year. Timing of seabird breeding is known to be influenced by the nutritional status of egg-laying females (Perrins 1970). Farallon auklets feed mostly on euphausiid crustaceans ('krill'). Coastal communities of *Euphausia pacifica* were comprised only of larval forms in January (Dorman et al. 2005). Our results show that upwelling during January and February is important to egg-laying of auklets and murres; therefore, it may be significant for the growth of krill as well. The prey of murres during the breeding season consists mainly of pacific hake, northern anchovy, and juvenile rockfish (Mills et al. 2007, Roth et al. 2008). Pacific hake spawn from January through March offshore of southern California, and juveniles and adults migrate northward to central California in the spring (Ressler et al. 2007, Agostini et al. 2008). Northern anchovy spawn year round, but late winter and early spring are peak spawning times (Parrish et al. 1986). Also, January through March is a very active period of fertilization/parturition for some species of rockfish in the California Current (Eschevarria & Lenarz 1984). Reed et al. (2009) used estimates of juvenile rockfish to show a relationship with murre phenology, although the forage fish data were obtained in May to June, after the egg-laying period of murres. Unfortunately, we lack data on the seasonal variation in food web components to estimate all the time lags involved. However, other studies on Farallon seabird phenology (Abraham & Sydeman 2004, Reed et al. 2009, Wolf et al. 2009) and seabird phenology elsewhere in the world (Frederiksen et al. 2004, Barbraud & Weimerskirch 2006, Reed et al. 2006, Byrd et al. 2008) have inferred, rather than demonstrated, that environmental relationships are due to variation in prey resources. In short, it seems that wintertime upwelling 'pre-conditions' the system and is important to the growth and development of many prey species that are likely related to the foraging success, body condition, and timing of breeding for these seabirds.

The seasonal cycle of water column structure in the California Current affects the biological utility of coastal upwelling. Surface stratification of the ocean off central-northern California is weakest in winter (Pennington & Chavez 2000, Palacios et al. 2004) and calculation of Brunt-Väisälä frequencies showed the lowest values in January-February at the M2 mooring located near Monterey Bay (data not shown). Thus the upwelling of nutrient-rich water in winter could occur with winds that are weaker or of shorter duration than the winds that would be required for significant nutrient-favorable upwelling later in the season. Thus anomalous (i.e. early) winter upwelling, even of weak magnitude or short duration, could seed the region with sufficient nutrients to enhance productivity and prey availability. This 'pre-conditioning' of the system would allow for a healthier adult breeding population, hence an earlier start to the breeding season.

To further illustrate these results, we have summarized wind patterns and SST for the 4 earliest (1989, 2002, 1999, 2001) and 4 latest (1995, 1996, 1998, 1992) years for auklet egg-laying (Fig. 2a). January-February meridional winds and February-March SSTs for these early/late years were averaged and then subtracted from the climatological means to form anomaly maps representing conditions that are favorable or unfavorable for early egg-laying. The anomalous wind patterns for the early egg-laying years correspond to an anomalously strong Subtropical High pressure system, resulting in anticyclonic wind anomalies and stronger coastal upwelling. The corresponding February-March SST anomalies over the region are cooler than the climatology by up to 1.5°C (Fig. 8a). In contrast, the January-February anomaly winds for the 4 latest years of auklet egg-laying show strongly downwelling favorable conditions along the entire coast, and February-March SST anomalies warmer by up to 1.5°C (Fig. 8b).

Within-season patterns: variance

Measures of central tendency (mean and/or median) and variance structures are often correlated as they are here (to some extent), but variance as a parameter provides a novel view of phenology. From a breeding success perspective, greater variance for auklets does not necessarily lead to better reproduction, but less variance for murres results in better reproductive output. We found that November winds of the previous year were related to murre variance in egg-laying dates, but we found no relationships for auklets. We do not understand why this difference exists between the species, although we assume November winds only have an effect on the prey of murres. Moreover, we found that murre and auklet variances were positively correlated before 1990 and negatively correlated thereafter. As noted in the 'Results', we surmise that greater variance for auklets and less variance for murres is a positive response to favorable environmental conditions, which means that it is the positive correlation between auklet and murre variance prior to 1990 that requires explanation. While we do not fully understand this relationship, before 1990 murre egg-laying dates advanced significantly (Sydeman 1999, Reed et al. 2009), and perhaps this change in overall breeding date was related to a change in the variance structure of the data. For auklets, the number of years with high variances (>150) only occurred after 1989, whereas there is no such shift to higher variances for the murres (Fig. 2b).

To illustrate the relationship between murre variance in egg-laying and environmental conditions, we applied the same process of looking at the average of the anomalous winds and SSTs for the 4 yr of smallest and largest variances. The 4 yr with the lowest variances are 1999, 2004, 1995, and 1994; the 4 yr with the highest variances are 2003, 1998, 1992, and 1989 (Fig. 2b). The wind and SST patterns associated with the largest/smallest variance years are very similar to those for the earliest/latest auklet egg-laying years (Fig. 8); because of the similarity the figure is not shown. Years with the smallest variances have anticyclonic November wind anomalies. The wind magnitudes are very large north of 45° N, with anomalies exceeding 4 m s^{-1} and directed from the northwest. The SST anomalies are cooler than the climatological mean over most of the region, with values between –0.5 to –1°C in the areas adjacent and to the north of the Farallones. The conditions for the highest variances are cyclonic wind anomalies; the SST anomalies over most of the region are warmer than the climatology. December SST anomalies of over 1.5°C are located just north of 45° N, with upwelling conditions around the Farallones with wind magnitudes ~1 m s^{-1} and SST anomalies of ~0.5°C.

Seabird phenology as an ecosystem indicator

Seabird phenology appears to be reflective of processes that determine ecosystem dynamics 3 to 5 mo prior to egg-laying for these species. Further refinements in understanding the mechanisms of the response are necessary, but we have a reasonable operational hypothesis, and have calibrated some of the functional relationships. Therefore, it seems appropriate to suggest seabird phenology as an indicator of wintertime ecosystem dynamics. Unlike for fish and other species in the system, the breeding timing of seabirds is relatively easy and inexpensive to measure. Indeed, it is hard to envision other taxa that could provide phenological indices of ecosystem dynamics early in each year. These indices could be extremely important in assessing ecosystem 'health' and resilience, and could be useful in a predictive context (Sydeman et al. 2008). Seabird phenology could provide a biological 'spring transition' index, which may be more meaningful to other biological organisms than a physically based index, such as changes in SST or sea level. Coupling both physical and biological indices of timing may be particularly useful for understanding ecosystem productivity.

CONCLUSIONS

Based on this investigation, we conclude that wintertime conditions are important determinants of ecosystem dynamics in the California Current and that future ecosystem studies should focus on physical forcing prior to the 'spring transition.' In some cases, the 'spring transition' may have been over-emphasized, when it is actually atmospheric–oceanographic interactions before the transition can be observed that are most significant to ecosystem productivity. The widespread correlations of winds and SST in January and February, and as early as November in the preceding year, support the notion that wintertime 'pre-conditioning' of the system is important. We have suggested that winds during periods of weak stratification may be mechanistically related to effectual upwelling in the system during winter, but this is certainly an area for future research.

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Appendix 1. *Ptychoramphus aleuticus* and *Uria aalge*. Summary statistics calculated and used for analysis of Cassin's auklet and common murre egg-laying dates

Year	Mean	Median	N	Max	Min	SD	Variance
Cassin's auklet							
1972	100.38	97.5	64	135	75	12.12	147.12
1973	98.13	96	62	124	90	7.29	53.22
1974	86.78	85	65	122	69	9.33	87.14
1975	94.69	91	70	131	77	11.91	141.89
1976	89.75	90	73	122	78	7.23	52.32
1977	105.35	105	71	133	93	7.28	53.11
1978	113.87	112	77	143	103	7.60	57.82
1979	90.59	90	75	112	78	5.53	30.62
1980	113.12	114	77	128	101	5.05	25.57
1981	98.94	99	80	120	88	7.67	58.86
1982	97.41	95	80	130	71	10.54	111.18
1983	152.35	155	37	162	148	3.81	14.56
1984	102.00	102	77	127	87	8.39	70.39
1985	94.46	91	78	146	81	11.90	141.75
1986	108.38	106	42	141	96	7.17	51.50
1987	98.43	96	39	121	86	7.24	52.46
1988	87.06	85	17	95	80	3.56	12.68
1989	82.83	81	41	131	66	14.60	213.44
1990	97.50	96	40	121	81	8.33	69.48
1991	99.03	96	40	146	81	15.73	247.56
1992	164.65	167	17	172	157	3.58	12.86
1993	124.38	121	37	161	116	10.00	100.07
1994	107.22	101	37	146	96	11.80	139.45
1995	126.97	126	31	161	121	8.50	72.36
1996	132.42	132	36	157	117	8.22	67.67
1997	99.59	96	39	146	86	12.61	159.14
1998	157.67	156	15	166	151	4.49	20.23
1999	91.63	86	32	121	71	13.18	173.79
2000	101.18	98	33	123	93	6.59	43.46

Appendix 1 (continued)

Year	Mean	Median	N	Max	Min	SD	Variance
2001	96.88	91	40	151	76	15.72	247.29
2002	83.50	81	36	106	71	8.49	72.14
2003	101.53	101	38	126	91	6.75	45.66
2004	107.36	104.5	42	142	97	8.51	72.43
2005	124.08	126	13	126	121	2.53	6.41
2006	106.16	106	32	111	101	2.97	8.84
Common murre							
1972	142.56	140	98	187	127	10.75	115.63
1973	141.00	139	130	161	130	7.45	55.59
1974	138.32	137	139	158	128	6.45	41.65
1975	138.17	136	137	162	130	6.55	42.99
1976	137.04	135	164	168	126	7.47	55.94
1977	137.69	137	108	160	126	7.42	55.07
1978	144.90	144	114	162	136	4.29	18.42
1979	129.20	130	135	161	116	5.47	29.99
1980	134.60	134	138	152	126	4.97	24.78
1981	128.55	128	135	160	117	6.25	39.17
1982	133.82	134	70	156	125	5.94	35.36
1983	161.08	162	45	181	143	8.70	75.76
1984	134.69	132	128	184	121	10.79	116.47
1985	129.27	128	110	166	118	7.62	58.14
1986	135.63	135	111	160	127	5.74	33.01
1987	130.17	130	114	156	118	5.06	25.66
1988	119.86	119	119	158	107	6.24	38.98
1989	123.01	121	126	162	107	9.35	87.42
1990	123.19	122	135	158	108	7.92	62.76
1991	126.65	126	125	146	110	4.60	21.22
1992	149.34	146	93	182	133	9.33	87.14
1993	130.53	128	112	169	119	8.31	69.09
1994	125.37	125	133	151	110	6.28	39.55
1995	134.04	134	142	162	123	6.03	36.47
1996	130.92	128	150	167	120	8.34	69.71
1997	125.96	125	143	157	115	6.62	43.83
1998	142.53	141	101	167	122	9.07	82.31
1999	126.17	125	102	164	114	8.54	73.07
2000	130.89	130	105	156	118	8.67	75.24
2001	127.16	127	130	157	113	6.37	40.64
2002	123.86	123	136	157	111	7.88	62.13
2003	130.84	128	147	164	116	8.92	79.65
2004	130.26	130	150	151	115	5.49	30.19
2005	143.94	144	168	177	131	6.48	42.01
2006	138.38	137	189	171	124	7.33	53.77

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Changes in the timing of egg-laying of a colonial seabird in relation to population size and environmental conditions

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ABSTRACT: An emerging consequence of global climate change is its potential effect on the timing of seasonal biological events. Analysis of long-term datasets reveals a high degree of plasticity in the nature of phenological responses both within and among species, and understanding these differences is central to understanding the mechanisms and implications of climate-related change. We investigated factors influencing timing of breeding (median laying date) in a colonial nesting seabird, the common guillemot *Uria aalge*, over 23 breeding seasons between 1973 and 2008. There was a trend for earlier laying over this period, and earlier laying was associated with higher average breeding success. Multiple regression models (with de-trended explanatory variables to control for linear trends over time) indicate that the timing of breeding is positively correlated with a wide-scale climatic driver, the winter North Atlantic Oscillation (WNAO), and negatively correlated with population size: guillemots lay later in years with high WNAO indices and earlier in years with larger populations. Responses to environmental conditions are probably related to indirect effects on timing or abundance of food availability, direct effects of weather or both. The mechanism(s) leading to a possible relationship between laying date and population size are less clear. They may be related to Allee-type effects associated with social stimulation, improved foraging efficiency or a density-dependent increase in breeding site quality. Given the correlative nature of these results, we are cautious about the role of non-climatic (intrinsic) factors, but we cannot exclude that they play a role alongside climatic (extrinsic) factors in influencing reproductive phenology.

KEY WORDS: Phenology · Climate change · Allee effect · Coloniality · NAO · Density dependence

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INTRODUCTION

An emergent characteristic of organisms living in seasonal environments is a shift in the timing of life-history events related to global climate change (Walther et al. 2002). For instance, many animals have altered their timing of reproduction in response to changes in the timing of peak food availability, which is linked with environmental change (Charmantier et al. 2008). The consequences and limits of this phenotypic plasticity are not fully understood, and current research indicates that responses to global climate change are highly variable both within and among taxa (Visser & Both 2005). The reasons for this variability are not clear, but it is probably linked to spatial variation in environmental change, different life-history characteristics among taxa or other non-climate related factors that influence phenology. An important goal is to understand why this variation exists, but to date few studies have investigated the combined influence of climate change with other non-climate related effects on phenology.

For social or colonial animals, the presence of conspecifics can directly affect various important life-history tactics. Although the mechanisms are complex, key benefits of breeding in large groups include

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improved anti-predator strategies, increased reproductive facilitation, greater chance of finding a mate or improved foraging efficiency via information transfer (Courchamp et al. 2008). Together these processes can lead to a positive relationship between population growth rate and population size, collectively termed positive density dependence, or Allee effects (Courchamp et al. 2008). Although Allee effects specifically relate to effects on demographic parameters, there is also evidence that population size may have implications for other important processes such as the timing of reproduction. For example, Coulson & White (1960) found that timing of egg-laying in colonial breeding black-legged kittiwakes *Rissa tridactyla* was related to local nesting density, while controlling for the potentially confounding effects of both environmental conditions and age. Despite this, the role of intrinsic factors influencing timing of breeding remains unclear.

Here we analysed long-term data from a colonial nesting seabird, the common guillemot *Uria aalge* (hereafter guillemot), to determine the factors influencing the timing of reproduction. We simultaneously assessed whether guillemot breeding phenology is influenced by a number of environmental covariates and investigated the relationship with annual population estimates. We also investigated whether the onset of breeding is related to reproductive performance. Guillemots breed in very close proximity (i.e. at very high densities) and therefore population size and population density are likely to be closely related. We therefore investigated whether any changes in population size are related to changes in breeding density during the period of this long-term study. This is important because previous work indicates that breeding density rather than population size may play a role in altering timing of breeding (Coulson & White 1960, Coulson 2002). Understanding phenological responses to environmental factors has been the subject of much research, but it is not clear whether the effect of density-dependent factors can be excluded.

MATERIALS AND METHODS

Study site and data collection. Observations were conducted at 3 guillemot sub-colonies on Skomer Island (51° 40′ N, 05° 15′ W), Wales, in 23 breeding seasons between 1973 and 2008. Date of first egg laid and breeding successes were estimated by checking sites almost daily throughout the breeding period using binoculars or a telescope (Birkhead & Nettleship 1980, Hatchwell 1991a). Data on the median lay date of the 1-egg clutches laid by guillemots were collected in all 23 years of observation. Breeding success, measured as chicks fledged per breeding pair, was recorded in 17 breeding seasons during the same period. The number of breeding attempts that were followed varied during the study period (mean = 188 ± 146 SD, n = 23; range: 42 to 574). The whole island guillemot population (including breeders, failed breeders and immatures) was counted annually in the first half of June using standard methodologies (Hatchwell & Birkhead 1991).

Photographic records of 9 guillemot sub-colonies on Skomer (specifically, Amos sub-colonies A, B, C and D and Bull Hole sub-colonies B, C, D, E and F) were used to obtain an index of breeding density for 5 years: 1973, 1984, 1991, 1995 and 2005, spread across the study period. The location of each breeding bird was marked on photographs, and a density index was calculated as the mean number of birds within 1 bird length of all breeding individuals in each sub-colony.

Explanatory covariates. We considered 2 candidate environmental variables; winter North Atlantic Oscillation Index (WNAO; www.cgd.ucar.edu/cas/jhurrell/indices.html) and 4 major oil pollution incidents that released large quantities of crude oil into the marine environment in the wintering grounds of Skomer guillemots (‘Aegean Sea’, December 1992, 74 000 tonnes, La Coruña, Spain; ‘Sea Empress’, February 1996, 72 000 tonnes, Pembrokeshire, Wales; ‘Erika’, December 1999, 10 000 tonnes, Brittany, France; ‘Prestige’, November 2002, 63 000 tonnes, Galicia, Spain).

Guillemots feed primarily on lipid-rich shoaling fish such as sprat *Sprattus sprattus* and sandeel *Ammodytes* spp., as well as a range of different clupeid species (Hatchwell 1991b). WNAO is known to influence recruitment and timing of fish availability (Ottersen et al. 2001, Attrill & Power 2002) via changes in a suite of environmental conditions such as temperature, salinity, oxygen, turbulence and advection (Stige et al. 2006). Alternatively, WNAO may have direct effects leading to differences in foraging conditions (Finney et al. 1999). Because WNAO may influence guillemots directly via conditions in the current year or via longer-term effects on the prey base, we modelled contemporaneous WNAO as well as WNAO lagged by 1 yr. Previous studies have found variable responses of seabird reproductive phenology to NAO (Durant et al. 2004, Frederiksen et al. 2004); therefore, it was unclear whether WNAO would have positive or negative influences on lay date. The 4 major oil pollution events have been found to increase adult mortality, either because of direct effects or because of effects on the prey base (Votier et al. 2005). Moreover, reduced adult survival was associated with a concomitant increase in juvenile recruitment probability, with young birds presumably buffering adult losses (Votier et al. 2008). Therefore, major oil spills may lead to later laying because of negative effects in adult breeders or because of an increase in inexperienced breeders in the colony.

WNAO was modelled as a continuous explanatory variable, and oil pollution was modelled as a 2-level factor (i.e. whether there was an oil spill the previous winter or not). We also considered the possibility of using sea surface temperature (SST), but previous work has shown that common guillemots do not adjust timing of breeding in response to local-scale SST (Frederiksen et al. 2004). For this reason, and to reduce the number of explanatory variables given the number of years studied, we did not include SST in our regression models.

To test for possible intrinsic effects, we modelled lay date as a function of the Skomer guillemot population estimate, with a natural log (ln) transformation to correct for the fact that count data has the variance equal to the mean (i.e. the data are Poisson distributed). To determine whether the total Skomer guillemot population is related to breeding density, we modelled this as a function of breeding density measured at 9 sub-colonies. The mechanisms behind any possible density-dependent effects are likely to be linked with the presence of conspecifics, so we only modelled the current estimate of breeding density rather than consider lagged effects. Previous studies have found evidence that social stimulation from an increased number of conspecifics can facilitate earlier onset of breeding (Coulson 2002), so we *a priori* predicted that, if laying date is related to breeding density, the effect will be positive. Although population size may have negative as well a positive effects on demographic parameters (Greene & Stamps 2001, Oro et al. 2006), because of the highly social nature of guillemot colonies, we considered only the positive effects of population size.

Statistical analysis. We used multiple regression models to investigate factors influencing breeding phenology. Models were selected using Akaike's Information Criterion, corrected for small sample size (AICc; Burnham & Anderson 2002). The most parsimonious model was selected on the basis of the lowest AICc value, and AICc weights provide weight of evidence for the preferred model. Strong temporal trends in the dataset (see Figs. 1 & 4) mean that explanatory variables may be confounded by some other unmeasured variables that also co-vary with time. To control for these effects, we de-trended the response and explanatory variables by taking the Studentised residuals of their relationship with year and used these in our analysis. After removing the variation due to a linear trend with year, we found no co-linearity among explanatory variables. To reduce the effects of annual variation in the number of breeding attempts monitored, regression models were weighted by the square-root of the sample size. To reduce the number of parameters fitted, we included only 2-way interactions (we had no *a priori* reason to fit higher-order interactions).

To determine whether timing of breeding may have consequences for fitness, we modelled breeding success as a function of lay date using least square regressions, weighted by the square-root of the sample size.

We used a generalised linear mixed model (GLMM) to determine whether our measure of breeding density increased in relation to changes in the overall Skomer guillemot population. Mean breeding density (log transformed to conform to assumptions of homoscedasticity) was the dependent variable, population size a 5-level fixed factor and sub-colony included as a random factor to account for repeat observations over time. All analyses were conducted using R version 7.1 (R Development Core Team 2008).

RESULTS

The median lay date of guillemots across years did not differ significantly from a normal distribution (Shapiro-Wilk $W = 0.941$, $p = 0.188$) and became significantly earlier from 1973 to 2008 ($F_{1,21} = 5.196$, $R^2 = 0.198$, $p = 0.03$; slope [± SE] = –0.172 [± 0.075]; Fig. 1a). The most parsimonious model (AICc weight = 0.307) describing variation in median lay date included the additive effect of (ln) population size and lagged WNAO (Table 1) and explained 34% of the variance in lay date. After controlling for a linear trend across years, timing of breeding was positively related to WNAO with a 1 yr lag (Table 2, Fig. 1b), and was significantly earlier in years with high breeding density (Table 2, Fig. 1c). In addition, mean breeding success (which did not differ significantly from a normal distribution; Shapiro-Wilk $W = 0.934$, $p = 0.230$) was negatively correlated with laying date ($F_{1,16} = 4.53$, $R^2 = 0.221$, $p = 0.05$, slope = –0.011 [± 0.005]; Fig. 2), i.e. years of early onset of breeding were associated with higher breeding success.

Mean breeding density increased significantly as a function of the Skomer population size (GLMM: $t = 5.119$, df = 3, $p = 0.014$, slope = 0.396 [± 0.077]; Fig. 3), indicating an increase in breeding density concomitant with increasing population size during our study.

DISCUSSION

We have shown that timing of egg-laying in a colonial seabird is positively correlated with a wide-scale climatic driver (WNAO) and negatively correlated with population size, while controlling for an effect of year (Table 1, Fig. 1). Although many studies have demonstrated phenological shifts in response to environmental cues (Visser & Both 2005), our results indicate that for colonial and social breeders, timing of breeding

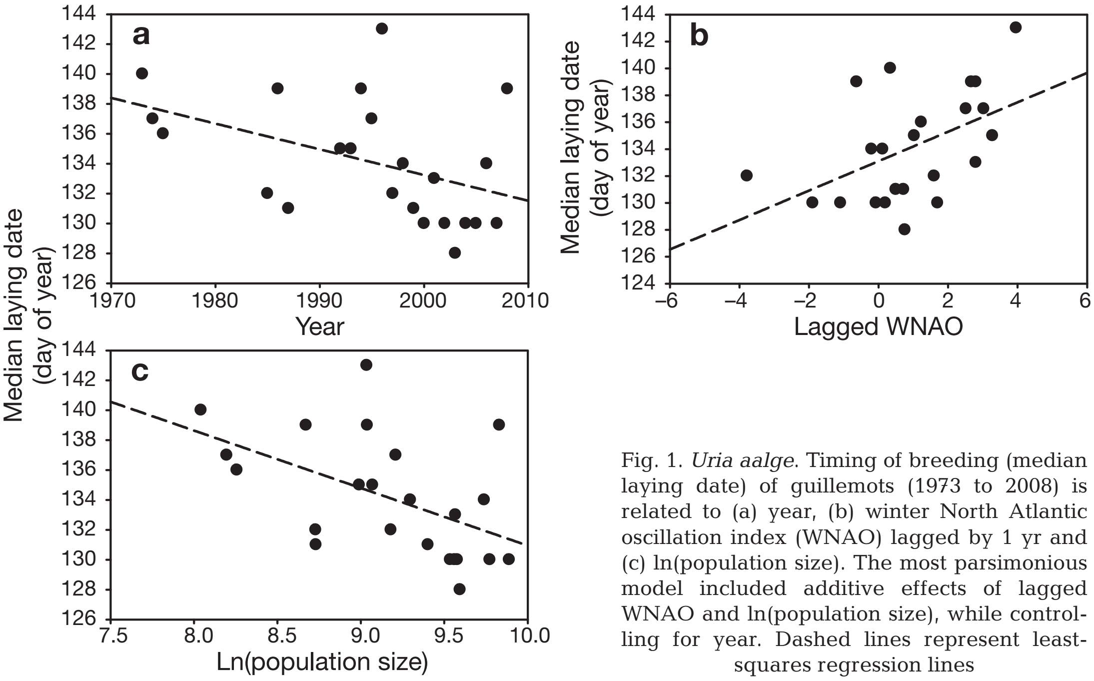

Fig. 1. *Uria aalge*. Timing of breeding (median laying date) of guillemots (1973 to 2008) is related to (a) year, (b) winter North Atlantic oscillation index (WNAO) lagged by 1 yr and (c) ln(population size). The most parsimonious model included additive effects of lagged WNAO and ln(population size), while controlling for year. Dashed lines represent least-squares regression lines

Table 1. *Uria aalge*. Model selection to estimate factors influencing timing of breeding in guillemots. Only the top 10 candidate models are shown, and the best supported model is in **bold**. df: degrees of freedom; LogLik: log likelihood; AICc: Akaike's Information Criteria (corrected); lnpop: natural log of guillemot population estimate on Skomer; WNAO: winter North Atlantic oscillation index; oil: incidence of 4 major oil pollution events

Model	df	LogLik	AICc	ΔAICc	AICc weight
lnpop + lagwnao	**4**	**–27.376**	**63.895**	**0.000**	**0.307**
lnpop + lagwnao + oil	5	–26.666	65.333	1.438	0.149
lnpop + wnao + oil	5	–29.655	65.476	1.581	0.139
lnpop + lagwnao + lnbreed ×lagwnao	5	–26.744	65.488	1.593	0.138
lnpop	3	–29.788	66.122	2.227	0.101
lnpop + lagwnao + wnao + oil	6	–26.412	67.981	4.087	0.040
lnpop + lagwnao + wnao + oil + lnpop ×wnao	7	–24.828	68.322	4.427	0.034
Intercept only	2	–32.145	68.463	4.569	0.031
lnpop + wnao + lagwnao	4	–27.165	68.474	4.580	0.031
lnpop + wnao	4	–29.666	68.512	4.617	0.030

Table 2. *Uria aalge*. Weighted multiple regression models explaining factors influencing variation in median laying date of guillemots on Skomer, Wales (1973 to 2008). The model including all main effects (but excluding interactions) and the model selected on the basis of Akaike's Information Criteria (corrected) (AICc) are presented along with slopes ± 1 SE (p-values); see Table 1 for definitions

	Full model	AICc selected model
Intercept	0.240 ± 0.230 (0.310)	0.775 ± 0.187 (0.684)
lnpop	–0.648 ± 0.222 (0.009)	–0.562 ± 0.207 (0.01)
wnao	0.132 ± 0.208 (0.533)	–
lagwnao	0.532 ± 0.220 (0.026)	0.430 ± 0.199 (0.04)
oil	–0.590 ± 0.534 (0.284)	–

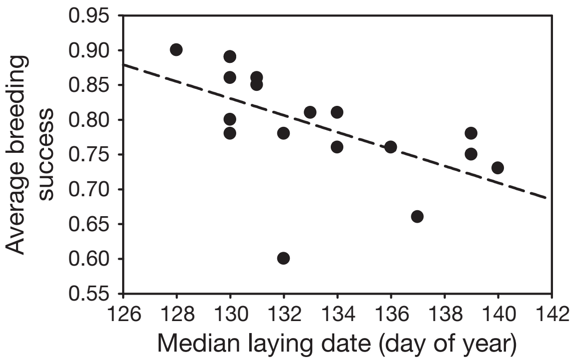

Fig. 2. *Uria aalge*. Average guillemot breeding success (number of chicks fledged per breeding pair) is negatively related to laying date in guillemots. Dashed line represents the least-squares regression line

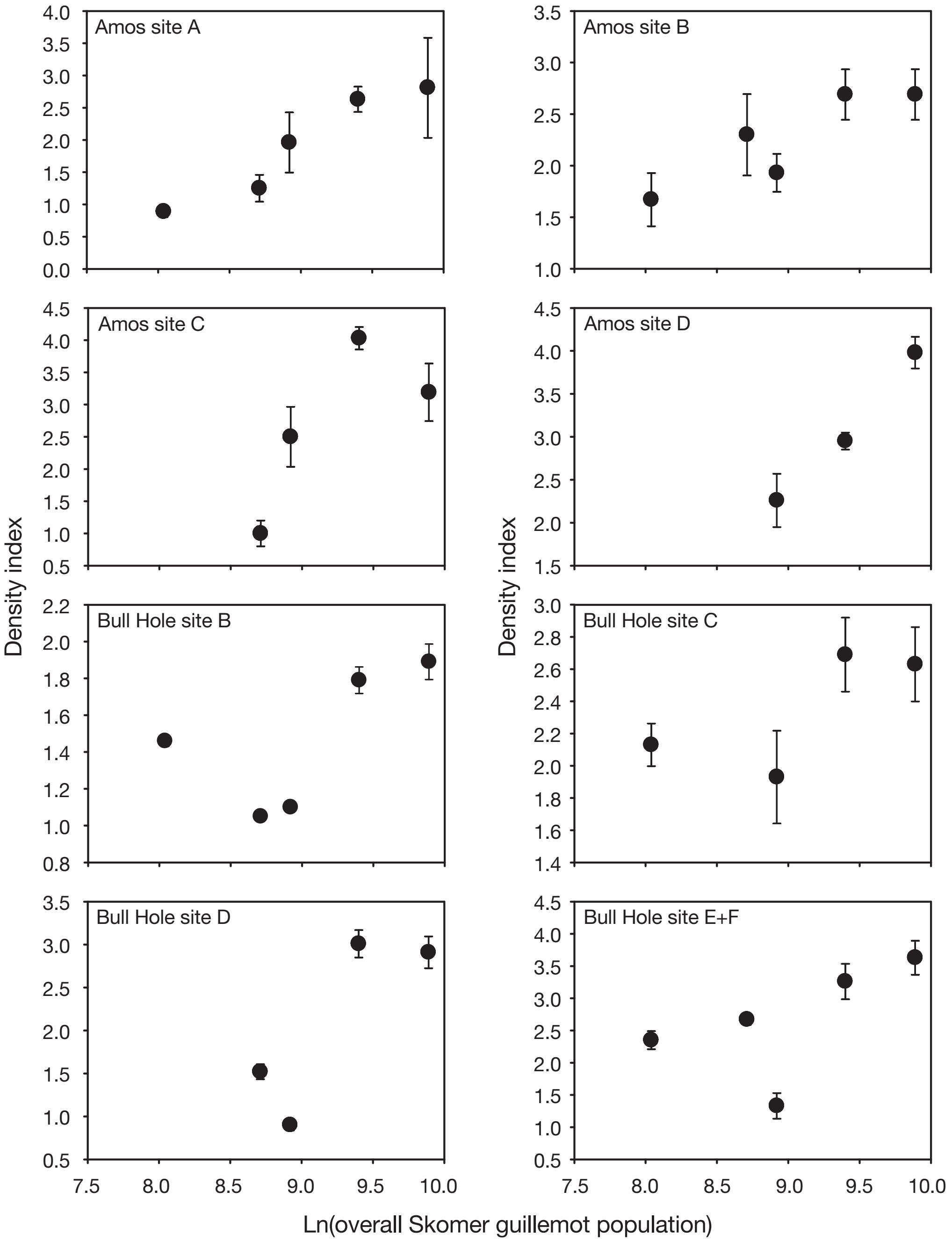

Fig. 3. *Uria aalge*. Mean breeding density (1 ± SE) of guillemots at 9 sub-colonies on Skomer, Wales (1973, 1984, 1991, 1999, 2005). The density index was calculated as the mean number of birds within 1 bird length of all breeding individuals in each sub-colony. On average, density increased significantly with increasing population size

may be influenced by density-dependent factors. Possible mechanisms and alternative explanations for these findings are discussed below.

The median lay date of our study population varied in response to environmental conditions lagged by 1 yr. The WNAO index is linked to large-scale oceanographic conditions in north-western Europe, which may affect guillemots either directly by increasing stormy conditions and therefore making foraging more difficult (Finney et al. 1999), indirectly via changes in prey fish abundance and timing (Finney et al. 1999, Ottersen et al. 2001, Attrill & Power 2002) or both. Although the direct effect of poor weather may be carried over from different periods of the annual cycle

(Sorensen et al. 2009), long-term effects from the winter 2 yr ago are unknown. Instead, the significant lagged effect probably reflects effects on the prey base. Therefore, changes in the timing of breeding most likely represent a response to changes in the timing of peak availability of forage fish (Durant et al. 2005). The inverse relationship between laying date and WNAO shown here is the opposite from a number of studies that have found positive relationships between seabird breeding phenology and WNAO in the North Sea (Durant et al. 2004, Frederiksen et al. 2004, Moller et al. 2006, Reed et al. 2006). Conversely, Durant et al. (2004) found that hatching date of Atlantic puffins *Fratercula arctica* in the Norwegian Sea was positively correlated with NAO during 1 climatic regime, although timing of breeding was independent of NAO following a regime shift. Such inter-population variation in the response of seabird reproductive phenology to the NAO are not well understood but probably reflect the complex nature of bottom-up effects of environmental conditions on fish population dynamics, including spatial differences in the effect of NAO on environmental conditions (Hallett et al. 2004, Stige et al. 2006) and non-linear effects of NAO (Durant et al. 2004). Further study of the relationship between the demographics and timing of peak abundance of forage fish at broad spatial scales might reveal more about the way in which different populations of top marine predators respond to environmental change.

To account for the trend for median lay date to become earlier during the course of this study (Fig. 1a), WNAO would have to show a negative trend over this period, but instead it did not change significantly with time ($F_{1,21}$ = 0.355, R^2 = 0.017, p = 0.558, slope [± SE] = –0.023 [± 0.039]; Fig. 4). SST showed a linear increase over the duration of this study (Fig. 4), but was not correlated with lay date ($F_{1,21}$ = 0.087, R^2 = 0.004, p = 0.087, slope [± SE] = –0.059 [± 0.201]). Therefore, some other factor must be influencing the long-term trend for earlier breeding in guillemots.

Early onset of breeding in guillemots was associated with higher population size in the current year (Tables 1 & 2). However, because our data are correlative, they do not necessarily show a causal relationship, and alternative explanations exist. For instance, years of high food availability may coincide with early breeding and an increase in breeder numbers at the colony. Guillemots exhibit delayed maturity and a protracted 2-stage recruitment (Votier et al. 2008), so breeder numbers change slowly over time and are relatively insensitive to annual fluctuations in food availability. However, the pre-breeding component of the population may be able to respond rapidly to environmental change and start breeding at a younger age in good years, and it has been shown that recruitment of this age class is negatively related to population size (Crespin et al. 2006) and is higher following increased oil-related adult mortality (Votier et al. 2005, 2008). On the other hand, young birds tend to lay later than older, more experienced birds (Hatchwell 1991a), and a growing population necessarily includes a number of inexperienced breeders, so increased recruitment of young birds would not necessarily be expected to drive

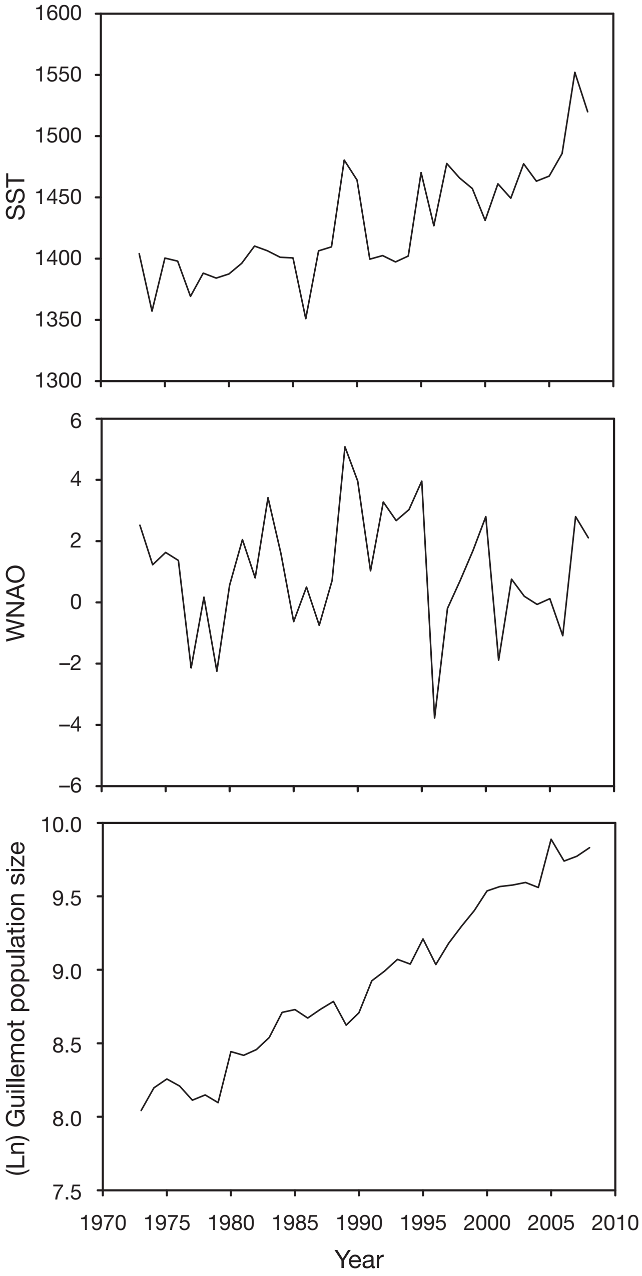

Fig. 4. Variation in explanatory variables used in the analysis (WNAO and population size), as well changes in SST, between 1973 and 2008

earlier laying. Furthermore, we found no significant effect of major oil spills on the timing of breeding (Table 2), an effect that would have been predicted under this scenario. An alternative explanation is that the proportion of sexually mature birds that breed each year is sensitive to variation in their social or ecological environment. If late breeders are less likely to breed at higher population sizes, the median lay date would be earlier in years when population size is large. Again, this idea is incompatible with the fact that the mean breeding density, as well as the overall population size, has increased over the study period (Fig. 3). Another potentially confounding factor is the possibility that detection probability of eggs laid early may increase with population size (Tryjanowski & Sparks 2001). Once again this explanation seems improbable. By using median laying date, we reduced the statistical influence of early or late laid eggs, and, given the intensive nature of the long-term study at Skomer, such methodological detection issues are doubtful. Finally, the trend for earlier breeding could be explained by the trend in population size. There is a negative relationship between population size and laying date (Fig. 1c) combined with a positive trend in population size ($F_{1,21}$ = 859.86, R^2 = 0.98, $p < 0.001$, slope = 0.050 [± 0.002]; Fig. 4), but despite this, we cannot exclude the influence of some other unmeasured factor. In summary, given the large number of possible alternative explanations for our findings, and without direct measures of prey availability, we cannot be certain that population size is causally linked with the timing of breeding in common guillemots.

Despite the uncertainty for a direct influence of density-dependent effect on timing of breeding, it is helpful to consider likely proximate causes of earlier laying in larger populations. Guillemots are present at the colony for several months prior to egg-laying (Birkhead 1978a), providing opportunity for much interaction, and the most plausible influence of increasing population size on phenology is a link with Allee-type density dependence, mediated in 2 possible ways. Firstly, social stimulation by conspecifics could lead to advancement in the timing of reproduction. Darling (1938) hypothesised that social stimulation among colonial-nesting birds could lead to an acceleration and synchronisation in reproduction. While the 'Fraser Darling effect' remains hypothetical, there is some evidence that local density, rather than population size, can influence laying date in black-legged kittiwakes (Coulson & White 1960, Coulson 2002). At Skomer, a significant increase in local breeding density is concomitant with an increase in overall population size on Skomer (Fig. 3). Secondly, increasing numbers of conspecifics may facilitate food location, improving average body condition and therefore leading to earlier onset of breeding. Colonies may act as information centres to enhance foraging efficiency (Sonerud et al. 2001, Wright et al. 2003) and although this has not been demonstrated at the colony level for seabirds, there is evidence of positive density dependence in foraging success at sea, mediated via local enhancement (Grünbaum & Veit 2003, Silverman et al. 2004). Alternatively, since strong stabilising selection favours synchronous breeding in this species (Reed et al. 2006), which is probably closely linked with social constraints (Birkhead 1978b), other components of social behaviour linked with synchrony may also be important. Finally, the increase in density at Skomer (Fig. 3) would also result in an increase in breeding site quality, because site quality in guillemots is positively related to density through its effect on communal defence against predators (Birkhead 1977, Hatchwell 1991a). Thus, if an earlier onset of egg-laying is linked to population size, this may be via inverse density dependence.

Given the reliance on correlative studies for this type of research, assessing the role of density-dependence on timing of breeding will require a more detailed body of evidence than that currently available to us. Latitudinal studies from a range of colonies with different breeding densities could prove fruitful, as could similar longitudinal studies from other sites as that presented here. As mentioned, there is already evidence that timing of breeding is related to breeding density in the colonial-nesting black-legged kittiwake (Coulson & White 1960, Coulson 2002), and work suggests that chinstrap penguins *Pygoscelis antarctica* nesting in large colonies in the South Shetlands have earlier hatching dates compared to those nesting in small colonies (Barbosa et al. 1997). Conversely, long-term trends in later laying of northern gannets *Morus bassanus* in the eastern Atlantic (Wanless et al. 2008) are associated with increasing population sizes of this species (Mitchell et al. 2004). With so few studies, it is not possible to draw any firm inference, so we urge other researchers conducting similar phenological studies to consider the effects of density dependence to test this further.

It is generally the case that an early onset of avian breeding leads to improved reproductive performance within seasons (Spear & Nur 1994). Guillemots are characterised by a high degree of breeding synchrony, and pairs that breed later than average have lower breeding success than the rest of the population (Birkhead 1977, Hatchwell 1991a, Reed et al. 2006). Thus, there is strong stabilising selection that should limit intra-population variation in timing of breeding (Reed et al. 2006). Here, we found that guillemot breeding success was negatively correlated with median lay date across years (Fig. 2) as well as within years (Birkhead 1977, Hatchwell 1991a). However, we think it unlikely that this between-year relationship is also mediated by reproductive synchrony, because previous studies have suggested that synchrony operates at the level of the sub-colony, so that timing relative to neighbours is the key determinant of breeding success (Birkhead 1977, Hatchwell 1991a).

To conclude, our results indicate that timing of guillemot laying date is influenced by environmental conditions linked with the NAO, but this does not explain a long-term trend for earlier breeding. This trend may in part be explained by an increase in population size or breeding density, but because our findings are open to multiple interpretations, and given problems with collecting experimental data to test the robustness of these findings, they are equivocal. Nevertheless, we urge other researchers conducting phenological studies to consider the influence of both climate- and non-climate-related factors to better understand the effects of global change.

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Contribution to the Theme Section 'Marine ecosystems, climate and phenology: impacts on top predators'

Climate change and phenological responses of two seabird species breeding in the high-Arctic

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ABSTRACT: The timing of breeding is a life-history trait that can greatly affect fitness, because successful reproduction depends on the match between the food requirements for raising young and the seasonal peak in food availability. We analysed phenology (hatch dates) in relation to climate change for 2 seabird species breeding in the high-Arctic, little auks *Alle alle* and black-legged kittiwakes *Rissa tridactyla*, for the periods 1963–2008 and 1970–2008, respectively. We show that spring climate has changed during the study period, with a strong increase in both air temperature (TEMP) and sea surface temperature (SST) and a decrease in sea ice concentration. Little auks showed a trend for earlier breeding over the study period, while kittiwakes showed a non-significant trend for later breeding, demonstrating different phenological responses in these 2 species. Little auks and kittiwakes adjusted their timing of breeding to different environmental signals. Spring TEMP was the best predictor of little auk phenology, with a significant negative effect. Spring SST was the strongest predictor of kittiwake phenology, with a non-significant negative effect. Spring sea ice concentration and the North Atlantic Oscillation (NAO) winter index had a low relative variable importance. Furthermore, in kittiwakes, years with late breeding were associated with low clutch size and mean annual breeding success, indicating poor investment and food availability. This study identifies some spring environmental factors important for regulating the timing of breeding in the high-Arctic, most likely through effects on snow cover limiting access to nest sites and the development of the polar marine food web. It remains to be investigated whether environmental factors are reliable predictors of marine prey phenology, and whether the decision to start breeding is constrained by food availability.

KEY WORDS: Phenology · Climate change · Seabirds · Match-mismatch · Svalbard · Sea ice · Temperature · Timing of breeding

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INTRODUCTION

Some of the strongest evidence for the effects of climate change on organisms comes from studies of phenology (e.g. Stenseth et al. 2002, Walther et al. 2002). Phenology is the timing of seasonal activities of animals and plants, and long-term trends for changes in arrival dates and breeding dates of birds have been regarded as 'fingerprints' of the ongoing climate change (Parmesan & Yohe 2003, Root et al. 2003).

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In regions where food availability is highly seasonal, reproduction is only possible during a short time period, usually during the spring and summer. The timing of the peak in food availability varies between years. Hence, the timing of breeding is crucial in order to match the energy requirements of breeding to the actual food availability (the temporal match-mismatch concept; Cushing 1990, Edwards & Richardson 2004, Frederiksen et al. 2004, Durant et al. 2005). Thus, the timing of breeding is among the key factors for successful reproduction in birds (Dunn 2004, Reed et al. 2009).

The decision to start breeding is under endocrine control, and the hormone levels involved in this control are influenced by a combination of fixed (photoperiod) and variable environmental cues (climatic factors, food availability; Wingfield 1983, Gwinner 1986). Birds experience variable environmental cues on different spatial and temporal scales, and evidence suggests that birds use these cues in optimal decisions on when to initiate breeding (e.g. Frederiksen et al. 2004). The decision is done before the peak in food availability occurs, so optimal decisions are possible if the environmental cues are reliable predictors of the peak in food availability (Visser & Both 2005). In addition, initiation of breeding could be constrained by the food availability during the pre-breeding period that is needed for investment in eggs. In extreme cases, egg production relies on endogenous reserves built up before and during migration ('capital breeders'; Drent & Daan 1980). However, most birds produce their eggs from resources acquired at the breeding grounds ('income breeders'; Drent & Daan 1980).

The Arctic region is currently undergoing a dramatic climate change, with a 2-fold higher increase in temperature compared to the global increase, a trend that is expected to continue (Kattsov et al. 2005, IPCC 2007). Advancement in the onset of spring is already evident, with the timing of snow melt becoming 15 d earlier over the last decade in Greenland (Høye et al. 2007). Furthermore, sea ice extent has decreased linearly by 3 to 9% per decade in the Arctic Ocean (Serreze et al. 2007), with substantial effects on polar marine ecosystems (Gaston et al. 2003, Moline et al. 2008). The development of the polar marine food web on which seabirds depend is closely linked to the timing of removal of sea ice and the warming and stratification of the surface waters to allow for a spring bloom. Consequently, there is a need to assess the effects of climate change on Arctic seabirds. With some exceptions, however, there are very few published long-term studies on breeding phenology from the Arctic. In the Canadian Arctic, years with low sea ice cover and early sea ice break-up were related to early breeding of Brünnich's guillemots *Uria lomvia* (Gaston et al. 2005a). While low sea ice cover negatively affected breeding success of the low-Arctic population, breeding success of the high-Arctic population was positively affected by early sea ice break-up (Gaston et al. 2005a). In East Antarctica, a decrease in sea ice cover and an increase in the length of the sea ice season were associated with a trend for later breeding of adelie penguins *Pygoscelis adeliae* and cape petrels *Daption capense* (Barbraud & Weimerskirch 2006). These studies suggest that sea ice affects seabird breeding phenology and breeding success in high-latitude regions. They also underline the fact that climate change has not affected all parts of the polar regions to the same extent or in the same direction (Vaughan et al. 2001).

In the present study, we analysed long-term data on breeding phenology of 2 high-Arctic breeding seabirds, black-legged kittiwakes *Rissa tridactyla* (hereafter 'kittiwakes') and little auks *Alle alle*, breeding at Ny-Ålesund and Hornsund, respectively, on the western coast of Svalbard (Fig. 1). These data cover the periods 1970–2008 and 1963–2008 for kittiwakes and little auks, respectively, and offer a great opportunity to detect long-term changes in the timing of breeding in relation to climate change in the high-Arctic and to test whether environmental conditions at different scales explain the variability in the timing of breeding. Migratory seabirds may use the winter conditions to initiate the spring migration (Frederiksen et al. 2004), and we used the North Atlantic Oscillation index (NAO) as a large-scale proxy for winter conditions. Our study populations spend the winter in the Northwest Atlantic Ocean, close to Greenland according to ring recoveries (Bakken et al. 2003). If they use the winter conditions to initiate the spring migration, and this in turn affects the timing of breeding, we expected NAO to affect the breeding phenology of both species.

When the seabirds arrive at the breeding grounds in spring, they may use local environmental cues or food availability to further adjust the timing of breeding (Frederiksen et al. 2004). Both of these birds are 'income breeders'. Just after arrival at their breeding grounds, kittiwakes and little auks feed at different trophic levels (Karnovsky et al. 2008). In the early part of the breeding season, little auks are primarily zooplanktivorous: they feed at a low trophic level on copepods (e.g. Karnovsky et al. 2003, 2008). Little auks from West Greenland have been known to arrive at their breeding grounds just when copepods such as *Calanus hyperboreus* rise to the surface waters to feed on the spring phytoplankton bloom that is linked to stratification of the water column (Karnovsky & Hunt 2002). In contrast, kittiwakes feed at a higher trophic level on fish, amphipods and krill (Hop et al. 2002, Karnovsky et al. 2008). We used spring sea surface temperature (SST) and sea ice concentration (ICE) to represent the environmental conditions in the foraging areas at sea, and we expected both species to breed earlier in years

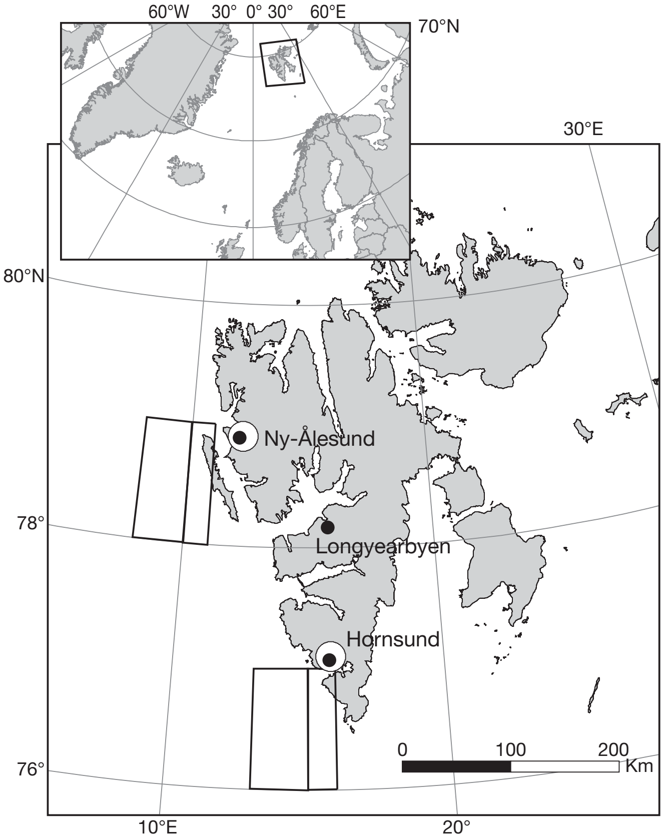

Fig. 1. Study area on Spitsbergen, Svalbard. Kittiwakes were studied at Ny-Ålesund and little auks in Hornsund, and large white circles indicate the 2 study colonies. Meteorological stations (small black circles) in Ny-Ålesund, Longyearbyen and Hornsund provided data on air temperature. The boxes show the areas from which data on sea surface temperatures (SST) and sea ice concentrations (ICE) were obtained (see 'Materials and methods: Environmental parameters')

with low ICE and high SST (Gaston et al. 2005a, Barbraud & Weimerskirch 2006).

The ground-nesting little auks breed in a rocky slope that is covered by snow during spring. Hence, access to the nests is only available when the snow cover has melted sufficiently. However, snow does not block access to nests for the cliff-nesting kittiwakes. By using spring air temperature (TEMP) as an indicator of timing of snow melt, we expected TEMP to affect little auk but not kittiwake phenology. Furthermore, in kittiwakes, we also tested the hypothesis that inter-annual variation in the timing of breeding would be related to fecundity and breeding success.

MATERIALS AND METHODS

Breeding phenology. Data on median hatch date of little auks was obtained in a large colony (~10 000 breeding pairs) at the Ariekammen slopes (77° 00′ N, 15° 33′ E) in Hornsund, Svalbard (Fig. 1). Published (Stempniewicz 2001, Harding et al. 2004) and unpublished data on median hatch date were obtained for 18 years in the period 1963–2008 (1963–65, 1974–75, 1980, 1983–84, 1986–87 and 2001–08). Hatch date was determined by regular visual inspections of 17 to 261 nests in the same area of the colony for all years, except for one. In 2003, hatch date was back-calculated from the median date of fledging (departure of 857 fledglings during 14 nights of observation that covered the whole fledging period; Wojczulanis et al. 2005) and the length of the nesting period (27 d; Stempniewicz 1981).

Median hatch dates of kittiwakes were obtained in the colony Krykkjefjellet (78° 54′ N, 12° 13′ E) in Kongsfjorden, 6 km from Ny-Ålesund in Svalbard (Fig. 1). Since 2002, we included a second colony (Irgensfjellet; 79° 00′ N, 12° 07′ E). It is located only 10 km away from the other and comprises approximately the same number of nests. This was done to maintain robust sample sizes after a substantial decline in the population size (during 1997–2003), and to maintain high precision in the measure of hatch date. Published (Mehlum 2006) and unpublished data were obtained for 18 years in the period 1970–2008 (1970–71, 1982–85 and 1997–2008). The median hatch dates for 2004–2008 were determined by regular visual inspections of ~180 nests, and in 1997–2000 we inspected ~100 nests. In 2002 and 2003, we used hatch dates of chicks (2002, N = 18; 2003, N = 5) that were hatched in an artificial egg incubator (A90, J. Hemel; T = 37.5–38°C, relative humidity 55–75%), because breeding was extremely late and the hatching occurred when the field workers were not present. The chicks originated from eggs that were collected in the colony, insulated with wool and brought to the laboratory in Ny-Ålesund within 1 h upon collection. Median hatch dates for 1970–1971, 1982–1985 and 2001 were determined from counts of hatched eggshells under the bird cliff in the same colony (Krykkjefjellet) by Mehlum (2006). We did a methodological study and observed hatch dates in the nests and counted hatched eggshells under the same nests (covering 112 nests). This showed that counts of hatched eggshells produced a 0.5 d later median hatch date, compared to direct observations in the nests. Accordingly, we adjusted the hatch dates obtained from Mehlum (2006) by –0.5 d.

Breeding success. For kittiwakes, data on clutch size and a measure of breeding success (number of chicks >12 d old per active nest) were obtained for all years in the period 1997–2008 (51 to 139 active nests), except for 2001. Data on breeding success of little auks were only available for a few years, and consequently were not analysed.

Environmental parameters. We used the NAO as a large-scale measure of winter conditions and 3 local measures of spring conditions (SST, ICE and TEMP).

Monthly NAO indices, standardised by the 1950–2000 base period monthly means and SD, were obtained from the National Oceanic and Atmospheric Administration (NOAA; www.cpc.ncep.noaa.gov) to produce a winter index (NAO_W, averaged over December to March). Measures averaged for April–May were used for local spring conditions, because both kittiwakes and little auks return to the breeding grounds in Svalbard in April, and egg-laying occurs in June.

Data on TEMP (°C) were obtained from the weather stations in Ny-Ålesund and Longyearbyen (Norwegian Meteorological Institute, DNMI) and Hornsund (Polish Polar Station Hornsund; Fig. 1). Data on TEMP from Ny-Ålesund were used in the analyses of kittiwake phenology. In analyses of little auk phenology, we used data on TEMP from Hornsund for the period 1979–2007 and estimated data on TEMP for Hornsund for the period 1963–1979. By using the estimates from a linear regression, we made a reliable estimate of TEMP for Hornsund from TEMP Longyearbyen (TEMP Hornsund = –0.36 [±0.27] + 0.794 [±0.037] × TEMP Longyearbyen), because these measures were highly correlated (1979–2008, N = 30, r = 0.97, $p < 0.0005$). The conclusions drawn in this study did not differ if we entirely used TEMP Longyearbyen to represent TEMP Hornsund. Furthermore, we expected the timing of snow melt to influence the breeding phenology of little auks. Data on snow depth or snow cover, however, do not exist for the appropriate time scales, so we used TEMP as a proxy for the timing of snow melt.

ICE (%) was extracted with the software ArcGIS Arcinfo (9.2) from sea ice maps. DNMI has produced daily maps (1979–2008) and weekly maps (1963–1979) by manual interpretation of satellite data and *in situ* observations. Sea ice maps were unavailable for May 1964 from Hornsund. We therefore estimated ICE May from ICE April (ICE May = 0.59 × ICE April – 0.127, $F_{1,41} = 25.5$, $p < 0.001$). Maps were unavailable for April and May in 1964 and 1965 for Ny-Ålesund. The sea ice cover at the western coast of Spitsbergen typically consists of different types of drift ice, ranging from 'very close drift ice' to 'open water', with 90–100% and 0–10% ice concentrations, respectively.

Data on sea temperature at 5 m depth were used as SST (°C). These data were obtained from the Carton-Giese SODA v2.0.2-4 database (Carton & Giese 2008) via the IRI/LDEO Climate Data Library (http://iridl.ldeo.columbia.edu). The SST data from Carton-Giese SODA v2.0.2-4 covered the whole study period except for the last year. SST for 2008 was therefore estimated from SST obtained from Reyn_Smith OIv2 (Reynolds et al. 2002) via the IRI/LDEO Climate Data Library. We simply multiplied the SST from 2007 by the 2008/2007 SST ratio from Reyn_Smith OIv2.

We used ICE data from the 1° box bounded by 78–79° N and 10–11°E for the kittiwakes breeding at Ny-Ålesund (Fig. 1) and by 76–77° N and 15–16° E for the little auks breeding in Hornsund (Fig. 1). The sea ice is more extensive close to the coast compared to farther west, so data from these areas are the best to reflect the sea ice conditions. We used SST data from the 2° boxes bounded by 78–79° N and 8–10° E and by 76–77° N and 13–15° E for the kittiwakes and the little auks, respectively (Fig. 1). We chose these boxes to cover a relatively large area that included both the shelf and the area to the west of the shelf break. From GPS-tracking, we know that this geographical sector correspond well to the foraging areas during the pre-breeding period for the kittiwakes breeding at Ny-Ålesund (O. Chastel unpubl. data). We do not have knowledge about the foraging grounds of the little auks during the pre-breeding period. However, the chosen area corresponds well to the foraging areas during the breeding period (Karnovsky et al. 2003).

Statistical analyses. Linear regressions and Pearson moment-product correlations were used to test for temporal trends in environmental factors and timing of breeding. We followed the approach by Frederiksen et al. (2004) to test how environmental variables affected breeding phenology. We entered TEMP, ICE, SST, NAO_W and YEAR as predictor variables in multiple linear models where median hatch date was the response. We used diagnostic plots (QQ, residuals versus fitted, residuals versus leverage) to assess whether the data sufficiently met the assumptions of the linear model. We fitted 32 models for each species and included no interactions. The selection of the best models was based on Akaike's Information Criterion adjusted for small samples size (AIC_c; Burnham & Anderson 2002). To avoid models with very limited support, we selected a redefined set of candidate models with $\Delta AIC_c < 4$ and calculated AIC_c weights. AIC_c weight is the likelihood of the model given the data and the set of candidate models, and evidence ratios summarise this for each predictor variable. Thus, AIC_c weight and evidence ratio represent the relative importance of a model and a predictor variable, respectively. Evidence ratios >10 indicate moderately strong support (Lukacs et al. 2007, Frederiksen et al. 2008). The effect of each environmental variable on breeding phenology was estimated using model-averaged estimates that were calculated using AIC_c weights according to Burnham & Anderson (2002). Hence, the effects were adjusted for model selection uncertainty.

It was important to include YEAR in these analyses, because some of the environmental variables showed a linear trend over time (Fig. 2, Table A1 in Appendix 1). Other predictor variables also correlated with each other (Table A1), so we carefully compared models

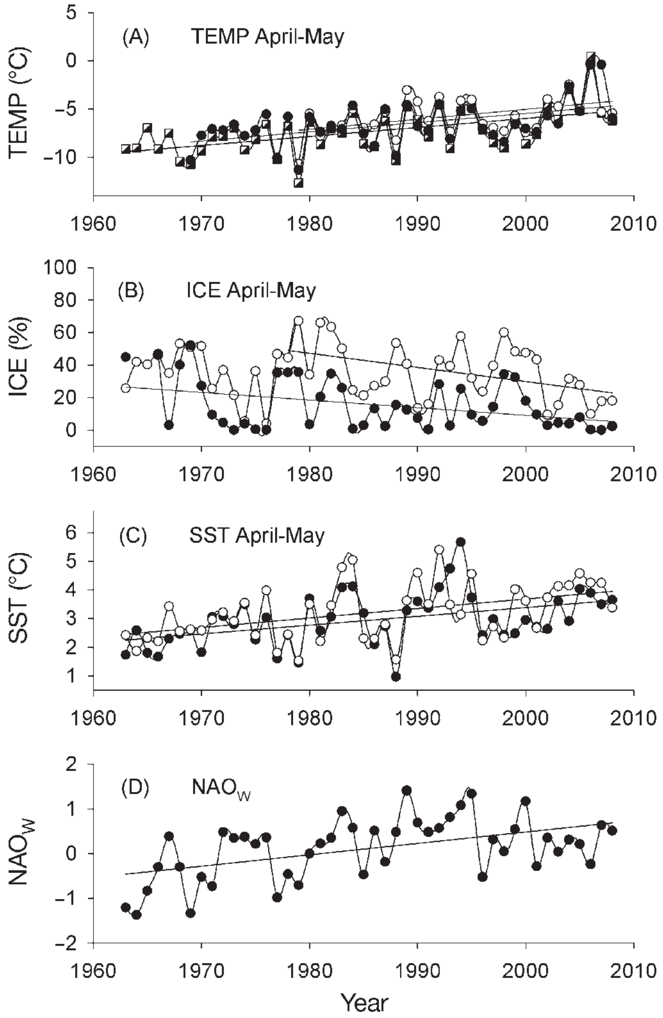

Fig 2. (A) Air temperature (TEMP), (B) sea ice concentration (ICE) and (C) sea surface temperature (SST) at (●) Ny-Ålesund, (○) Hornsund and (◪) Longyearbyen as a function of year. (D) North Atlantic Oscillation winter index (NAO_W) as a function of year. The data on TEMP are from the periods 1963–2008, 1969–2008 and 1979–2008 from Longyearbyen, Ny-Ålesund and Hornsund, respectively. Regression lines indicate significant linear relationships. (A) TEMP Longyearbyen = −194.3 (±42.4) + 0.094 (±0.021) × year; TEMP Ny-Ålesund = −196.6 (±53.3) + 0.096 (±0.027) × year; TEMP Hornsund = −213.3 (±76.2) + 0.104 (±0.038) × year, (B) ICE Ny-Ålesund = 958.8 (±333.7) − 0.475 (±0.168) × year; ICE Hornsund = 1775.8 (±617.4) − 0.873 (±0.310) × year; (C) SST Ny-Ålesund = −57.8 (±18.2) + 0.031 (±0.009) × year; SST Hornsund = −63.1 (±19.0) + 0.034 (±0.010) × year; (D) NAO_W = −50.7 (±13.0) + 0.026 (±0.007) × year

containing only 1 variable to those of multiple variables. The SEs of the estimates were not severely inflated when multiple variables were included in the same models, so the conclusions drawn from these analyses are not assumed to be influenced by problems related to multiple collinearity.

The analyses could potentially be affected by the fact that different methods had been used to obtain hatch dates. For kittiwakes, data from 2002 and 2003 were special because hatch dates were obtained from eggs in incubators, and because these years were extremely late and poor. For little auks, data from 2003 was special because hatch date was back-calculated from fledging dates. We therefore performed reanalyses to test how environmental variables affected breeding phenology when these years were excluded. However, the results from these reanalyses did not change the conclusions drawn from the full analyses with all years included. The statistical analyses were performed with the software R 2.6.0 (R Development Core Team 2007). The seabird and environmental data used in this study are given in Appendix 1, Table A2.

RESULTS

Spring TEMP increased in Svalbard over the study period (1963–2008), with TEMP becoming 0.9 (±0.2)°C warmer per decade in Longyearbyen ($F_{1,44}$ = 19.4, p < 0.001, Fig. 2A). The strongest increase in TEMP took place during the later part of this period, with an increase of 0.47 (±0.18)°C per year from 1997 to 2008 ($F_{1,10}$ = 6.9, p = 0.03, Fig. 2A). The increase in TEMP was similar for Hornsund and Ny-Ålesund (Fig. 2A). This trend was accompanied by a decrease in spring ICE and by an increase in spring SST. During the whole study period, the decrease in ICE was significant for Ny-Ålesund ($F_{1,42}$ = 8.0, p = 0.007, Fig. 2B), but not entirely for Hornsund ($F_{1,44}$ = 2.3, p = 0.14, Fig. 2B). During the last 30 yr, however, it was significant for both locations (1978–2008, $F_{1,29}$ > 5.5, p < 0.02, Fig. 2B). SST increased significantly over the study period for Ny-Ålesund ($F_{1,44}$ = 11.2, p = 0.002, Fig. 2C) and Hornsund ($F_{1,44}$ = 12.1, p = 0.001, Fig. 2C). The NAO_W also increased significantly during the study period ($F_{1,44}$ = 15.3, p < 0.001, Fig. 2D).

Little auks showed a significant trend for earlier breeding ($F_{1,16}$ = 4.5, p = 0.05, Fig. 3); median hatch date became 4.5 (±2.1) d earlier over the study period. The kittiwakes showed a trend for later hatching, but it was not significant ($F_{1,16}$ = 1.7, p = 0.21, Fig. 3). For the years with data from both species, there was no correlation between the median hatch dates of kittiwakes and little auks (r = 0.06, df = 8, p = 0.86), indicating that the 2 species have shown different phenological responses over time.

Different environmental factors were related to the breeding phenology of little auks than kittiwakes (Tables 1 & 2). The best models were TEMP for little auks and SST+ICE for kittiwakes (Table 1), with coefficients of determination (R^2) of 0.40 and 0.30, respec-

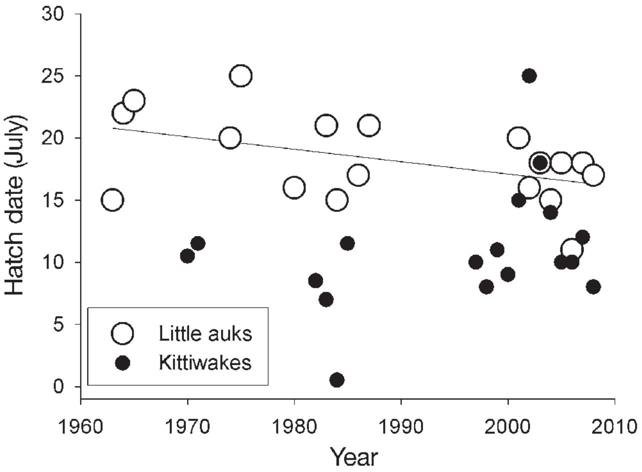

Fig 3. *Alle alle* and *Rissa tridactyla*. Median hatch dates in July of little auks (open circles) and kittiwakes (filled circles) breeding in Svalbard, as a function of year (kittiwakes, 18 yr, 1970–2008; little auks, 18 yr, 1963–2008). The regression line represents a significant linear trend for earlier breeding of little auks; hatch date = 217.2 (±93.7) – 0.100 (±0.047) × year

Table 1. *Alle alle* and *Rissa tridactyla*. Rank of linear models explaining breeding phenology of little auks and kittiwakes based on Akaike's Information Criterion corrected for small sample size (AIC_c). k is the number of parameters, and w is the Akaike weight calculated from the set of models with $\Delta AIC_c < 4$. See 'Materials and methods: Environmental parameters' for an explanation of model parameters

	Rank	Model	k	ΔAIC_c	w
Little auks	1	TEMP	2	0.0	0.33
	2	TEMP, ICE	3	0.1	0.31
	3	TEMP, SST	3	2.6	0.09
	4	TEMP, YEAR	3	3.3	0.06
	5	TEMP, NAO_W	3	3.4	0.06
	6	TEMP, ICE, SST	4	3.5	0.06
	7	TEMP, ICE, NAO_W	4	3.9	0.05
	8	ICE	2	3.9	0.05
Kittiwakes	1	SST, ICE	3	0.0	0.34
	2	SST, ICE, YEAR	4	1.9	0.13
	3	SST, YEAR	3	2.2	0.11
	4	intercept only	1	2.3	0.11
	5	SST	2	2.7	0.09
	6	YEAR	2	3.3	0.06
	7	YEAR, NAO_W	3	3.6	0.06
	8	SST, ICE, NAO_W	4	3.9	0.05
	9	SST, ICE, TEMP	4	3.9	0.05

Table 2. *Alle alle* and *Rissa tridactyla*. Effects of environmental variables on breeding phenology of little auks and kittiwakes. Effects are model-averaged slope estimates derived from the models in Table 1. Variables are ranked according to the evidence ratio (ER), which reflects their relative importance. Shown are unconditional SEs and 95% confidence intervals. ER was calculated as the summed Akaike weights of all models including the variable divided by the summed weight of models not including the variable. ER > 10 indicates moderate to strong support. Units are °C for TEMP and SST and % for ICE. See 'Materials and methods: Environmental parameters' for an explanation of model parameters

Variable	Effect	SE	95% CI	ER
Little auks				
TEMP	–1.02	0.45	–1.89, –0.14	19.0
ICE	0.04	0.06	–0.07, 0.16	0.9
SST	–0.09	0.22	–0.51, 0.34	0.2
NAO_W	0.02	0.14	–0.26, 0.30	0.1
YEAR	–0.001	0.005	–0.010, 0.008	0.1
Kittiwakes				
SST	–3.54	2.66	–8.75, 1.67	3.3
ICE	–0.13	0.14	–0.39, 0.14	1.3
YEAR	0.05	0.08	–0.11, 0.22	0.6
NAO_W	–0.20	0.57	–1.33, 0.92	0.1
TEMP	–0.003	0.032	–0.066, 0.060	0.1

tively. TEMP was the best predictor of little auk phenology, while SST was the best predictor of kittiwake phenology (Tables 1 & 2). High TEMP was associated with early breeding of little auks, while high SST was associated with early breeding of kittiwakes (Table 2). For little auks, TEMP had an evidence ratio that indicated moderately strong support relative to the other predictor variables (Table 2), and the confidence interval of the model-averaged slope estimate did not overlap with 0 (Table 2). Hence, TEMP seemed to have an important negative relationship with breeding phenology of little auks. For kittiwakes, however, the model-averaged slope estimate for SST overlapped slightly with 0 and the evidence ratio was relatively low (Table 2), and we cannot conclude firmly about the effect or the relative importance of the variable.

Although ranked second best, ICE had low relative variable importance, and the effects were highly uncertain (Table 2). Furthermore, NAO_W and YEAR had the lowest evidence ratios, and the model-averaged slope estimates were very close to 0 (Table 2). Notably, the significant correlation between YEAR and little auk phenology (Fig. 3) disappeared when TEMP was included in the models (Table 2). Hence, it seems likely that the trend for increased spring TEMP (Fig. 2) has caused the trend for earlier breeding of little auks (Fig. 3).

In kittiwakes, clutch size ($r = -0.84$, df = 9, $p = 0.001$, Fig. 4) and breeding success ($r = -0.80$, df = 9, $p = 0.003$, Fig. 4) were negatively correlated to median hatch dates. When breeding success was calculated as the number of chicks per egg laid, instead of the number of chicks per active nest, the negative correlation with phenology was still significant ($r = -0.83$, df = 9, $p = 0.001$). Thus, late breeding was associated with low clutch size and poor breeding success (Fig. 4). These relationships, however, were strongly driven by the 2 extremely late years, i.e. 2002 and 2003, and the correlations were not significant when these years were excluded.

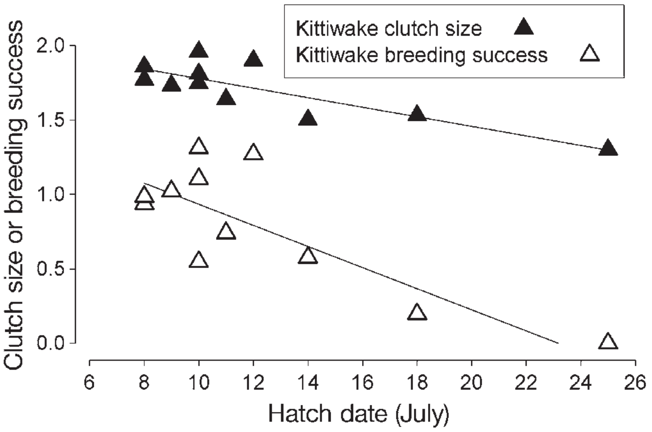

Fig. 4. *Rissa tridactyla*. Mean annual clutch size (filled triangles) and breeding success (number of chicks >12 d old per active nest; open triangles) of kittiwakes in relation to median hatch date (in July) during the breeding seasons 1997–2008 (N = 11, no data on clutch size or breeding success in 2001). Regression lines indicate significant linear relationships

DISCUSSION

The main findings of this study were that (1) median hatch date of little auks advanced during the study period, while hatch dates of kittiwakes tended to become later (albeit not significantly); (2) spring TEMP was a strong environmental predictor of little auk phenology, while spring SST tended to be an important environmental predictor of kittiwake phenology; and (3) clutch size and breeding success of kittiwakes was negatively related to the timing of breeding. Kittiwakes and little auks thus showed some different phenological responses.

Temporal trends in the timing of breeding

To our knowledge, this is the first little auk study with long-term phenology data and, consequently, the first to detect a trend for earlier breeding. The timing of breeding advanced by 4.5 d during 1963–2008. Another alcid species, Brünnich's guillemot, advanced breeding by 5 d during 1988–2007 in the Canadian low-Arctic but showed no trend in the high-Arctic (Gaston et al. 2005a, 2009). The trend for later breeding of kittiwakes, although not significant, is in accordance with trends for later breeding of British kittiwake populations (Frederiksen et al. 2004, Wanless et al. 2009). The finding that kittiwakes and little auks showed different phenological responses adds to a diverse picture of seabird phenology in polar and temperate regions. Studies have reported trends for earlier (*Catharacta maccormicki*, *Fratercula cirrhata*, *Sterna paradisaea*, *Uria lomvia*) and later breeding (*Daption capense*, *Fulmarus glacialis*, *Pygoscelis adeliae*, *Rissa tridactyla*, *U. aalge*), as well as no detectable trends (*Aptenodytes forsteri*, *Fratercula arctica*, *Fulmarus glacialis, Pagodroma nivea*, *Ptychoramphus aleuticus*, *U. aalge, U. lomvia*; e.g. Gjerdrum et al. 2003, Abraham & Sydeman 2004, Durant et al. 2004, Frederiksen et al. 2004, Gaston et al. 2005a, 2009, Barbraud & Weimerskirch 2006, Møller et al. 2006, Wanless et al. 2008, 2009, Reed et al. 2009). This diverse pattern may indicate that the phenology of specific seabird species is regulated by different environmental factors (e.g. Frederiksen et al. 2004, Barbraud & Weimerskirch 2006), or that climate has changed in different degrees or directions in different parts of the world (e.g. Vaughan et al. 2001). Hornsund and Ny-Ålesund are located relatively close (Fig. 1) and are strongly correlated environments (Table 3, Fig. 2), and it is not likely that the different trends are caused by climate change having acted differently on Hornsund and Ny-Ålesund. Rather, we think that the different ecologies of the 2 species have created the different phenological responses.

Environmental predictors of seabird phenology

TEMP and SST in combination with ICE were the highest ranked models explaining little auk and kittiwake phenology, respectively (Table 1), and TEMP and SST were the variables with the highest relative importance (Table 2). Conditional on the candidate models and the data, this suggests that local environmental factors during spring are the most important predictors of timing of breeding in these 2 high-Arctic populations. Indeed, we think spring TEMP is strongly linked to the timing of snow melt and to the time when ground-nesting little auks can have access to snow-

Table 3. Mean and SE of environmental variables (TEMP, SST and ICE) of Ny-Ålesund and Hornsund in April–May of the periods 1963–2008 (SST and ICE) and 1979–2008 (TEMP). Shown are the correlations of the environmental variables between the 2 locations and a comparison of the means (paired *t*-test). The difference in SST between the locations was reversed if data on SST were obtained closer to the coast

	Ny-Ålesund		Hornsund		Correlation			Paired *t*-test	
	Mean	SE	Mean	SE	N	r	p	*t*	p
TEMP	−6.5	0.43	−5.7	0.37	30	0.84	<0.01	−2.3	0.03
SST	2.9	0.13	3.2	0.14	46	0.71	<0.01	−2.4	0.02
ICE	15.4	2.31	35.6	2.42	44	0.70	<0.01	−10.5	<0.01

free nest sites in the rock debris colony slope. Unfortunately, we do not have appropriate data on snow cover, but behavioural observations and temperature measurements at Hornsund in 2006 strengthen this interpretation. The little auk colony was constantly occupied by birds in the colony only after the ground temperature and the nest temperature were permanently above 0°C (Fig. 5). The little auks then occupied nests as soon as the snow cover melted sufficiently to allow access to the nests. Therefore, the timing of egg-laying seemed to be strongly determined by temperature and snow melt in the colony (Fig. 5), consistent with a study on ground-nesting auklets (*Aethia pusilia, A. cristatella, Cyclorrhynchus psittacula*) in Alaska (Sealy 1975). Effects of spring snow cover and TEMP on phenology have also been reported in other ground-nesting bird species in the high-Arctic, such as waders (*Calidris alba, C. alpina, Arenaria interpres*; Meltofte et al. 2007), greater snow geese *Chen caerulescens atlantica* (Bêty et al. 2003, Dickey et al. 2008) and pink-footed geese *Anser brachyrhynchus* (Madsen et al. 2007). In addition to effects via snow cover, temperature could also directly impose energetic constraints on little auk phenology. Temperatures are often below the thermoneutral zone (TNZ) when they lay eggs (TNZ >4.5°C, Gabrielsen et al. 1991), and costs of egg production and incubation are elevated under such conditions (Stevenson & Bryant 2000).

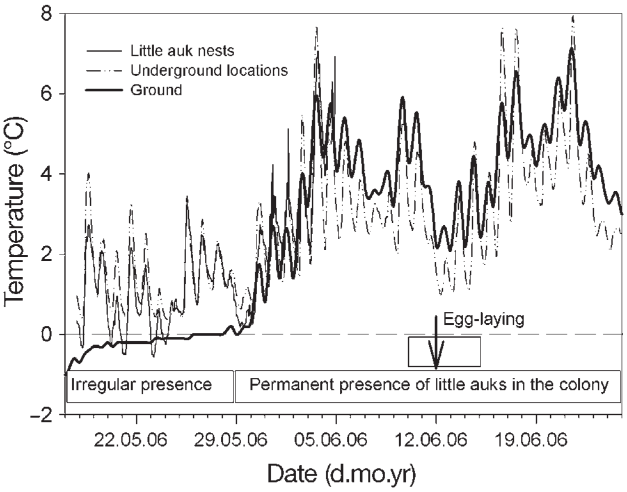

Fig. 5. *Alle alle*. Temperature (°C) in little auk nests (solid line), underground locations in the colony slope (broken line) and ground (measured ~20 cm above flat tundra; thick solid line) as a function of date in 2006. 'Irregular presence' means that the colony attendance alternated between periods without any birds and periods with many birds in the colony. 'Permanent presence' means that the colony was constantly attended by little auks. The arrow indicates median egg-laying date in 2006, and the box indicates the egg-laying period. Ground temperature was measured 3 times d^{-1}. Temperature was measured every hour in 3 nests and 4 underground locations, and this graph presents the hourly means for these 3 nests and 4 underground locations, respectively. Temperature loggers in the 3 nests were removed on 4 June, i.e. before egg laying occurred

SST correlated negatively to kittiwake phenology, but we cannot conclude firmly that SST had an effect, because the confidence intervals of the model-averaged slope estimate slightly overlapped with 0 (Table 2). This is in accordance with studies of kittiwakes (Frederiksen et al. 2004) and tufted puffins *Fratercula cirrhata* (Gjerdrum et al. 2003) at lower latitudes. Those studies reported significant negative correlations with local SST, but they disappeared when a longer time series was analysed for the kittiwakes (Frederiksen et al. 2004, Wanless et al. 2009) and when all years were included in the tufted puffin data (Gjerdrum et al. 2003). Wanless et al. (2009) reported long-term phenology data for British seabirds, and SST did not correlate significantly to phenology of any of the 11 investigated species. Hence, the effect of SST on seabird phenology seems weak or unclear.

Studies from the Arctic and the Antarctic have shown that seabirds breed later in years with more sea ice or a longer sea ice season (Gaston et al. 2005a,b, Barbraud & Weimerskirch 2006). Extensive ICE could force arctic seabirds to forage in more distant waters and make early breeding energetically expensive, and late disappearance of sea ice and development of the polar marine food web could delay the optimal timing of breeding (Moline et al. 2008). However, we did not detect a clear effect of ICE on phenology, as the signs of the model-average slope estimates differed between kittiwakes and little auks and the confidence intervals considerably overlapped with 0 (Table 2). This result is somewhat unexpected, especially for little auks breeding at Hornsund, because the sea ice cover can be rather extensive in this area (Fig. 2B, Table 3).

We used NAO_W as a large-scale proxy for winter conditions, and detected no effect on phenology (Fig. 2). However, we cannot rule out the possibility that kittiwakes breeding in the high-Arctic assess their winter conditions to adjust the timing of breeding, as reported for kittiwakes, common guillemots *Uria aalge*, Atlantic puffins *Fratercula arctica* and razorbills *Alca torda* breeding in Great Britain (Frederiksen et al. 2004, Wanless et al. 2009). Kittiwakes and little auks are likely to disperse over a large area in the North Atlantic during winter, and the evidence for wintering close to Greenland is sparse (Bakken et al. 2003). Because the correlation between NAO and local climate (e.g. SST) is highly spatially variable, it is not clear how well NAO_W captures the winter conditions of kittiwakes and little auks.

Our phenological time series covered substantial time periods (1963–2008, 1970–2008, Fig. 3). However, data were not available for all the years within these periods, and the time series had some substantial gaps (Fig. 3). Complete time series would have provided (1) better precision in the descriptions of the temporal trends in the timing of breeding and (2) more statistical power to detect potential relationships between environmental factors and timing.

It is not clear whether kittiwakes and little auks use the environmental cues in optimal decisions on when to initiate breeding. We have no data on phenology of the main prey items of little auks and kittiwakes (copepods versus fish/amphipods/krill). Therefore, we are consequently unable to test whether specific environmental variables are reliable predictors of marine prey phenology (Visser & Both 2005). We do not think TEMP is a direct predictor of marine prey phenology. SST and ICE could be such predictors through their effects on the timing of spring bloom and phenology of phytoplankton and zooplankton (Edwards & Richardson 2004, Scott et al. 2006, Moline et al. 2008). Alternatively, the ability of kittiwakes and little auks to initiate breeding could be constrained by food availability, because they rely on food acquired at the breeding grounds for investment in their eggs. Reed et al. (2009) reported that fish abundance affected phenology of common guillemots in California, but appropriate data to test this for our populations do not exist. Thus, our results are not conclusive on whether breeding phenology is regulated by optimal decisions or constrained by food availability.

Breeding success and phenology

Kittiwake clutch size and breeding success were significantly negatively related to the timing of breeding (Fig. 4), indicating poor investment and poor food availability in years with very late breeding. The same relationship has been found for other Arctic kittiwake populations in Alaska (Murphy et al. 1991) and Canada (Gaston et al. 2005b), but not at lower latitudes in Scotland (Frederiksen et al. 2004). The Arctic summer is very short, so this relationship could indicate that a late peak in food availability is associated with a very short peak or a very low peak in food availability, and that the low breeding success achieved in the late years is the best possible in these years. However, we do not know how well kittiwakes are able to match the peak in food availability.

CONCLUSIONS AND FUTURE CONSIDERATIONS

The spring climate is currently undergoing big changes in this part of Svalbard. The increase in air temperature and SST and the decrease in sea ice concentration are consistent with rapidly advancing spring and timing of snow melt in Greenland (Høye et al. 2007). Thus, further advancements in the timing of breeding could be expected for little auks and other ground-nesting high-Arctic species. A possible consequence of an earlier snow melt is the opening of new breeding grounds at the limits of the species' range (Jensen et al. 2008), with a displacement of the population towards the colder areas (e.g. Gaston et al. 2005a, Stempniewicz et al. 2007). Although SST tended to have some importance, it is not sufficiently clear how kittiwake phenology is affected by environmental factors to make sound future predictions.

We investigated seabird phenology in the high-Arctic in relation to environmental factors. Local environmental factors during spring seem to be stronger predictors than winter conditions, but it is unclear how well the considered variable (NAO_W) captures the winter conditions. It remains to be investigated whether specific environmental variables are reliable predictors of marine prey phenology, whether the initiation of breeding is constrained by food availability, and how well seabirds are able to match the peak in food availability in the high-Arctic. Since phenology, abundance and composition of marine prey species may change as climate changes (Edwards & Richardson 2004, Wassmann et al. 2006), this is important for understanding the fitness consequences of future climate change.

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Appendix 1. Data used in models of phenology for little auks *Alle alle* and black-legged kittiwakes *Rissa tridactyla* and of climate change in Svalbard

Table A1. *Rissa tridactyla* and *Alle alle.* Correlation matrix of predictor variables used in the linear models analysing hatch date in relation to environmental variables (Table 1). Pearson's product moment correlations are presented with p-values in parentheses. See 'Materials and methods: Environmental parameters' for an explanation of model parameters

		YEAR	NAO_W	TEMP	SST
Kittiwakes	NAO_W	0.38 (0.12)	–		
(1970–2008)	TEMP	0.47 (0.05)	0.14 (0.57)	–	
N = 18	SST	0.23 (0.36)	0.31 (0.20)	0.44 (0.07)	–
	ICE	−0.39 (0.11)	0.12 (0.62)	−0.58 (0.01)	−0.50 (0.04)
Little auks	NAO_W	0.54 (0.02)	–		
(1963–2008)	TEMP	0.65 (0.004)	0.20 (0.43)	–	
N = 18	SST	0.57 (0.01)	0.66 (0.003)	0.53 (0.03)	–
	ICE	−0.40 (0.10)	−0.23 (0.35)	−0.40 (0.10)	−0.31 (0.21)

Table A2. *Alle alle* and *Rissa tridactyla*. Seabird and environmental data used in the study. See 'Materials and methods' for details on data collection, calculations, units and abbreviations. HD: hatch date; BS: breeding success; CS: clutch size; NA: data not available

	Little auk	Hornsund			Kittiwake			Ny-Ålesund			Longyearbyen	
YEAR	HD	TEMP	ICE	SST	HD	BS	CS	TEMP	ICE	SST	TEMP	NAO_W
1963	15	−7.66	25.60	2.42	NA	NA	NA	NA	44.86	1.73	−9.15	−1.21
1964	22	−7.58	41.86	1.87	NA	NA	NA	NA	NA	2.58	−9.05	−1.38
1965	23	−5.91	40.35	2.32	NA	NA	NA	NA	NA	1.80	−6.95	−0.83
1966	NA	NA	45.92	2.20	NA	NA	NA	NA	46.78	1.66	−9.15	−0.30
1967	NA	NA	35.05	3.43	NA	NA	NA	NA	3.08	2.29	−7.50	0.38
1968	NA	NA	53.09	2.55	NA	NA	NA	NA	40.08	2.46	−10.45	−0.30
1969	NA	NA	50.93	2.62	NA	NA	NA	−10.30	52.14	2.60	−10.75	−1.34
1970	NA	NA	51.58	2.58	10.5	NA	NA	−7.75	27.21	1.82	−9.35	−0.53
1971	NA	NA	25.43	2.95	11.5	NA	NA	−7.10	9.43	3.05	−7.90	−0.73
1972	NA	NA	36.84	3.21	NA	NA	NA	−7.20	4.47	3.08	−7.85	0.48
1973	NA	NA	21.51	2.90	NA	NA	NA	−6.65	0.05	2.79	−6.95	0.35
1974	20	−7.74	5.33	3.55	NA	NA	NA	−7.80	3.80	3.49	−9.25	0.37
1975	25	−6.86	36.25	2.41	NA	NA	NA	−7.20	0.48	2.26	−8.15	0.21
1976	NA	NA	3.95	3.98	NA	NA	NA	−5.55	0.17	3.03	−6.60	0.36
1977	NA	NA	46.66	1.81	NA	NA	NA	−10.10	35.27	1.60	−10.25	−0.99
1978	NA	NA	44.45	2.45	NA	NA	NA	−5.80	35.32	2.42	−6.80	−0.46
1979	NA	−10.70	67.18	1.53	NA	NA	NA	−11.35	35.62	1.45	−12.70	−0.71
1980	16	−5.50	34.10	3.50	NA	NA	NA	−5.85	3.45	3.70	−6.40	0.00
1981	NA	−7.80	66.03	2.20	NA	NA	NA	−7.40	20.43	2.57	−8.70	0.22
1982	NA	−6.80	63.41	3.45	8.5	NA	NA	−6.75	34.75	3.06	−7.00	0.35
1983	21	−6.70	50.08	4.79	7	NA	NA	−7.10	25.92	4.08	−7.50	0.95
1984	15	−5.03	24.56	5.04	0.5	NA	NA	−4.65	0.85	4.12	−5.45	0.58
1985	NA	−6.99	21.31	2.30	11.5	NA	NA	−7.55	2.94	3.19	−8.60	−0.48
1986	17	−6.62	27.26	2.29	NA	NA	NA	−8.85	13.10	2.10	−8.90	0.51
1987	21	−5.30	29.81	2.79	NA	NA	NA	−5.05	2.41	2.73	−6.25	−0.19
1988	NA	−8.25	53.49	1.56	NA	NA	NA	−9.85	15.43	0.96	−10.40	0.48
1989	NA	−3.05	40.63	3.62	NA	NA	NA	−4.60	12.49	3.27	−4.80	1.41
1990	NA	−4.25	13.49	4.59	NA	NA	NA	−6.80	7.31	3.60	−6.10	0.69
1991	NA	−6.25	15.99	3.51	NA	NA	NA	−7.25	0.28	3.37	−7.90	0.48
1992	NA	−3.75	42.95	5.40	NA	NA	NA	−4.50	28.21	4.09	−4.60	0.57
1993	NA	−7.35	39.30	3.48	NA	NA	NA	−8.10	2.65	4.74	−9.10	0.81
1994	NA	−4.15	57.70	3.14	NA	NA	NA	−5.20	25.37	5.67	−5.25	1.08
1995	NA	−4.05	32.03	4.55	NA	NA	NA	−5.00	9.41	3.73	−4.65	1.34
1996	NA	−6.55	23.68	2.24	NA	NA	NA	−7.05	5.47	2.42	−7.15	−0.53
1997	NA	−6.95	39.52	2.72	10	1.10	1.81	−7.70	14.29	2.98	−8.50	0.32
1998	NA	−7.30	60.07	2.33	8	0.94	1.77	−8.40	34.38	2.43	−9.05	0.05
1999	NA	−5.70	48.33	4.01	11	0.74	1.64	−6.60	32.42	2.48	−6.30	0.54
2000	NA	−7.45	47.50	3.62	9	1.02	1.73	−7.05	17.94	2.94	−8.60	1.17
2001	20	−7.00	43.39	2.67	15	NA	NA	−7.40	9.62	2.71	−7.65	−0.29
2002	16	−4.00	9.36	3.73	25	0.00	1.30	−5.70	2.95	2.63	−4.70	0.35
2003	18	−4.75	15.29	4.13	18	0.25	1.53	−6.55	4.40	3.59	−6.05	0.04
2004	15	−2.50	31.46	4.15	14	0.58	1.50	−2.70	3.88	2.90	−3.00	0.31
2005	18	−5.05	27.71	4.58	10	1.31	1.96	−5.25	7.90	4.03	−5.15	0.21
2006	11	−0.25	9.89	4.24	10	0.55	1.74	−0.40	0.21	3.89	0.45	−0.24
2007	18	−5.33	17.67	4.24	12	1.27	1.90	−0.40	0.00	3.49	−5.40	0.63
2008	17	−5.45	18.02	3.38	8	0.98	1.86	−5.95	2.39	3.65	−6.20	0.51

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Timing of breeding and reproductive performance in murres and kittiwakes reflect mismatched seasonal prey dynamics

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ABSTRACT: Seabirds are thought to time breeding to match the seasonal peak of food availability with peak chick energetic demands, but warming ocean temperatures have altered the timing of spring events, creating the potential for mismatches. The resilience of seabird populations to climate change depends on their ability to anticipate changes in the timing and magnitude of peak food availability and 'fine-tune' efforts to match ('Anticipation Hypothesis'). The degree that inter-annual variation in seabird timing of breeding and reproductive performance represents anticipated food availability versus energetic constraints ('Constraint Hypothesis') is poorly understood. We examined the relative merits of the Constraint and Anticipation Hypotheses by testing 2 predictions of the Constraint Hypothesis: (1) seabird timing of breeding is related to food availability prior to egg laying rather than the date of peak food availability, (2) initial reproductive output (e.g. laying success, clutch size) is related to pre-lay food availability rather than anticipated chick-rearing food availability. We analyzed breeding biology data of common murres *Uria aalge* and black-legged kittiwakes *Rissa tridactyla* and 2 proxies of the seasonal dynamics of their food availability (near-shore forage fish abundance and sea-surface temperature) at 2 colonies in Lower Cook Inlet, Alaska, USA, from 1996 to 1999. Our results support the Constraint Hypothesis: (1) for both species, egg laying was later in years with warmer sea-surface temperature and lower food availability prior to egg laying, but was not related to the date of peak food availability, (2) pre-egg laying food availability explained variation in kittiwake laying success and clutch size. Murre reproductive success was best explained by food availability during chick rearing.

KEY WORDS: Phenology · Climate change · Food availability · Forage fish · *Rissa tridactyla* · *Uria aalge*

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INTRODUCTION

The frequency of warm sea-surface temperature (SST) anomalies has increased across the globe (Mackas et al. 2007), which may be having dramatic consequences for the timing, abundance, and community composition of primary and secondary producers. Through a cascade of complex events, these effects may be transferred through the food web, resulting in the altered timing and abundance of key prey items for seasonally breeding seabirds or marine mammals (Litzow & Ciannelli 2007, Mackas et al. 2007). This may result in mismatches between seabird timing of breeding, reproductive investment, and food availability, ultimately decreasing the fitness of individuals in a population (Visser & Both 2005). The potential for mis-

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matches between predator and prey dynamics are compounded for high-latitude breeding seabirds: the time window during which conditions are suitable for reproduction is short and may limit their ability to adjust timing of breeding to match shifts in timing of seasonal increases in food abundance.

Seabirds are long-lived, and trade-offs between costs of current reproduction versus maintaining residual reproductive value should be tightly regulated (Goodman 1974, Stearns 1992). Timing of reproduction in seabirds and the majority of other high-latitude nesting birds is ultimately timed to coincide with the seasonal peak of food availability (Lack 1968, Perrins 1970): those individuals that feed chicks when food is most abundant produce more offspring (e.g. Perrins 1991, Nager & Van Noordwijk 1995, Svensson & Nilsson 1995, Van Noordwijk et al. 1995) and have higher survival (Golet et al. 1998). Reproductive effort should also match food abundance during the period of peak energetic demand: having a larger brood than resources allow may result in the reduced condition of parents and chicks (Heaney & Monaghan 1995), and reduced survival (Golet et al. 1998).

Extensive effort has gone into monitoring the reproductive performance of seabirds as indicators of these changes and to predict their effects on seabird population dynamics. Across the globe, strong relationships have been found between seabird reproduction, climate, and food availability (e.g. North Atlantic: Wanless et al. 2007, Regular et al. 2009; North Pacific: Bertram et al. 2001, Mackas et al. 2007, Piatt et al. 2007; Central Pacific: Sydeman et al. 2001, Abraham et al. 2004; Antarctic: Le Bohec et al. 2008; tropical Pacific: Erwin & Congdon 2007). In other cases, due to the complex interactions of large and small-scale physical and biological processes, it is often unclear how environmental changes, food availability, and seabird reproductive biology are linked (Springer 2007). In light of efforts to understand these relationships, the need to distinguish between the role of adaptive adjustments in reproductive effort (‘Anticipation Hypothesis’) versus energetic constraints imposed by current food availability (‘Constraint Hypothesis;’ Durant et al. 2005, Visser & Both 2005) has become apparent. Species and populations capable of adjusting effort to match changes in the dynamics of their food availability will be more resilient to a changing environment.

Adaptive adjustments may be impossible for high-latitude nesting seabirds with a limited time window to reproduce (Svensson 1995) and potential energetic constraints on egg formation. To do so requires a lack of physiological constraint and the existence of reliable cues prior to egg laying that enable them to predict the timing and abundance of peak food availability, months or weeks in advance. The onset of reproduction in birds is regulated by a combination of proximate cues that are fixed (e.g. photoperiod) and variable, which interact to modify timing of breeding and reproductive effort (Hahn et al. 1997). Variable proximate cues or ‘supplemental cues’ may include any environmental features (e.g. ocean temperature, food availability, weather); the only requirement is that they provide reliable information about variation in the timing and/or abundance of food during the period of peak energetic demand on parents (Wingfield et al. 1992). For seabirds, SST may be a useful supplemental cue, as timing of breeding in seabirds has been associated with changes in climate indices partially derived from SST (Rindorf et al. 2000, Durant et al. 2003, Frederiksen et al. 2004), as well as SST itself (Ainley et al. 1996, Bertram et al. 2001, Frederiksen et al. 2004). However, spring SST and food availability may be correlated (Ainley et al. 1996, Bertram et al. 2001) making it difficult to distinguish between its role as a supplemental cue or because it reflects food limitations.

Egg production is costly in terms of energy and nutrients (reviewed by Monaghan & Nager 1997) and is a common phenomenon in birds in general (reviewed by Svensson 1995). These costs increase for larger species (Meijer & Drent 1999). Seabird laying success is related to their physiological condition prior to egg laying (Daunt et al. 2002). Murre reproductive success and survival are related to stress hormone levels and food availability (Kitaysky et al. 2007). Supplemental feeding experiments with seabirds have produced mixed results, possibly because the act of feeding may interfere with a bird's perception of proximate cues: supplementally fed kittiwakes laid eggs earlier (Gill & Hatch 2002, Gill et al. 2002), laid larger clutches (Gill & Hatch 2002, Gill et al. 2002), and had higher laying success (Lanctot et al. 2003) than unsupplemented controls. However, they advanced the laying date relatively little compared to natural variation, and laying success was unchanged in 2 yr (Gill et al. 2002). Supplementally fed lesser black-backed gulls *Larus fuscus* did not advance laying (Hiom et al. 1991, Bolton et al. 1993), but increased clutch size (Bolton et al. 1993). Thus, timing of breeding and reproductive performance may reflect a combination of adaptive adjustments and physiological constraints, and the relative importance of these factors is unclear.

To estimate the extent to which seabird timing of breeding and reproductive performance reflect current food limitations versus anticipated food, it is necessary to simultaneously measure the seasonal dynamics of prey availability and seabird reproductive performance. We quantified the seasonal dynamics of seabird food availability using 2 proxies (SST and near-shore fish abundance) while simultaneously measuring timing of breeding and reproductive performance of 2 colonial seabird species, the common murre and black-legged kittiwake. The goals of this analysis were: (1) to assess the degree to which interannual variation in the seasonal dynamics of food availability accounted for variation in seabird timing and breeding and reproductive performance, (2) evaluate the strength of evidence in support for the 'Anticipation' versus 'Constraint' Hypotheses. For the second goal, we specifically addressed 2 predictions of the 'Constraint Hypothesis': (1) seabird timing of breeding is related to food availability prior to egg laying rather than to the date of peak food availability, (2) initial reproductive output (e.g. laying success, clutch size) is related to pre-lay food availability rather than to anticipated chick-rearing food availability.

MATERIALS AND METHODS

Study area. Our work was conducted at and around 2 seabird colonies in Lower Cook Inlet, Gulf of Alaska, from May to September in 1996 to 1999. The colonies, Gull Island (east side of Cook Inlet; 59° 35′ N, 151° 19′ W) and the Barren Islands at the mouth of Cook Inlet (58° 55′ N, 152° 10′ W), are separated by about 100 km. The data presented here were collected as part of a larger study and have been published elsewhere (see Piatt & Harding 2007 for references and references herein).

Proxies of food availability. To assess the seasonal dynamics of food availability for murres and kittiwakes, we used 2 proxies: SST and near-shore fish abundance. To examine the effects of small-scale, regional differences in oceanographic conditions (Abookire & Piatt 2005, Speckman et al. 2005), we measured SST and near-shore fish abundance immediately adjacent to each study colony.

SST may be a reliable reflection of food availability in Cook Inlet (for both birds and scientists): (1) colder spring SST reflects stronger winter upwelling, more nutrient-rich surface water, a prolonged phytoplankton bloom, greater zooplankton abundance, and potentially higher survival and recruitment of forage fish (Cooney 2007); (2) the distribution and abundance of principle prey species of murres and kittiwakes are closely tied to surface temperatures in Cook Inlet (Robards et al. 2002, Abookire & Piatt 2005, Speckman et al. 2005); and (3) approximately 80 % of the principle prey species for murres and kittiwakes in Cook Inlet feed in the top 30 m of the water column (Abookire & Piatt 2005, Speckman et al. 2005, Piatt & Harding 2007).

SSTs were obtained by deploying temperature loggers (StowAway and TidbiT models, Onset Electronics) 3 to 10 m below the low tide line. They recorded temperatures every 10 min during June to August. Data were unavailable until August in 1996 at the Barrens. Average daily temperatures were used in the analyses.

We used beach seines to sample near-shore fish abundance in surface waters adjacent to breeding colonies where birds were known to actively forage (Speckman 2004). We used small-meshed nets designed to capture small schooling fish that are the appropriate size for seabird prey (80 to 150 mm). For detailed methods see Robards et al. (1999). Sites were sampled every 2 wk, weather permitting, near Gull Island from late May to early September and at the Barren Islands during June through August, 1996 to 1999. Seines were also conducted year round at Gull Island in 1996. Nets were deployed from a small boat and set parallel to shore, about 25 m from the beach. Two sites were sampled at the Barrens and 12 sites at Gull Island (except at Gull Island in 1996 where an additional 26 sites were sampled). Beach seine trawling was conducted within a 1.5 h window on either side of low tides. A single set was carried out on each site visit as this provided adequate representation of species richness and dominant species rank (Allen et al. 1992, Robards et al. 1999).

Catch per unit effort (CPUE) was calculated as the total catch of all forage fish taxa (80 to 150 mm) per seine (Litzow et al. 2000). Forage species included in the analyses were sand lance *Ammodytes hexapterus*, herring *Clupea pallasi*, and all species of salmonids (*Oncorhynchus* spp.), *Osmeridae*, and *Gadidae*. These fish species and size classes comprised >90 % of the diet (frequency of occurrence in stomach samples) of kittiwake and murre adults in this study (Shultz et al. 2002, Van Pelt et al. 2002). CPUE data were log(x+1) transformed to meet assumptions of homoscedasticity for parametric statistical procedures (Zar 1999), then averaged by site and day (Litzow et al. 2000).

Timing of clutch initiation and reproductive performance. Egg-lay dates and reproductive performance were measured at both colonies during 1996 to 1999, using sample plots and standardized methods (Birkhead & Nettleship 1980, 1982, Hatch & Hatch 1988, 1989, 1990). We monitored 10 to 11 kittiwake plots, containing 25 to 30 nests. Kittiwake plots were checked every 3 d.

We monitored 5 to 10 murre plots with an average of 20 and 22 nest sites with eggs. Murre plots were checked every 1 to 2 d at Gull Island and every 3 d at the Barren Islands from observation points on the island using binoculars and telescopes.

Murre chicks were considered 'fledged' if they disappeared from the nest site ≥15 d after hatching — the minimum nest departure age (Swennen 1977). Kittiwake chicks were considered fledged if they were observed at the nest until 32 d old (fledging age is typically 42 d; Baird 1994).

For kittiwakes, laying success (LS) was defined as the percentage of nest structures in which 1 or more eggs were laid. We could not estimate this for murres, as many eggs are laid and lost and it is nearly impossible for us to keep track of these failed attempts. Clutch size (CS) is the mean number of eggs per nest in which eggs were laid. Hatching success (HS) is the percentage of eggs laid that hatched. Total reproductive success (RS) is the number of chicks fledged per nest built for kittiwakes, and chicks fledged per egg for murres.

Data analysis. ***Proxies for food availability:*** We estimated 'lay SST' by calculating the average SST for the first half of June for kittiwakes and the first half of July for murres, as average lay date differed between species: the first half of June for kittiwakes and the first half of July for murres.

We estimated near-shore fish abundance for the exact dates of interest by fitting non-linear regressions and interpolation. We determined the best fitting non-linear function by averaging all from all years at each colony, including year round data from 1996 at Gull Island. The data followed a uni-modal distribution, and we compared the fit of a quadratic function to a Gaussian distribution. The Gaussian function provided the best fit to the data (Table 1, Fig. 1) and was defined by the equation:

$$y = \frac{1}{\sigma\sqrt{2\pi}}\,e^{\left(-\frac{1}{2}\left[\frac{x-\mu}{\sigma}\right]^{2}\right)} \qquad (1)$$

We used the fitted curves to estimate several parameters of near-shore abundance: 'lay CPUE', 'chick CPUE', and 'peak CPUE date'. Lay CPUE was defined as fish abundance at the onset of egg formation, or the average lay date minus the egg formation duration (14 d for kittiwakes; 15 d for murres; Baird 1994, Ainley et al. 2002). We defined 'chick CPUE' as near-shore fish abundance from average hatch date through the peak demand date (PDD). We defined PDD as the average date when chicks reach maximum energetic demands (kittiwakes: 26 d, Gabrielsen et al. 1992; murres: 20 d). Murre growth rates increase roughly linearly through fledging (Benowitz-Fredericks et al. 2006), and we defined murre PDD as the average fledging age of murres in this study. Peak CPUE date was the date when near-shore fish abundance reached its highest level.

Timing of clutch initiation and reproductive performance: In order to pool data from both colonies, between which geographic differences in water temperature, food supply and breeding biology persisted among years (Robards et al. 1999, Abookire & Piatt 2005; Speckman et al. 2005, Piatt et al. 2007), data were converted into colony-specific annual residuals by subtracting the average of all years from the value of a given parameter for each year. Each colony-year was treated as a sample unit. Before pooling data from different colonies for analyses, we first used analysis of covariance (ANCOVA) on annual residuals to test for colony effects. All ANCOVA tests for colony-effects were non-significant.

Table 1. Summary of goodness of fit statistics for the seasonal dynamics of forage fish abundance (catch per unit effort, CPUE) around Gull and the Barren Islands, 1996–1999, fitted using Gaussian functions

Island	Year	R^2	SD of residuals	df (n – 3)
Gull	1996	0.95	0.64	4
	1997	0.91	0.32	3
	1998	0.86	1.36	5
	1999	0.74	0.60	4
Barren	1996	0.93	0.25	2
	1997	0.90	0.32	2
	1998	0.83	1.22	2
	1999	0.91	0.31	3

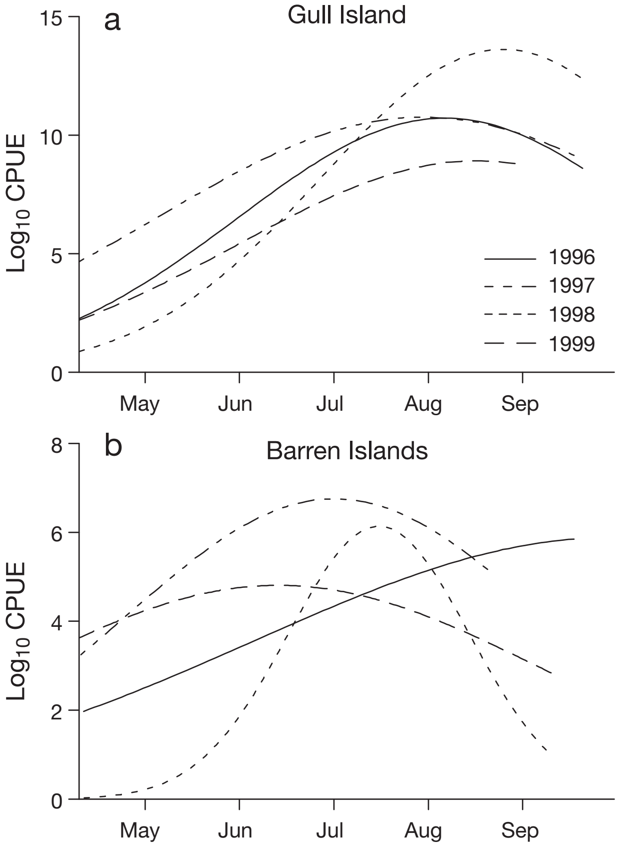

Fig. 1. Seasonal dynamics of forage fish abundance among years (1996–1999) at (a) Gull Island and (b) Barren Islands. Curves represent data fitted with a Gaussian function. Goodness of fit statistics are presented in Table 1. Curves were used to estimates forage fish abundance at the onset of egg laying, forage fish abundance at the period of peak energetic demand, and the date of peak food abundance. CPUE: catch per unit effort

We used the Akaike Information Criterion adjusted for small sample size (AIC_c) to evaluate models of the data for lay date and reproductive performance. The model with the lowest AIC_c was the best model (Burnham & Anderson 2002). We calculated AIC_c weight (w_i) to evaluate the relative probability of each model representing the true model. The ratios of Akaike weights (Evidence Ratio, ER: w_{min}/w_j) were compared to assess the strength of evidence for a particular model compared to others in the model set (Burnham & Anderson 2002)

Models of timing of laying and reproductive performance: We modeled lay date using all combinations of the variables lay CPUE, lay SST, and peak CPUE date. We modeled reproductive performance parameters that potentially reflect decisions made at egg laying, using the explanatory variables lay date, lay CPUE, and chick CPUE. For kittiwakes, these parameters included LS and CS. For murres, because we were unable to measure LS, and CS is 1, we modeled HS, the parameter most likely to reflect pre-lay conditions. We refer to these parameters as 'initial reproductive output' (IRO). We modeled total RS for both species (combination of LS, CS, HS, and FS for kittiwakes; HS and FS for murres) to evaluate the relative importance of lay date itself versus food abundance (lay CPUE and chick CPUE) for explaining variability in total RS.

Environment: Pearson's correlation was used to examine the relationship between lay SST and lay CPUE. Non-linear regressions were performed with Graphpad Prism version 4.00 for Windows. All other statistical analyses were performed with SAS (ver 91, 2003).

RESULTS

Beach seine catch composition

In total, 815 398 fish representing at least 70 species were captured in 717 seine nets deployed from June to August, 1996 to 1999 (Table 2). Pacific sand lance dominated the near-shore community, and herring was the second most important taxon at Gull Island, while gadids (primarily walleye pollock) were second at the Barrens. As reported elsewhere (Shultz et al. 2002, Van Pelt 2002), fish species and size classes caught in seines comprised >90% of the diet of kittiwake and murre adults (Shultz et al. 2002, Van Pelt et al. 2002).

Seasonal dynamics of near-shore fish and peak demand date

As reported elsewhere, near-shore fish abundance around Gull Island was low from October through April (<2% of total catch), but increased rapidly in

Table 2. Catch per unit effort (CPUE) of the major taxonomic groups caught in beach seine sets in June to August 1996–1999 at Gull and Barren Islands

Island	Year	No. of Species	No. of Sets	CPUE	SE	Median	Herring	Salmonids	Osmerids	Gadids	Sand lance	Sculpins	Flatfish	Other	Total
Barren	1996	12	32	4032	2588	467	0	417	34	480	127 830	242	8	22	129 033
	1997	12	24	1909	712	433	0	0	6	9286	26 516	7983	35	1995	45 821
	1998	15	26	751	234	97	0	36	64	425	15 261	277	1	3469	19 533
	1999	13	24	108	32	55	0	229	1	63	8	876	22	1381	2580
Gull	1996	43	202	545	162	65	15 241	9128	22	4715	78 069	1999	326	650	110 150
	1997	41	161	621	173	116	7152	3483	5147	3203	78 847	484	599	1140	100 055
	1998	51	149	1879	555	122	61 862	4750	108	3353	205 104	821	656	3300	279 954
	1999	52	99	1258	643	131	219	8338	21	1194	114 587	752	556	2605	128 272
Total Barren		22	106	6800	3566	1052	0	682	105	10 254	169 615	9378	66	6867	196 967
Total Gull		70	611	4303	1533	434	84 474	25 699	5298	12 465	476 607	4056	2137	7695	618 431
Total Both sites			717	11103	5099	1486	84474	26 381	5403	22 719	646 222	13 434	2203	14 562	815 398

May to early June (Robards et al. 1999). Peak near-shore fish abundance (peak CPUE date) was 22 August (26 June to 21 August) at Gull Island, and 26 July (4 July to 22 August) at the Barren Islands (Fig. 1). Lay date and PDD were not correlated with peak CPUE date. PDD was calculated by adding the peak demand age for each species to mean lay date, so the correlation statistics are identical (kittiwake: r = 0.10, p = 0.81, n = 8; murre: r = 0.26, p = 0.53, n = 8).

SST and near-shore fish abundance

Lay SST and lay CPUE were negatively correlated for both species (murre: $r^2 = 0.63$, p = 0.03, n = 7; kittiwake: $r^2 = 0.98$, p = 0.0001, n = 7) and was similar between colonies (ANCOVA; SST × Colony: $F_{2,4} = 0.68$, p = 0.43).

Lay date, SST, and food availability

The model that best explained variation in timing of breeding for murres and kittiwakes contained the single variable of lay SST; however, there was nearly equal support for the model containing lay CPUE for kittiwakes (ER = 1.45; Fig. 2, Table 3). There was no evidence in support of other models for either species (ER > 77 for the next competing model; Table 4).

As lay SST increased, lay CPUE decreased, and both species laid eggs later. This relationship was similar among colonies (ANCOVA; SST × Colony, murre: $F_{2,4} = 0.0$, p = 0.99; kittiwake: $F_{2,4} = 0.27$, p = 0.64; lay CPUE × Colony, kittiwake: $F_{2,4} = 0.28$, p = 0.66, murre: $F_{2,4} = 0.11$, p = 0.76).

IRO and food availability

The best model contained only the variable lay CPUE: it explained over 66 % of variation in kittiwake clutch size (Table 4). The best model for kittiwake LS contained only lay date, with weak support for the

Table 3. *Rissa tridactyla* and *Uria aalge*. Models of egg-laying date for kittiwakes and murres nesting at Gull and the Barren Islands, Cook Inlet, Alaska, 1996–1999, using Akaike's Information Criterion adjusted for small sample size (AIC_c). K: number of model parameters + 1, R^2: coefficient of determination

Variable	K	R^2	SSE	ΔAIC_c	w_i	Evidence Ratio
Kittiwake						
Lay SST	3	0.95	5.53	0.00	0.59	1.0
Lay CPUE	3	0.96	6.17	0.76	0.40	1.5
Peak CPUE date	3	0.93	19.19	8.70	0.01	77.6
Lay CPUE + peak CPUE date	4	0.92	3.87	11.50	0.00	314.8
Lay SST + peak CPUE date	4	0.93	5.30	13.70	0.00	945.4
Lay SST + lay CPUE	4	0.93	5.31	13.70	0.00	946.0
Lay SST + lay CPUE + peak CPUE date	5	0.75	3.16	52.07	0.00	2.0×10^{11}
Murre						
Lay SST	3	0.96	3.08	0.00	0.98	1.0
Lay SST + lay CPUE	4	0.96	1.46	8.77	0.01	80.2
Lay SST + peak CPUE date	4	0.94	2.27	11.87	0.00	377.8
Lay CPUE	3	0.91	30.36	16.01	0.00	2998.2
Peak CPUE date	3	0.16	32.55	16.50	0.00	3826.4
Lay CPUE + peak CPUE date	4	0.10	29.93	29.91	0.00	3.1×10^6
Lay SST + lay CPUE + peak CPUE date	5	0.17	1.27	49.82	0.00	6.6×10^{10}

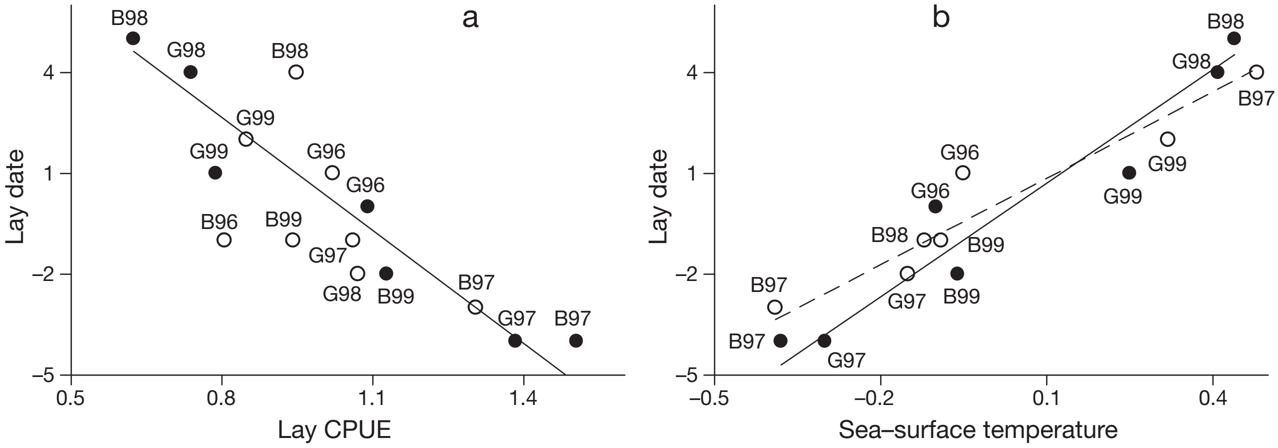

Fig. 2. *Uria aalge* and *Rissa tridactyla*. Relationships between (a) the residuals of average forage fish abundance during egg laying (lay catch per unit effort, CPUE) and (b) sea-surface temperature (SST) during egg laying, and egg lay date for murres (○) and kittiwakes (●) nesting at Gull (G) and the Barren (B) Islands, 1996–1999. Lines are Deming Model II regression lines shown for significant correlations

Table 4. *Rissa tridactyla* and *Uria aalge*. Models examining the relative importance of average lay date, average forage fish abundance during egg laying (lay catch per unit effort, CPUE) and during chick-rearing (chick CPUE) for explaining variation in reproductive output of kittiwakes and murres nesting at Gull and the Barren Islands, Cook Inlet, Alaska, 1996–1999. K: number of model parameters + 1, R^2: coefficient of determination

Variable	K	R^2	SSE	ΔAIC_c	w_i	Evidence Ratio
Kittiwake clutch size						
Lay CPUE	3	0.66	0.02	0.00	0.97	1.0
Chick CPUE	3	0.00	0.07	7.52	0.02	43.0
Lay CPUE + chick CPUE	4	0.67	0.02	13.00	0.00	664.2
Lay date + lay CPUE	4	0.70	0.02	13.02	0.00	673.0
Lay date + chick CPUE	4	0.67	0.02	13.69	0.00	939.4
Lay date	3	0.65	0.25	16.19	0.00	3285.9
Lay date + lay CPUE + chick CPUE	5	0.71	0.02	54.89	0.00	8.3×10^{10}
Kittiwake laying success						
Lay date	3	0.78	0.04	0.00	0.94	1.0
Lay CPUE	3	0.47	0.09	6.15	0.04	21.7
Chick CPUE	3	0.17	0.13	9.28	0.01	103.7
Lay date + chick CPUE	4	0.85	0.02	11.13	0.00	260.5
Lay date + lay CPUE	4	0.81	0.03	13.12	0.00	705.9
Lay CPUE + chick CPUE	4	0.84	0.25	27.77	0.00	1.1×10^{6}
Lay date + lay CPUE + chick CPUE	5	0.87	0.02	52.60	0.00	2.6×10^{11}
Kittiwake reproductive success						
Lay date	3	0.94	0.06	0.00	0.43	1.0
Lay CPUE + chick CPUE	4	0.94	0.01	0.74	0.30	1.4
Chick CPUE	3	0.91	0.08	2.11	0.15	2.9
Lay date + chick CPUE	4	0.73	0.01	3.36	0.08	5.4
Lay CPUE	3	0.60	0.11	4.47	0.05	9.3
Lay date + lay CPUE	4	0.46	0.04	11.34	0.00	289.9
Lay date + lay CPUE + chick CPUE	5	0.25	0.01	42.56	0.00	1.7×10^{9}
Murre hatching success						
Chick CPUE	3	0.64	0.03	0.00	0.96	1.0
Lay CPUE	3	0.05	0.09	6.81	0.03	30.1
Lay CPUE + chick CPUE	4	0.77	0.02	10.85	0.00	227.0
Lay date + chick CPUE	4	0.72	0.03	12.39	0.00	489.3
Lay date	3	0.51	0.44	18.27	0.00	9289.5
Lay date + lay CPUE	4	0.56	0.40	31.52	0.00	7.0×10^{6}
Lay date + lay CPUE + chick CPUE	5	0.93	0.01	44.90	0.00	5.6×10^{9}
Murre reproductive success						
Chick CPUE	3	0.99	0.03	0.00	0.90	1.0
Lay date	3	0.87	0.06	4.88	0.08	11.5
Lay CPUE	3	0.82	0.11	9.50	0.01	115.3
Lay CPUE + chick CPUE	4	0.77	0.02	9.76	0.01	131.3
Lay date + chick CPUE	4	0.53	0.02	12.25	0.00	457.5
Lay date + lay CPUE	4	0.55	0.06	18.57	0.00	10776.1
Lay date + lay CPUE + chick CPUE	5	0.09	0.00	36.31	0.00	7.7×10^{7}

model containing lay CPUE (ER = 21.66; Fig. 3, Table 4). CS increased with increasing lay CPUE. LS increased with earlier lay date. Murre HS was best explained by the model containing only chick CPUE, with weak evidence that lay CPUE might be important (ER = 30.06). HS increased with increasing chick CPUE. Relationships were similar among colonies (ANCOVA; LS × Colony: $F_{2,4}$ = 0.35, p = 0.59; CS × Colony: $F_{2,4}$ = 0.05, p = 0.84; HS × Colony: $F_{2,4}$ = 1.05, p = 0.39).

Near-shore fish abundance, lay date, and RS

The model that best explained variation in total RS of kittiwakes contained only the variable lay date (R^2 = 0.94); however, there was strong support for the model containing the combination of lay CPUE and chick CPUE (ER = 1.45; Table 4). For murres, the best model of total RS contained only the variable chick CPUE (R^2 = 0.99) There was also some support for the model containing lay date only (ER > 11, R^2 = 0.87).

DISCUSSION

Breeding biology and proxies of food availability

Colder spring SST was associated with higher near-shore fish abundance prior to egg laying, earlier mean lay date, and higher average reproductive performance. Global SST has increased 1 to 2°C in the last 50 yr (Mackas et al. 2007), and evidence indicates that these changes have decreased the availability of key prey items for seabirds and marine mammals in the Gulf of Alaska (Litzow 2006, Litzow & Ciannelli 2007) and elsewhere (e.g. North Sea: Edwards & Richardson 2004; Antarctic: Le Bohec et al. 2008). The mechanisms linking colder spring SST and higher forage fish abundance in our study area (Gulf of Alaska) are unclear, although it is likely that colder spring temperatures reflect stronger winter upwelling (Litzow 2006), resulting in cold, nutrient-rich water being brought to the surface. In spring, this cold, nutrient-rich water promotes the growth of sub-arctic zooplankton communities (Mackas et al. 2007), possibly by promoting the production of slow-growing, large diatoms that are high in nutrient content and are a valuable

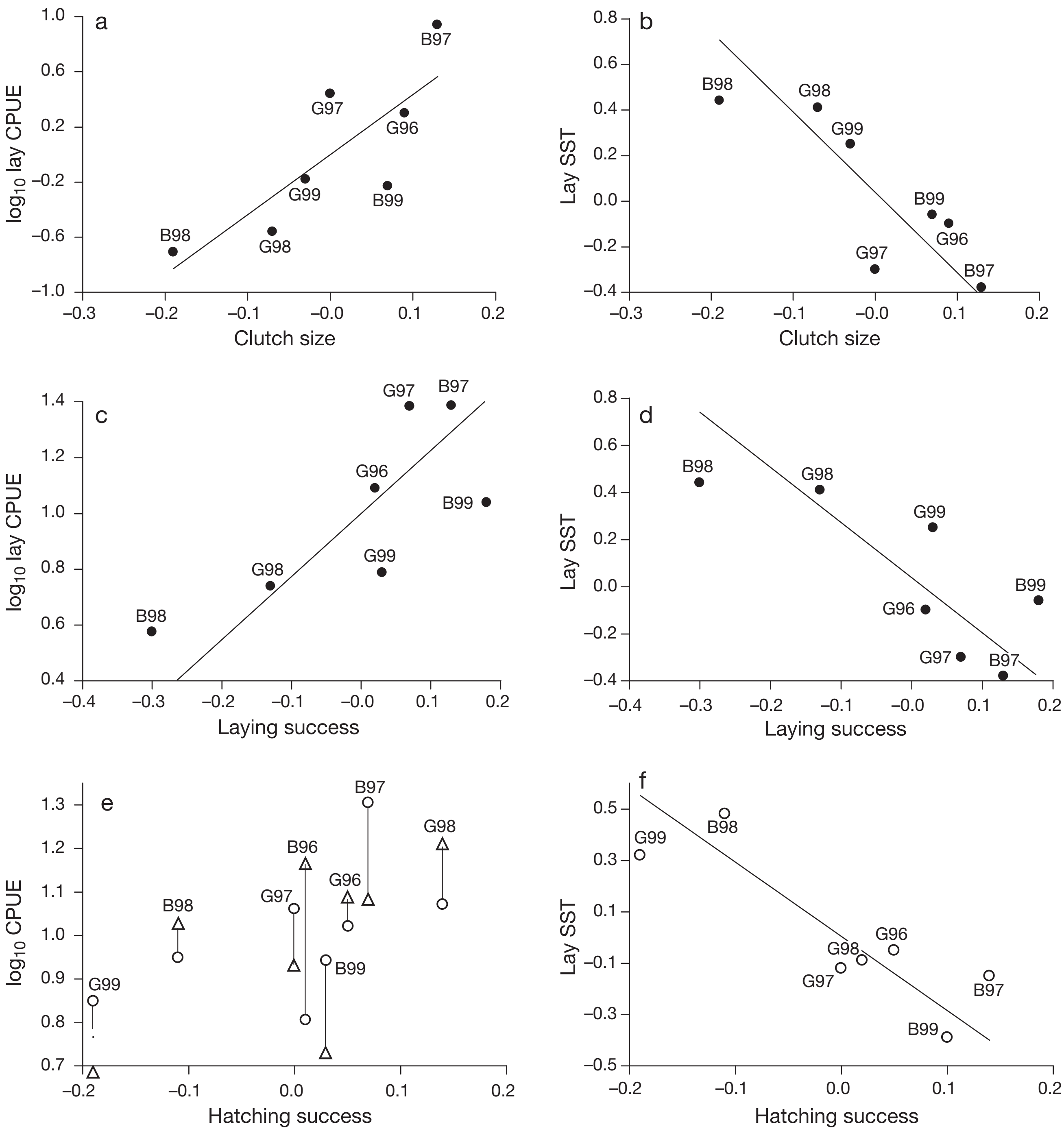

Fig. 3. *Uria aalge* and *Rissa tridactyla*. Relationships between the residuals of average forage fish abundance during egg laying (lay catch per unit effort, CPUE), sea-surface temperature (SST) during egg laying, and components of reproductive performance for (a,b,c,d) kittiwakes (clutch size, laying success) and (e,f) murres (hatching success) breeding at Gull (G) and the Barren (B) Islands, 1996–1999. (e) Murre is plotted versus lay CPUE and chick CPUE (forage fish abundance during chick rearing). (●) Lay period kittiwake, (○) lay period murre, (△) chick period murre. Lines are Deming Model II regression lines shown for significant correlations

food source for grazing zooplankton (Cooney 2007). The benefits associated with colder spring temperatures for forage fish may be related to the timing of their peak biomass — large, lipid-rich copepods (*Neocalanus plumchrus*) peak in abundance later during colder springs (Mackas et al. 2007), and this is correlated with higher seabird reproductive performance. Our study encompassed the end of a relatively warm 'regime shift' in the Gulf of Alaska (Litzow & Ciannelli 2007) that resulted in seabird and marine mammal population declines (Anderson & Piatt 1999). Years with colder spring SST may more closely resemble those prior to this regime shift, which were more productive for seabirds and marine mammals. Capelin are high quality forage fish (Van Pelt et al. 1997) that are important in the diet of murres and kittiwakes in our study area (Van Pelt et al. 2002), and warmer ocean temperatures have been linked to fewer capelin in the Gulf of Alaska (Anderson & Piatt 1999, Litzow & Ciannelli 2007). Capelin were more abundant in colder years of our study and were found primarily in cold water (Abookire & Piatt 2005).

Similar relationships between cold spring SST, higher food availability for seabirds, and higher RS have been found elsewhere (Ainley et al. 1996, Abraham & Sydeman 2004, Mackas et al. 2007). However, the relationships between physical oceanographic processes and the transfer of energy through the food web are complex, and we do not expect to see the same relationships everywhere. In the Sea of Okhotsk, the reproductive performance of planktivorous and piscivorous seabirds responded in opposite ways to the same changes in SST: piscivorous species were more successful in warm years (Kitaysky et al. 2000). In the North Atlantic, warmer ocean temperatures (e.g. positive North Atlantic Oscillation and SST anomalies) were associated with advanced timing of seabird breeding (Durant et al. 2004, Frederiksen et al. 2004, Regular et al. 2009). In British Columbia, Canada, rhinoceros auklets *Cerorhinca monocerata*, Cassin's auklet *Ptychoramphus aleuticus*, and tufted puffin *Fratercula cirrhata* breed earlier in warmer years, but in contrast to results presented here, this was associated with reduced reproductive performance and greater mismatch with macrozooplankton prey abundance (Bertram et al. 2001, Gjerdrum et al. 2003).

'Anticipation' or 'Constraint'?

Forage fish abundance increased after the onset of egg laying in all years and usually peaked during chick rearing. Inter-annual variation in food availability (near-shore fish abundance and SST) prior to egg laying accounted for nearly all of the observed variation in timing of egg laying for both species and the majority of kittiwake reproductive performance; when near-shore fish abundance was low, reproduction was delayed and birds produced fewer young. This delay in the onset of egg laying was apparently not an attempt to better match peak energetic demands of chicks with peak food availability, as the date of peak forage fish abundance was not related to timing of breeding. These results support the Constraint Hypothesis; the ability of birds to initiate reproduction was likely constrained by current food availability. Lay SST was apparently not a cue allowing birds to predict the timing of peak food abundance, but simply reflected current near-shore fish abundance and the degree of food limitation. Thus, in concordance with life-history theory, birds appeared to prioritize their own condition over their current RS.

Although food availability prior to egg laying was not important for explaining variation in murre RS, several lines of evidence suggest that its importance may be underestimated here: (1) lay date explained 87% of variability in RS and was the second best model, (2) lay date was related to pre-lay food availability, but not timing of peak food, (3) our estimate of murre RS does not include LS. Taken together, these results suggest that murre RS may have been limited by food availability prior to egg laying. This is supported by results from a concurrent study showing that murres with high peak stress hormone levels during incubation (indicative of prior nutritional stress) had reduced hatching success (Kitaysky et al. 2007).

Inter-annual variation in murre lay dates was half that of kittiwakes, suggesting that murres may have been less food limited prior to egg laying. Food abundance during egg formation was always higher for murres than kittiwakes, which laid eggs 3 to 4 wk earlier. However, our interpretation is confounded by a number of factors, including differential costs of egg production, about which we know little. Also, there is strong selection pressure for murres to lay eggs and fledge chicks synchronously with neighbors (Benowitz-Fredericks & Kitaysky 2005), and social cues may play an important role in reducing variability in murre egg laying.

Implications for climate change

The results of this study provide insight into how seabird populations may respond to long-term changes in climate. Here we demonstrate that seabird reproductive performance is sensitive to ocean temperature and food availability; small increases in spring SST (<1°C) accounted for over 94% of variability in seabird timing of breeding and near-shore fish abundance, which in turn, accounted for over 94% of variability in seabird RS. The rate of seabird population declines in response to climate change will largely depend on adult survival rates, and to a lesser degree, RS, and recruitment. However, when food availability is low, adult seabirds increase energy expenditure (Kitaysky et al. 2000, Harding et al. 2007) and stress hormone levels (Kitaysky et al. 2007, Shultz & Kitaysky 2008, Benowitz-Fredericks et al. 2008) which are associated with reduced RS and survival (Golet et al. 2004, Kitaysky et al. 2007). Also, chicks reared during periods of low food availability may have reduced chances of survival (Kitaysky et al. 2006). Thus, warmer spring ocean temperatures are likely to result in population declines of seabirds in the Gulf of Alaska, due to decreased RS, recruitment, and adult survival.

The results presented here highlight the importance of a multi-species approach to monitoring environmental changes; kittiwake lay date may best reflect spring near-shore forage fish abundance and SST, while murre RS may be most indicative of near-shore fish abundance during August.

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Climate-forced seasonal mismatch between the hatching of rhinoceros auklets and the availability of anchovy

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ABSTRACT: Predator–prey relationships are key to understanding complex marine ecosystem dynamics. The match–mismatch hypothesis posits that predators time energy-intensive activities, such as reproduction, to periods of high food availability. However, predators may be constrained by various ecological or physiological processes, leading to mistimed activities relative to prey availability. We investigated inter-annual variation in the timing of breeding for a piscivorous seabird (rhinoceros auklet *Cerorhinca monocerata*) in relation to availability of a preferred prey item, Japanese anchovy *Engraulis japonicus*, using data collected over 18 yr between 1984 and 2006 at Teuri Island in the northern Japan Sea. Our primary goals were (1) to identify the climatic factors that affect the seabirds' timing of breeding, proxied by hatching date, and anchovy seasonal availability, and (2) to quantify the fitness effects of predator–prey matches and mismatches relative to climate variability. Hatching date was later in years with lower spring air temperatures. Auklets switched their feeding from sandlance and juvenile greenling to anchovy when it was transported into the birds' foraging range with the seasonal northern expansion of 13°C warm water from the south. The mismatch between hatching date and the period of high anchovy availability was most pronounced when spring air temperatures were warm, and there was a weak Tsushima (warm) Current. Spring air temperature was influenced by spring atmospheric pressure gradients in the Arctic and northern Eurasia, which drive the east Asian winter monsoon, whereas timing of the Tsushima warm water expansion was influenced by winter surface pressures over the western North Pacific. Chick growth rates, mass at fledging, and overall fledging success (fitness) were lower during mismatch years when the auklets fed less on anchovy. The auklets were constrained to adjust hatching date because the seasonal mismatch appeared to be driven by independent and unpredictable surface pressure patterns.

KEY WORDS: Climate change · Match–mismatch · Seabirds · Atmospheric pressure systems · Reproductive consequences

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INTRODUCTION

Most species of birds mate, lay eggs, hatch, grow, and migrate during specific, well-defined periods of the year when physical and biological conditions (e.g. light, temperature, precipitation, prey availability) are suitable for these activities (Lack 1968, Stenseth & Mysterud 2002). Climate fluctuations are known to shift these specific periods ('phenological' shifts), sometimes differently across species (Stenseth & Mysterud 2002, Visser & Both 2005). Different phenological responses in species of varying trophic levels may lead to mismatches between functionally different components of an ecosystem (e.g. prey and predator), with important effects on ecological structure and function (Stenseth et al. 2002).

Terrestrial birds provide a good example. As these birds have high energy requirements during the chick-rearing period (Drent & Daan 1980), parents time the

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onset of breeding so that the availability of prey is highest during this period. Many bird species have advanced their laying date in response to the increase in spring air temperatures over the past 2 decades (Crick et al. 1997, Visser et al. 2003), although this response varies among species and regions. Weak responses in migrating (Both et al. 2005) and predatory (Both et al. 2009) birds have caused seasonal mismatches between the birds and their prey, which has led in some cases to population declines (Both et al. 2006).

In marine ecosystems, upper trophic level predators demonstrate high metabolic needs during breeding. Inter-annual variation in the abundance and distribution of prey may similarly result in mismatches between food availability and predator needs, with substantial reproductive consequences (Anderson & Piatt 1999, Hunt & Stabeno 2002, Platt et al. 2003, Edwards & Richardson 2004). In seabirds, the date of arrival at the breeding area or the egg-laying date depends on inter-annual variation in ocean climate (Durant et al. 2004, Frederiksen et al. 2004, Barbraud & Weimerskirch 2006, Schroeder et al. 2009 this Theme Section). Biological determinants of breeding data have also been established. In relation to a change in the date of zooplankton peak availability, there is a seasonal mismatch between zooplanktivorous Cassin's auklets *Ptychoramphus aleuticus* and their prey (Bertram et al. 2001, Hipfner 2008) in British Columbia, Canada. However, parent birds of the same species in California (Abraham & Sydeman 2004) and other seabird species (e.g. tufted puffins *Fratercula cirrhata*, Gjerdrum et al. 2003; kittiwakes *Rissa tridactyla* and common murres *Uria aalge*, Frederiksen et al. 2004) may be able to adjust hatching dates so that peak prey availability coincides with the chick-rearing period.

To understand the impacts of climate change on seabird populations, it is important to identify factors affecting the onset of breeding, the timing of peak prey availability, and factors constraining adjustment. In the North Pacific, the widely distributed rhinoceros auklet *Cerorhinca monocerata* provides an excellent system to test ideas pertaining to climate change and the match–mismatch hypothesis. The auklets feed mainly on epipelagic fishes within a limited range from the colony (Gaston & Jones 1998, Thayer et al. 2008). The relationships between ocean climate, food habits, and reproductive success of rhinoceros auklets differ among British Columbia (Bertram et al. 2001, Hedd et al. 2006), California (Thayer and Sydeman 2007), and Japan (Deguchi et al. 2004a), but the influence of ocean climate on the match or mismatch of predator and prey has yet to be investigated.

Using data collected over 18 years between 1984 and 2006 at Teuri Island in the Japan Sea (Fig. 1), we identified local climate factors affecting the hatching date of rhinoceros auklets and the period of peak availability of their prey, and examined the effects of a seasonal mismatch between these dates on breeding success. To illustrate the relationships between local ocean climate and global climate, we examined the linkage between surface atmospheric pressure patterns in the Arctic and northwestern Pacific that drive wind and water currents in the Japan Sea (Minobe et al. 2004). At Teuri Island, when summer sea surface temperature (SST) within about 100 km of the colony is high, the auklets switch prey from energy-poor age-0 sandlance *Ammodytes personatus* and age-0 greenling *Pleurogrammus azonus* to the energy-rich anchovy earlier in the year, and chick growth is faster (Takahashi et al. 2001, Deguchi et al. 2004a). Therefore, we investigated specifically (1) how the local climate factors such as air temperature and SST affected auklet hatch date and the date of prey-switching to anchovy, (2) the degree of mismatch between these 2 dates and the effects of mismatch on the mass proportion of anchovy in the diet, (3) the link between the sea surface pressure pattern over the Northern Hemisphere and local climate factors, and (4) the effects of the proportion of anchovy in the diet of chicks on chick growth and fledging success.

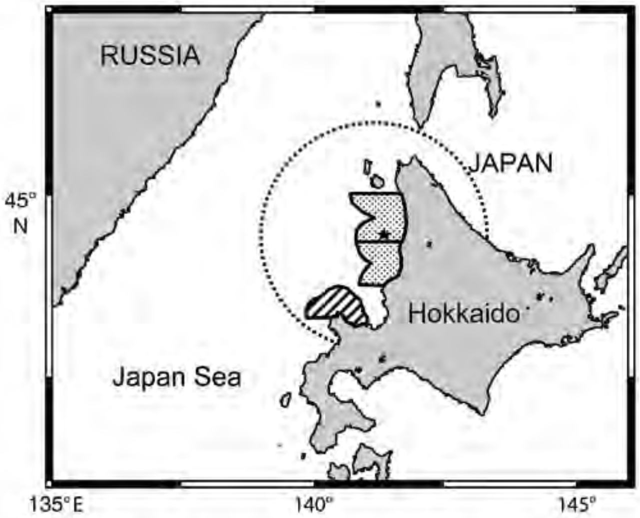

Fig. 1. Teuri Island (star), the area where local sea surface temperature (*LSST*) was measured (stippled), and the area where SST at the southern edge of the foraging range of auklets was measured (hatched). Potential foraging range of rhinoceros auklets from Teuri Island (Kato et al. 2003, 164 km) is within the dotted line

MATERIALS AND METHODS

Field work. Data were collected over 18 yr at Teuri Island (44° 25′ N, 141° 19′ E, Fig. 1) from 1984 to 1985, in 1987, and from 1992 to 2006. The breeding performance of birds in natural burrows and artificial nest boxes (Kuroki et al. 1998) was studied. Nests were checked between 16:00 and 18:00 h every 3 to 5 d to determine the hatching date and mass of chicks. Between 10 and 66 nests with hatchlings were monitored each year (Deguchi et al. 2004b). When newly hatched chicks were found, these were assumed to have hatched at the midpoint of the interval between the nest censuses. Chicks were weighed with a Pesola spring balance to the nearest 5 g. The growth rate of each chick was defined as a slope of the linear regression line of chick mass (g) against age (d) for chicks 5 to 20 d old (Takahashi et al. 2001). Chicks that disappeared from the nest after attaining the age of 40 d were considered to have fledged.

Diets were sampled by capturing birds with food loads along a road in the colony within ~100 m of the nest-monitoring site. Birds were captured as they landed between 19:00 and 22:00 h with either a swooping net or by hand. Sampling was initiated as soon as birds were observed carrying fish to nest sites, typically from mid-May to early June. Diet was sampled once every 2 wk during 1984 to 1995 (except for the years 1986, 1988 to 1991), every 3 to 5 d during 1996 to 2001 and every week during 2002 to 2006. Each food load was put into a separate bag, which was brought back to the laboratory for identification. Fish species were identified using a key by Amaoka et al. (1995) and weighed to the nearest 0.1 g with an electronic balance, and fork length was measured to the nearest 1 mm. On each sampling date, 3 to 76 food loads were collected, for a total of 64 to 226 food loads each year.

To determine the ocean climate, proxied by SST, in the areas where rhinoceros auklets feed on anchovy, we recorded the diving behavior of the parents and water temperature at the feeding site by using bird-borne data-loggers in 2006. With quick-set glue and plastic netting, we attached 2.7 g data-loggers (Cefas G5, CTL), which recorded depth (0.1 m accuracy) and temperature (0.1°C accuracy) at 3 s intervals for up to 8 d, to 5 birds that were rearing chicks in artificial nests (Kuroki et al. 2003). The loggers were retrieved 7 to 10 d after deployment. To identify the species of prey brought back to the chicks by these birds, we videotaped the nest chambers of the same birds using a video camera and infrared light (SH-6B, Wireless Tsukamoto). The resulting video images were clear enough to identify the fish species.

Determination of the date of prey-switching. Japanese anchovy migrate northward with the Tsushima Current, which flows from the southern Japan Sea during the spring and summer (Naganuma 2000). We defined the date of prey-switching to anchovy (*SWITCH*) as the date when 50 % of rhinoceros auklets brought anchovy in their food loads. To determine *SWITCH*, we used logistic regression (SPSS v.14), where an assignment of each food load ('anchovy' = 1 or 'non-anchovy' = 0) was the dependent variable and the day of year was the independent variable. Most food loads (98 %) contained only a single species of fish. Of the other 2 %, those whose mass was more than 50 % anchovy were considered anchovy food loads and the others were considered non-anchovy food loads.

We verified this analysis using detailed data from 2006. Between 30 May and 30 June in 2006, prey species of fish carried by auklets (8 to 57 birds night^{-1}) were identified by direct observation every evening (19:30 to 20:30 h) at an observation site (about 5 × 5 m) beside the nest-monitoring site. Rhinoceros auklets brought age-0 sandlance, age-0 greenling, and herring *Clupea pallasi* before mid-June, but food loads were composed mostly of anchovy after that (Fig. 2a). The prey-switching occurred within 1 wk. Using the logistic regression approach ($p < 0.001$), *SWITCH* was found to occur on 21 June (day of year 172; Fig. 2a). According to the direct daily observation of birds with food loads, *SWITCH* occurred on 18 June (Fig. 2b); these data are in agreement.

SST and anchovy distribution. Rhinoceros auklets perform several dive bouts, each consisting of 3 to 212 consecutive dives, during daylight hours each day. In the evening, they stop diving and bring food back to the chicks (Kuroki et al. 2003). The SST recorded during the final dive bout of each day should be that of the water where the auklet obtains the fish in each food load. However, the temperature sensor has a slow response time (i.e. the time needed to reach 66 % of the temperature difference; 28 s), making direct measurement of SST problematic. Therefore, we excluded temperature records during the first and the second dives of each bout, because these might reflect the air temperature (Watanuki et al. 2001). We averaged the temperatures recorded at the start and at the end of each dive, then defined the grand average across all dives during each dive bout as the 'SST.' To check the reliability of this procedure, we simulated 10 dives as 1 dive bout and repeated the simulation 3 times. In each dive, the data-logger was submerged in 13°C water for 10 s (descent in the 'surface layer'), then in 11°C water for 10 s (foraging in the 'deeper layer'), again in 13°C water for 10 s again (ascent in the 'surface layer'), and then placed in the air at 23°C for 10 to 60 s (post-dive surface time). The 'SST' range of the 3 simulated dive bouts was 12.5 to 13.0°C, which is the same (within 0.5°C of accuracy) as the water temperature of the 'surface layer'. Thus, the grand mean of the temperatures recorded at the start and end of each dive during dive bouts including more than 10 dives gave a reasonable approximation of the SST where the birds were diving.

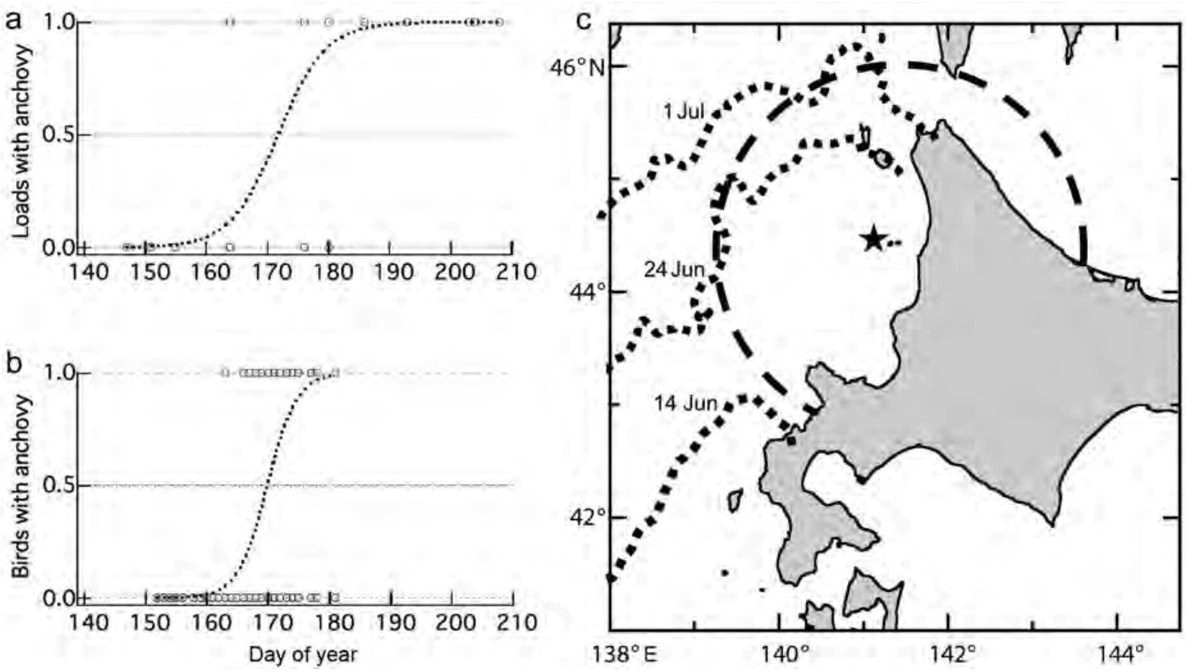

Fig. 2. Seasonal changes in (a) the occurrence of food loads with (designated as 1) and without (designated as 0) anchovy (n = 85 food loads), and (b) birds carrying anchovy (1) or other fish (0) (n = 787 birds) in 2006. Symbols for multiple samples on the same day overlap. Significant logistic regression lines are shown as broken lines. (c) The seasonal northern expansion of the 13°C SST (dotted lines with dates) in 2006 and the potential foraging range of auklets (broken line). Star indicates Teuri Island

Using data from 5 birds collected in 2006 and excluding dive bouts with fewer than 10 dives, the SST of waters where rhinoceros auklets fed on age-0 sandlance (8 bouts) varied between 11.8 and 14.4°C, and SST where they fed on age-0 greenling (6 bouts) varied between 8.0°C and 13.7°C. The SST where they fed on herring (2 bouts) was less than 11.6°C, whereas that where they fed on anchovy (6 bouts) was higher than 13°C. In the fishery off eastern Hokkaido, anchovy are harvested in relatively warm waters with an SST of 12 to 15°C (Mihara 1998). Thus, we inferred that anchovy expand their distribution northward as waters of ~13°C SST move northward with the northern expansion of the Tsushima Current.

Using the flight time determined by measuring acceleration with a bird-borne data-logger, and assuming flight speed to be 18 m s^{-1} and feeding frequency to be once per night, we estimated the average foraging ambit of rhinoceros auklets at Teuri Island to be 87 km with a maximum of 164 km (Kato et al. 2003; Fig. 2c). In 2006, the auklets switched their prey to anchovy between 18 and 21 June (Fig. 2a,b) when the northern limit of the 13°C SST crossed the maximum foraging range (164 km; Fig. 2c). Therefore, we used the date when the SST of waters near the southern edge of the maximum foraging range of the auklets became higher than 13°C as the critical factor determining *SWITCH*.

Local climate and anchovy stock size. To examine the effects of local climate on the mean hatching date between years (*HATCH*, day of year), we used monthly mean air temperature (*AIRTEMP*) and total precipitation (*RAIN*) at Yagishiri Island (4 km west of Teuri Island) and total snowfall (*SNOW*) at the nearest weather station in Haboro (30 km west of Teuri Island) in March (Japan Meteorological Agency, JMA, www.data.jma.go.jp/). For ocean climate, we used monthly mean SSTs in the northeastern and the southeastern coastal area of northern Hokkaido (stipped area in Fig. 1, *LSST*). We used the Merged Satellite and *In Situ* Data Global Daily SST (MGDSST), which is based on SST data collected by the AVHRR sensor on NOAA and Multi-functional Transport Satellite (MTSAT) satellites, reported by Hakodate Kaiyou Kishodai from 1985 to the present, to estimate SST in these regions (www.data.kishou.go.jp, in Japanese).

We used the daily mean SST in the coastal area off southern Hokkaido (hatched area in Fig. 1) to determine when warm waters of the Tsushima Current arrived in the study area. The date when the SST in this area exceeded 13°C was defined as the date that warm water arrived in the birds' foraging habitat (*WARMARR*). The index of the flow rate of the Tsushima Current in the Japan Sea (*FLOW*; area of water at 100 m depth having temperatures higher than 10°C) was obtained from the JMA (www.data.kishou.

go.jp/kaiyou/shindan/e_2/maizuru_tsushima/maizuru_tsushima.html, in Japanese).

The Tsushima anchovy stock is distributed from the west coast of Kyusyu to the Japan Sea coast of northern Japan, and should be available to rhinoceros auklets at Teuri Island in the summer. The stock size (*ENGSTOCK*) has been estimated annually since 1991 by monthly cohort analysis, and its trend has been validated by local acoustic surveys (Fisheries Agency http://abchan.job.affrc.go.jp/, in Japanese).

Statistical analyses. We used path analysis to identify the local climate factors explaining variation in mean hatch date (*HATCH*), the date of prey-switching to anchovy (*SWITCH*), the proportional mass of anchovy in the diet (*ENGDIET*), and chick growth (*GROWTH*), fledgling mass (*MASS*), and the number of fledglings per nest with chicks (*FLEDGLING*) (Amos 6.0, Amos Development Corporation). We only used years where values of all independent factors were collected. Path analysis was selected in order to test direct and co-varying effects of independent variables. In addition to local climate factors, year (*YEAR*) was included as a potential independent factor to look at trends. To make the analyses simple, indirect effects were not included. The model giving the smallest value of the 0-adjusted Akaike Information Criterion ($AIC_0 = 0$) was selected as the best-fitting model; the top 5 models with $AIC_0 < 2.0$ are shown in ‘Results (see Tables 1 & 2) as these are believed to be appropriate models (Burnham & Anderson 1998). Following Frederiksen et al. (2004), we also examined whether the slopes of factors were significant.

To find factors determining *HATCH*, the model included *AIRTEMP*, *LSST*, *SNOW*, and *RAIN* in March, and *YEAR* (n = 17 yr, as LSST was not available in 1984). There were significant correlations between *AIRTEMP* and *LSST* ($r = 0.601$, $p < 0.05$) and between *AIRTEMP* and *SNOW* ($r = -0.519$, $p < 0.05$, Fig. 3a). Thus the model also included covariance between these. We found no significant correlations between other combinations of independent variables (*SNOW*, *RAIN*, *YEAR*; $r = -0.08$ to $+0.33$, $p > 0.05$).

WARMARR, the index of Tsushima Current flow in June (*FLOW*) when *SWITCH* mainly occurred (Fig. 3b,d), *LSST* in June, *ENGSTOCK*, and *YEAR* (n = 11) were candidate factors determining *SWITCH; SWITCH* was not defined in 7 years. We found significant correlations between *WARMARR* and *FLOW* ($r = -0.837$, $p < 0.001$, see Fig. 3b), *WARMARR* and *LSST* ($r = -0.787$, $p < 0.01$), and *FLOW* and *LSST* ($r = 0.791$, $p < 0.01$). It is obvious that strong Tsushima Current flow results in both a higher SST and the earlier arrival of warm 13°C water. Therefore, the model included *WARMARR* as the most proximate factor instead of *FLOW* or *LSST*. *ENGSTOCK* and *YEAR* were also included as independent factors. Since there were no significant correlations among these independent factors ($r = -0.321$ to 0.065, $p > 0.05$, see Fig. 3b,c), no covariance was included.

To find factors affecting *ENGDIET*, the model included degree of mismatch (*MISMATCH*), *ENGSTOCK*, and *YEAR* as independent variables. *MISMATCH* was defined as the difference between hatch date and date of prey-switching to anchovy, i.e. *SWITCH* – *HATCH*. Since there were no significant correlations among these independent factors ($r = -0.370$ to 0.192, NS), no covariance was included.

Last, effects of *ENGDIET* on *GROWTH*, *MASS*, and *FLEDGLINGS* were examined with *AIRTEMP* and *RAIN* in June and *YEAR* included as independent factors (n = 18 years). Covariance between *ENGDIET* and *YEAR* was positive and significant ($r = 0.776$, $p < 0.01$), meaning that the auklets fed more on anchovy in later years, and was included in the model.

Atmospheric pressure and local climate. To investigate how large-scale climate affects *HATCH* and *SWITCH*, we constructed a correlation map of the monthly surface pressure in the Northern Hemisphere, based on NCEP/NCAR Reanalysis data (NOAA/OAR/ESRL PSD; Kalnay et al. 1996) against the local climate factors most strongly affecting *HATCH* and *SWITCH;* the time series used information from 1984 to 2006 (1986 and 1988–1991 were excluded). We used local climate data from 1950 to 2007 to confirm results.

RESULTS

Hatch date

HATCH varied between 16 May and 6 June (Fig. 3d). In 4 out of 5 appropriate models, *AIRTEMP* in March had a significant effect on *HATCH* (Table 1). The slope of *AIRTEMP* on *HATCH* was negative, meaning that the auklets advanced hatching date by 3.7 to 4.9 d per 1°C increase in *AIRTEMP* (Table 1, Fig. 4). The first hatch date was similarly advanced as *AIRTEMP* increased (Fig. 4). The marginally significant positive slope of *YEAR* on *HATCH* indicates that *HATCH* was delayed slightly (0.32 to 0.4 d yr^{-1}) across years. *SNOW*, *RAIN*, and *LSST* in March had no significant direct effects.

Date of prey-switching

Rhinoceros auklets fed on sardine *Sardinops melanostictus* and sandlance and did not feed chicks with anchovy in 1984, 1985, or 1987, and rarely in 1992 (Fig. 3c). In 1994, 2003 and 2004, birds were already bringing back anchovy at the beginning of hatching and fed mostly on anchovy after that, so we did not find any significant logistic regressions. Thus, *SWITCH* was not determined in these years (see Fig. 3d). Excluding these years, *SWITCH* varied between 21 April and 31 July (Fig. 3d; n = 11 years).

All appropriate models included *WARMARR* as a significant factor (Table 1). The positive slope of *WARMARR* on *SWITCH* indicates that the auklets delayed *SWITCH* by 3.3 d per day of delayed 13°C water (Table 1, Fig. 5). *YEAR* was included as a factor in the best-fitting model. The marginally significant and negative slope of *YEAR* on *SWITCH* indicates that *SWITCH* was advanced by 1.1 d yr^{-1} over the time series (Table 1). *ENGSTOCK* had no significant effects.

Mismatch between *HATCH* and *SWITCH*

ENGDIET varied between 1 and 94% during 1984 to 2006 (Fig. 3c). Using data of 11 years when *SWITCH* was determined, all 3 models included *MISMATCH* as a significant factor (Table 1). The negative slope of *MIS-*

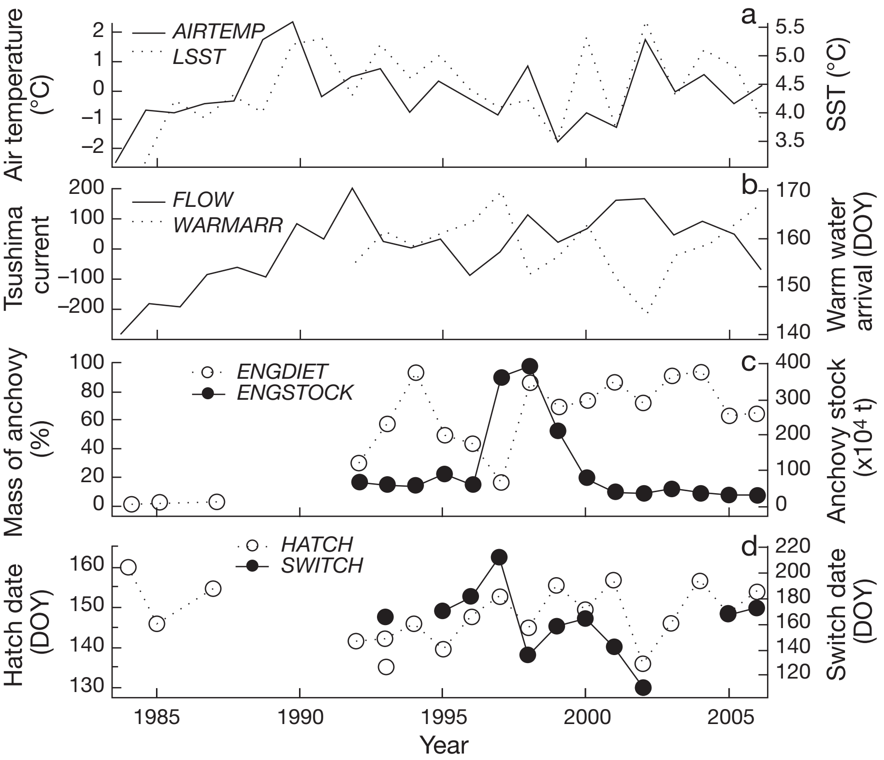

Fig. 3. *Cerorhinca monocerata.* Interannual changes in local climate factors and responses of rhinoceros auklets. (a) Mean monthly air temperature (*AIRTEMP*) in March at Yagishiri Island (3 km west of the colony), which was defined as the colony air temperature, and local monthly mean SST in March (*LSST*, see Fig. 1). (b) Flow rate index of the Tsushima Current (deviation from 1971–2000 average shown as % of SD) in the Japan Sea (*FLOW*) in June and the date of the arrival of warm (13°C) water at the southern edge of the potential foraging range of the auklets (*WARMARR*). (c) Size of the Tsushima anchovy stock (*ENGSTOCK*) and mass proportion of anchovy in food loads (*ENGDIET*). (d) Mean hatch date (*HATCH*) and date of prey switching to anchovy (*SWITCH*). DOY: day of year

Table 1. *Cerorhinca monocerata.* Summary of the fitted path models relating hatch date (*HATCH*, day of year) to monthly mean air temperature in March (*AIRTEMP*, °C), total snow fall in March (*SNOW*, cm), total precipitation in March (*RAIN*, mm), and mean monthly local sea surface temperature in March (*LSST*, °C); those relating the date of prey switching to anchovy (*SWITCH*, day of year) to the date of arrival of 13°C water within the birds' foraging range (*WARMARR*, day of year), and the stock size of anchovy (*ENGSTOCK*, 10^4 t); and those relating the mass proportion of anchovy in the auklet diet (*ENGDIET*, %) to the degree of mismatch between *HATCH* and *SWITCH* (*MISMATCH*, d) and *ENGSTOCK*. *YEAR* is also included as a factor. The 0-adjusted AIC (AIC_0), the coefficent (SE, significance level), and the coefficient of determination (R^2) are shown. For *HATCH*, the covariance between *AIRTEMP* and *LSST* ($r = 0.601$, $p < 0.05$) and bewteen *AIRTEMP* and *SNOW* ($r = -0.515$, $p < 0.05$) are significant and are included in all models. For *SWITCH* and *ENGDIET*, covariance between *WARMARR*, *ENGSTOCK*, and *YEAR* or between *MISMATCH*, *ENGSTOCK*, and *YEAR* are not significant. Models having $AIC_0 < 2.0$ but up to the fifth-best model are shown

Dependent		Independent					R^2
HATCH	AIC_0	*YEAR*	*AIRTEMP*	*SNOW*	*RAIN*	*LSST*	
	0.000	0.319(0.178, 0.073)	−4.916(1.239, <0.001)				0.542
	0.304	0.396(0.169, 0.019)	−3.735(1.467, <0.001)			−2.605(1.841, 0.157)	0.615
	0.890		−4.648(1.356, <0.001)				0.423
	1.775	0.318(0.177, 0.072)	−4.866(1.231, <0.001)		0.058(0.122, 0.478)		0.544
	1.881	0.344(0.166, 0.038)	−2.828(1.885, 0.133)	0.028(0.036, 0.434)		−3.132(2.028, 0.122)	0.609
SWITCH	AIC_0	*YEAR*	*WARMARR*	*ENGSTOCK*			
	0.000	−1.087(0.603, 0.072)	3.270(0.329, <0.001)				0.911
	0.527		3.292(0.337, <0.001)	0.030(0.019, 0.110)			0.907
	0.644	−0.859(0.563, 0.127)	3.257(0.307, <0.001)	0.022(0.017, 0.203)			0.921
	0.790		3.327(0.378, <0.001)				0.886
ENGDIET	AIC_0	*YEAR*	*MISMATCH*	*ENGSTOCK*			
	0.000		−0.754(0.166, <0.001)				0.808
	1.847	0.294(0.694, 0.672)	−0.736(0.115, <0.001)				0.804
	1.891		−0.747(0.116, <0.001)	-0.007(0.021, 0.736)			0.807

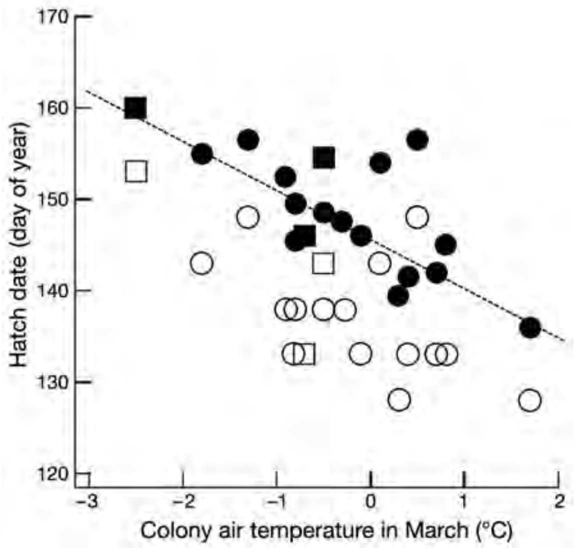

Fig. 4. *Cerorhinca monocerata.* Relationships of air temperature in March at the colony (*AIRTEMP*) with the mean hatch date (*HATCH*; closed symbols), and with the first hatch date (open symbols). Circles are data from 1992 to 2006 (15 yr), when auklets fed mainly on anchovy, and squares are data from 1984 to 1985 and 1987 (3 yr), when auklets rarely fed on anchovy. The broken line is the significant linear regression line of *HATCH* on *AIRTEMP* to show the trend

MATCH on *ENGDIET* indicates that as the degree of mismatch increased, the auklets fed less on anchovy (Fig. 6), because in years when the hatch date was earlier and the date of prey switching to anchovy was later, anchovy were available to the auklets for a shorter part of the chick-rearing period. The effect of *YEAR* was positive, but not significant, and *ENGSTOCK* had no effect (Table 1).

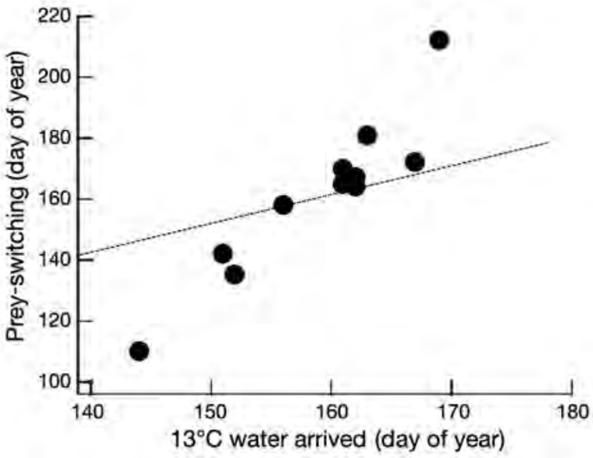

Fig. 5. *Cerorhinca monocerata.* Relationship between the date of the arrival of the 13°C water at the southern edge of the foraging range of the auklets from the colony (*WARMARR*) and the date of prey-switching to anchovy (*SWITCH*). Only data from years when *SWITCH* was determined (n = 11) are shown. The broken line shows the 1-to-1 relationship (slope = 1)

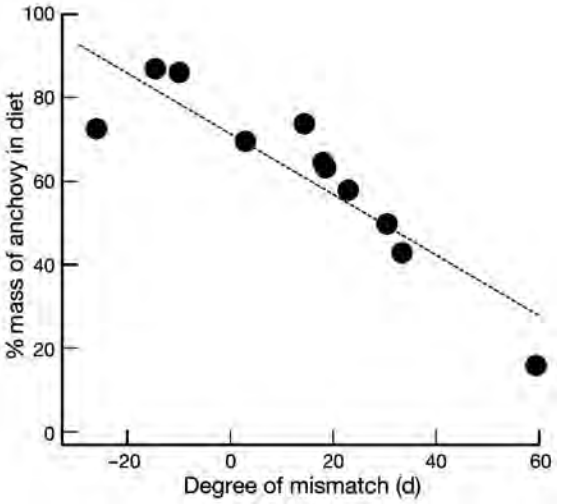

Fig. 6. *Cerorhinca monocerata.* Relationship between the number of days of mismatch (*MISMATCH*; difference between hatch date and date of prey-switching to anchovy, i.e. *SWITCH* – *HATCH*) and the mass proportion of anchovy in the chick diet (*ENGDIET*). Only data from years when *SWITCH* was determined (n = 11) are shown. The broken line is the significant linear regression to show the trend

Global surface pressure and local climate

AIRTEMP in March, which mainly determined *HATCH*, correlated negatively with surface pressure in March over the Arctic Sea and northern Eurasia, whereas the correlation was positive in areas surrounding the Arctic (Fig. 7a). This indicates that in years when pressure in the Arctic Sea and northern Eurasia was low, *AIRTEMP* was high. *WARMARR*, which determined *SWITCH,* was negatively correlated with the winter (December to February) surface pressure in the North Pacific east of Japan (Fig. 7c). Thus, in years when surface pressure in the North Pacific east of Japan was high in winter, the warm water arrived in the foraging range earlier in the season.

To extend the time series of local climate, we used surface air temperature (NECP/NCAR Reanalysis data) in March at the grid point nearest to the colony instead of *AIRTEMP* in March (r^2 = 0.627). *WARMARR* was most strongly correlated with SST anomalies in the southwestern Japan Sea (35–40° N, 130–135° E) in April and May (r^2 = 0.422). When a longer time-series (1950 to 2007) is used, the correlation maps of pressure with local climate factors show similar patterns. When the March surface pressure in the Arctic was high, the air temperature in the grid nearest to the colony in March was lower (Fig. 7b). When the winter (December to February) pressure in the North Pacific east of Japan was higher, the April–May SST in the southwestern Japan Sea was also high (Fig. 7d).

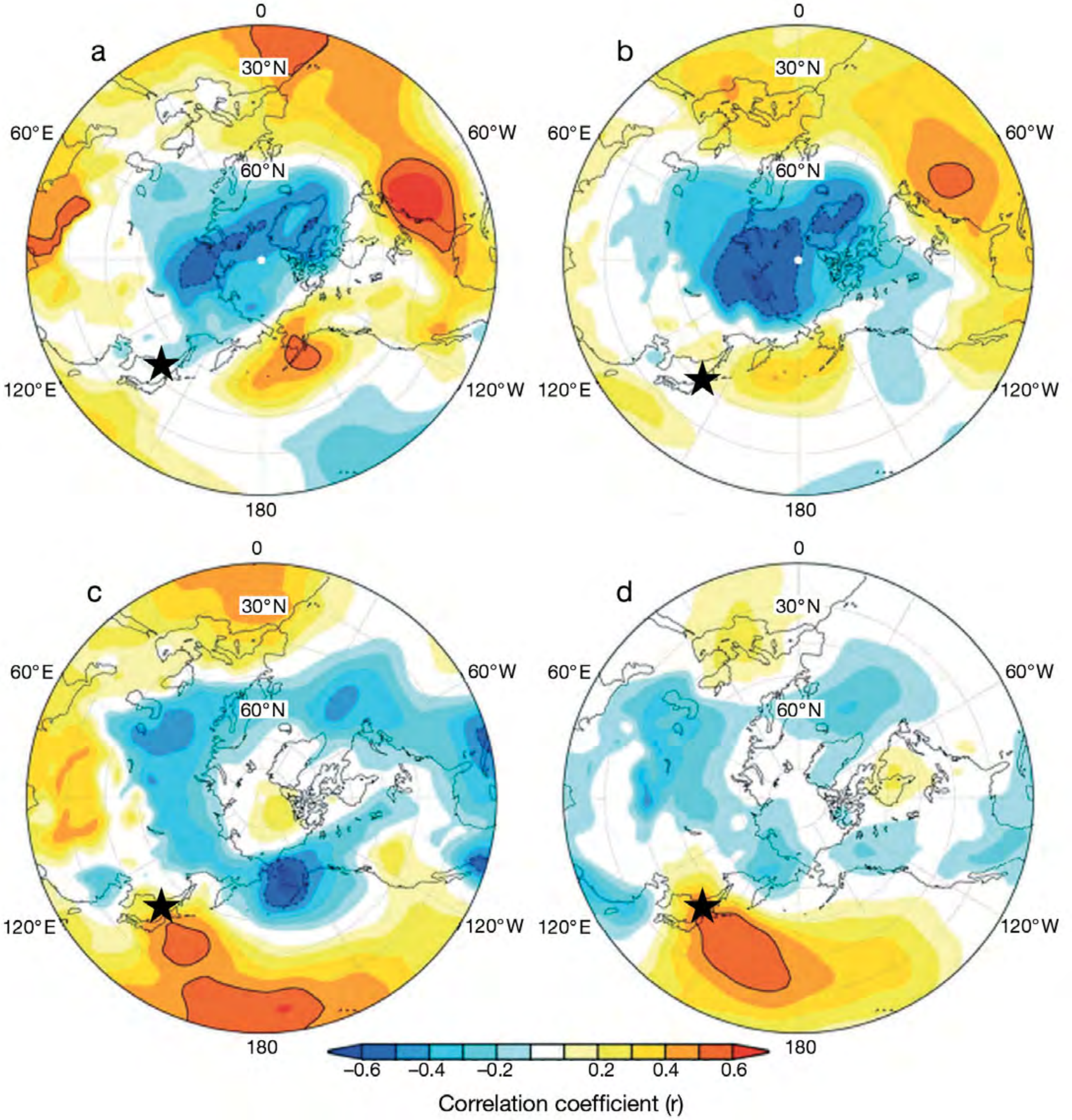

Fig. 7. Correlation maps (a) between March air temperature at the colony (*AIRTEMP*, which determined the hatch date) and March surface pressure (SP) in the Northern Hemisphere, and (c) between the minus date of the arrival of the 13°C SST water at the southern edge of the foraging range of the rhinoceros auklets (*WARMARR*, which determined the date of prey-switching) and winter (December to February) SP in the Northern Hemisphere, based on local climate data collected during the study period. Note that the sign is negative in panel (c). Correlation maps based on longer time series of local climate data (NCEP-NCAR reanalysis data; 1950 to 2007) between (b) the March air temperature at the grid point nearest to the colony and the March SP, and (d) between the SST averaged over the southwestern Japan Sea from April to May and the winter (December to February) SPI. A color contour interval of 0.1 is used for the simple product-moment correlation coefficient (r). The star shows the position of the colony

Table 2. *Cerorhinca monocerata.* Summary of the fitted path models relating the chick growth rate (*GROWTH*, g per 5 d), the fledgling mass (*MASS*, g), and the number of fledglings per nest (*FLEDGLING*) to the proportional mass of anchovy in the chick diet (*ENGDIET*, %), mean air temperature in June (*AIRTEMP*, °C), and total precipitation in June (*RAIN*, mm). *YEAR* is also included as a factor. The covariance between *YEAR* and *ENGDIET* (r = 0.776, $p < 0.01$) is significant and positive and is therefore included in the model. The covariances among other factors are not significant. The 0-adjusted AIC(AIC_0), the coefficent (SE, significance level), and the coefficient of determination (R^2) are shown. Models having $AIC_0 < 2.0$ are shown

Dependent	AIC_0	Independent				R^2
		YEAR	*ENGDIET*	*AIRTEMP*	*RAIN*	
GROWTH	0.000		0.281(0.057, <0.001)		−0.270(0.079, <0.001)	0.680
	0.592	−0.537(0.426, 0.207)	0.358(0.087, <0.001)		−0.242(0.076, 0.001)	0.684
	1.921		0.284(0.057, <0.001)	−0.610(2.130, 0.774)	−0.269(0.079, <0.001)	0.684
MASS	0.000		1.623(0.305, <0.001)		−0.927(0.422, 0.028)	0.661
	1.709		1.373(0.340, <0.001)			0.489
	1.992	−0.217(2.379, 0.927)	1.654(0.484, <0.001)		−0.916(0.442, 0.030)	0.659
	1.996		1.619(0.305, <0.001)	0.770(11.443, 0.946)	−0.928(0.422, 0.028)	0.666
FLEDGLING	0.000		0.004(0.001, <0.001)	−0.085(0.039, 0.031)	−0.004(0.001, 0.010)	0.604
	1.998		0.004(0.001, 0.002)		−0.004(0.002, 0.018)	0.467

Chick growth and fledging success

In years when rhinoceros auklets fed chicks with more anchovy (ENGDIET), *GROWTH*, *MASS*, and *FLEDGLINGS* were greater (Table 2, Fig. 8a–c). *RAIN* in June had significant negative effects on each of these variables as well (Table 2). *AIRTEMP* in June had no significant effects on *GROWTH* and *MASS* but negatively affected *FLEDGLINGS* in the best-fitting model (Table 2).

DISCUSSION

Timing of breeding

When the March air temperature was higher, hatching dates were earlier. According to the mean annual hatch date observed in this study (16 May to 6 June), and the reported incubation period for this species (39 to 52 d, Gaston & Jones 1998), the auklets laid eggs between late March and late April. Therefore, auklets

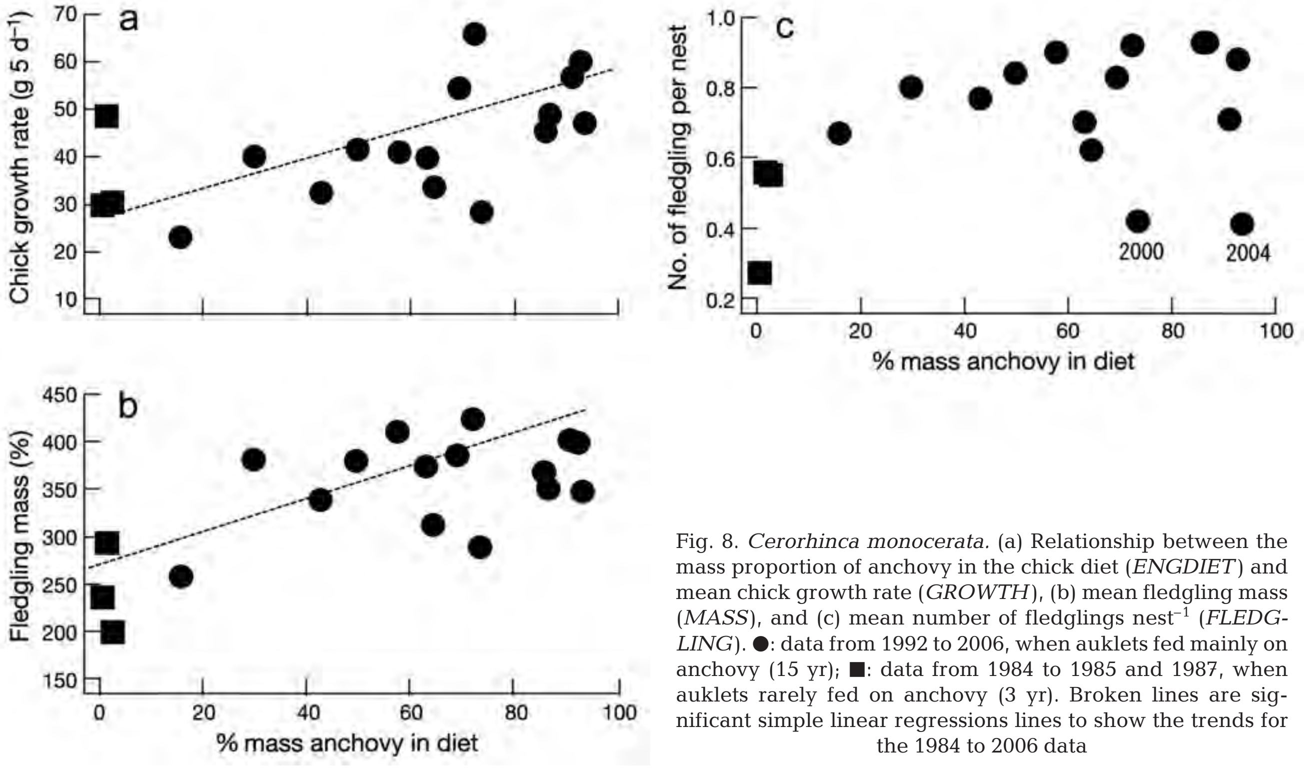

Fig. 8. *Cerorhinca monocerata.* (a) Relationship between the mass proportion of anchovy in the chick diet (*ENGDIET*) and mean chick growth rate (*GROWTH*), (b) mean fledgling mass (*MASS*), and (c) mean number of fledglings nest^{-1} (*FLEDGLING*). ●: data from 1992 to 2006, when auklets fed mainly on anchovy (15 yr); ■: data from 1984 to 1985 and 1987, when auklets rarely fed on anchovy (3 yr). Broken lines are significant simple linear regressions lines to show the trends for the 1984 to 2006 data

started excavating burrows in March, and possibly earlier in February. In 1984, the auklets started egg-laying in late April, which was 3 wk later than in 1985 (see Fig. 3d). As a result of lower spring air temperature (below freezing, see Fig. 3a) and the later disappearance of snow (mid-April) in 1984 than 1985, frozen soil in spring 1984 may have prevented the birds from excavating nest burrows (Watanuki 1987). Similarly, for prions *Pachyptila desolata* in the sub-Antarctic, hatching can be delayed if snow blocks their burrows in spring (Liddle 1994). Although total snowfall in March was negatively correlated with temperature in the Teuri region, snow did not influence hatching date directly.

Spring SST affects timing of breeding in several seabird species (Bertram et al. 2001, Gjerdrum et al. 2003, Frederiksen et al. 2004, Thayer & Sydeman 2007), but wintertime conditions may also be influential (Schroeder et al. 2009). The covariance between air temperature near the colony (*AIRTEMP*) and SST around the colony (*LSST*) in March was significantly positive. *LSST* showed negative, though non-significant, effects on *HATCH* in the second- and fifth-best fitting models (Table 1). Therefore, a higher SST in spring might cause timing to be advanced. Rhinoceros auklets at Teuri Island feed on krill and fishes in the egg-laying season (Ito et al. 2009, this Theme Section). *Thysanoessa inermis* is the predominant krill species in coastal waters near Teuri Island (T. Deguchi pers. obs.). In spring, this species congregates to spawn at the sea surface off the western coast of Hokkaido when SST rises to 3–4°C, and submerges when SST increases to 7–8°C (Hanamura et al. 1989). Thus, we cannot rule out the possibility that *LSST* in March, which ranged from 3.1 to 5.6°C (Fig. 3a) during the study years, affected the date of egg-laying through trophic effects.

Timing of prey-switching

Earlier arrival of warm waters at the southern edge of the auklets' foraging range (*WARMARR*), associated with the Tsushima Current, advanced the date of prey-switching to anchovy. Unexpectedly, the stock size of anchovy did not influence the date of prey-switching. The seasonal expansion of the distribution of anchovy was therefore more important than prey abundance in determining prey availability to the auklets. Similarly, the transport timing of herring *Clupea harengus* into the foraging range of Atlantic puffins *Fratercula arctica* in Norway was found to be the primary determinant of prey composition in that system (Durant et al. 2005).

However, it was not just the timing of arrival of warm waters that affected the take of anchovy by auklets in the Japan Sea. Overall, in years of generally warm SST, auklets switched to anchovy earlier than predicted by the Tsushima warm water arrival (Fig. 5). Flow rates and distribution of the Tsushima Current in the Japan Sea are complex and variable (Hase et al. 1999, Nakata & Tanaka 2002). Variability in the meanders and eddies of the warm water mass along the coast of northern Japan (Naganuma 2000) might make anchovy locally available at small scales within the auklets foraging range earlier than predicted by the increase of mean surface temperature.

Atmospheric pressure and degree of mismatch

The spring air temperature, which determined hatching date, and the arrival of warm water within the foraging range, which determined the date of prey-switching, were each affected by different atmospheric pressure patterns. These patterns are not tightly linked, and hence can lead to a mismatch between the date of hatching and the date of prey-switching. When atmospheric pressure over the Arctic Sea and northern Eurasia is lower than normal and that over the northern Aleutian region is higher than normal (Arctic Oscillation; Thompson & Wallace 1998), the eastern Asian winter monsoon is weakened, resulting in warming around the northern Japan Sea in proximity to the auklet colonies (Minobe et al. 2004), the southern Okhotsk Sea, and the northwestern North Pacific overall (Minobe & Nakamura 2004). Higher air pressures over the Pacific Ocean east of Japan, which is associated with northward wind stress over the Tsushima Strait, may enhance the flow of the Tsushima Current in the Japan Sea (Minobe et al. 2004), thus causing an earlier northern expansion of anchovy.

Birds may adjust breeding dates so that they raise dependent offspring when prey availability is highest (Lack 1968). For example, tufted puffins *Fratercula cirrhata* in British Columbia breed later during cold years, which are less productive for their prey, in this case sandlance (Gjerdrum et al. 2003). This adjustment is possible if birds use environmental cues, such as climate signals during winter or spring, to 'predict' the timing of peak prey (Frederiksen et al. 2004). Rhinoceros auklets at Teuri Island were not able to adjust timing of breeding to match the date of anchovy arrival. Correlations between SST in March and warm water arrival date (r = –0.266, n = 16, NS) and between SST in March and SST in June (r = 0.326, n = 17, NS) were weak, suggesting that environmental conditions early in the breeding season do not predict conditions later in the season. The long incubation period of the auklets coupled with this environmental unpredictability apparently makes adjustment of timing of breeding difficult. In addition, snow at Teuri Island makes it more difficult for the auklets to excavate burrows, a problem not encountered by tufted puffins in British Columbia, where the climate is milder (http://climate.weatheroffice.ec.gc.ca). Thus the auklets at Teuri Island are constrained in both burrow excavation and environmental sensitivity, and apparently cannot adjust their timing of breeding as well as related species in other locations.

Long-term trends

Rhinoceros auklets at Teuri Island fed on sardines, herring, and sandlance in the 1980s and mainly on anchovy in the 1990s and 2000s (Fig. 3c, Deguchi et al. 2004a). Accordingly, we found a positive correlation in the proportion of anchovy in the diet during the 18 yr study period (Table 2). Effect of year on the date of prey switching was negative (Table 1). These time trends reflect a recruitment failure of sardine in 1988 to 1991, when a cold-to-warm regime shift occurred in the western Pacific (Watanabe et al. 1995), as well as an increase in the anchovy stock, which may be related to greater productivity or re-distribution.

Because of limited availability of data during the cold regime (3 yr; 1984 to 1987), we cannot determine the relative importance of the effects of this regime shift versus inter-annual climate change. However, correlation maps of surface pressure in relation to the local climate factors that determined the hatching date based on 1950 to 2007 data show similar patterns to those observed during our study period. The effect of air temperature in March on hatching date during 1984 to 1987 seemed to be similar to that during 1992 to 2006 (Fig. 4). These results suggest that the surface pressure pattern may influence the onset of breeding similarly during both cold and warm regimes.

Fitness consequences

In years with high spring air temperatures and a weak Tsushima Current, the mismatch between the hatch date and the date of prey switching to anchovy was most pronounced, and the proportion of anchovy in the diet was smaller. When the auklets' food loads contain only anchovy, they are heavier than when they contain other fish species (Takahashi et al. 2001). As expected, in years when anchovy dominated the diet, food loads were heavier ($r^2 = 0.417$, $n = 18$ years, $p = 0.004$). However, the interannual variation in the energy density of food loads, calculated using published data (sardine, 10.5 kJ g^{-1} (in wet weight); anchovy, 6.3 kJ g^{-1}; 0-year sandlance, 3.8 kJ g^{-1}; 1-year sandlance, 5.5 kJ g^{-1}; 0-year greenling, 4. 8 kJ g^{-1}; herring, 5.8 kJ g^{-1}; other fish, 5.0 kJ g^{-1}; Watanuki 1992, Takahashi et al. 2001), was not related to the amount of anchovy in the diet ($r^2 = 0.047$, $n = 18$ years, not significant).

Thus, in years when anchovy was the primary prey species, auklets brought back heavier food loads, and chick growth rates, fledgling mass, and the number of fledglings produced increased. When 2 outlier years (2000 and 2004) were excluded, the effect of the proportion of anchovy in the diet on the number of fledglings was most apparent (Fig. 8c). Short-term food shortage, and/or prey that are too large during the early stage of chick development, might be critical to chick growth and survival and explain these outliers; this has been suggested for rhinoceros auklets in British Columbia (Vermeer 1980). In addition, precipitation in June negatively affected the number of fledglings (Table 2). Relatively high June precipitation in 2000 (114 mm) and 2004 (61 mm) compared to other years (43 ± 17 mm, 13–82 mm) might also have lowered survival of chicks in these 2 years (Table 2). Thus the mismatch between the hatch date and the date of prey switching apparently affects population processes for rhinoceros auklets at Teuri Island through changes in growth, survival, and fledging mass of offspring.

The amplitude and direction of the effects of local climate on the reproductive success of rhinoceros auklets vary among regions. In British Columbia, rhinoceros auklets hatch earlier and chick growth and survival is lower in years with higher spring SST, presumably because warm spring conditions in this region favor an early peak in the zooplankton biomass, leading to a seasonal mismatch between zooplankton abundance and sandlance, the main prey given to auklet chicks (Bertram et al. 2001, Hedd et al. 2006). In contrast, in California, rhinoceros auklets start breeding earlier and have higher chick survival in years with lower SST, possibly because strong upwelling and cold-water conditions induce high primary and secondary productivity, including 1 of the auklets' main prey (juvenile rockfish, *Sebastes* spp.; Thayer & Sydeman 2007). At Teuri Island, however, low spring air temperatures constrained the date of egg laying more strongly than spring SST, indicating that the physical nesting-ground conditions were more critical than trophic effects. There are no strong upwelling regions in the Japan Sea off Hokkaido (Naganuma 2000), so the transportation of anchovy via the Tsushima Current from the south in summer is the main mechanism determining the period of availability. Thus, local climate factors driven by different surface pressure patterns directly influence the seasonal mismatch of the auklets' hatching date, anchovy availability, and auklet reproductive success. Local marine physical and biological systems should therefore result in local rhinoceros auklet populations having unique responses to climate change.

CONCLUSION

We have shown how large-scale atmospheric surface pressure affects local air temperature and flow rates of the warm Tsushima Current in the Japan Sea. In turn, variations in air temperature and the Tsushima Current can create a seasonal mismatch between the timing of breeding of rhinoceros auklets and the availability of their primary prey, anchovy, in our study region, with reproductive consequences. Such climate-mediated mechanisms vary among regions and populations. Therefore, local relationships must be analyzed and understood before changes in productivity relative to global climate changes can be predicted.

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Seasonal and inter-annual oceanographic changes induce diet switching in a piscivorous seabird

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ABSTRACT: The structure of a marine food web can change quickly within seasons as well as inter-annually in response to physical oceanographic changes. In this study, we examined the relationship between temporal changes in the marine ecosystem of northern Hokkaido, Japan, and diets of rhinoceros auklets *Cerorhinca monocerata* breeding in this region. To obtain an integrated measure of changes in diet composition on short (days) and inter-annual (2004 and 2005) time scales, we used a 2-pronged approach. We examined (1) the diets of adults using stomach contents and stable isotope signatures in tissues, and (2) chick diets using the composition of bill-loads delivered to chicks. During the incubation period, the diet of adults comprised euphausiids (*Thysanoessa longipes* and *T. inermis*). During the chick-rearing period, the diet of adults was age 0 Japanese sandlance *Ammodytes personatus* and age 0 Japan Sea greenling *Pleurogrammus azonus* in the early period, but switched quickly (<10 d) to warm-water-preferring Japanese anchovy *Engraulis japonicus* when the warm Tsushima Current intruded into their foraging range. Adult blood plasma stable isotope ratios reflected these seasonal changes in stomach content. Diets did not differ between age categories. Furthermore, the timing of diet switching to anchovy differed inter-annually, and was about 10 d later in 2005 than 2004, reflecting a difference in the timing of the intrusion of warm water. We conclude that rhinoceros auklets respond sensitively to current-related rapid marine food web changes.

KEY WORDS: Prey switching · Stable isotope signatures · Rhinoceros auklets · Anchovy · Tsushima Current

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INTRODUCTION

The structure of a local marine food web can change quickly both seasonally and inter-annually in response to physical oceanographic changes (i.e. current systems and seasonal upwelling). The resulting seasonal and inter-annual changes in prey availability can then affect the breeding performance of seabirds, which are marine top predators, through trophic effects (Guinet et al. 1998, Kitaysky & Golubova 2000, Durant et al. 2003, Gjerdrum et al. 2003, Boyd et al. 2006, Wanless et al. 2007). Knowledge on how seabirds respond to physical oceanographic changes may shed light on the trophic effects induced by physical oceanographic changes on seabird breeding, one of the driving mechanisms of the population dynamics of marine top predators. To investigate the interaction between seabirds and marine resources, and rapid seasonal and inter-annual ecosystem changes, it is important to collect unbiased information on their diet over short time scales (1 to 3 d).

Previous studies have often surveyed diets provisioned to seabird chicks, as these data are easily collected (Harris & Wanless 1985, Watanuki 1987, Barrett & Furness 1990, Burger et al. 1993, Lewis et al. 2001, Litzow et al. 2002). However, the diets of adults have not been studied as much, since they are difficult to sample without sacrificing the birds (Gaston & Jones 1998). Several studies have suggested that adult seabirds, as central place foragers (Orians & Pearson 1979), feed chicks with large and higher quality prey, such as age >1 (>1+) sandlance or age >1 herring, while adults fed themselves on smaller, more easily collected prey, such as age 0 (0+) sandlance or euphausiids (Gaston & Nettleship 1981, Ydenberg 1994, Butler & Buckley 2002, Wilson et al. 2004). If adults select dif-

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ferent prey types for their chicks and themselves, seasonal and inter-annual oceanographic changes may affect adults and chicks differently. Furthermore, adult diet during egg formation and incubation is likely to be critical in determining the timing of breeding, clutch size, egg quality, and parental body condition in seabirds (Chastel et al. 1995, Oro et al. 1996, Barbraud & Chastel 1999, Gasparini et al. 2007). Thus, prey availability before hatching strongly affects fitness. Therefore, to gain an improved understanding of the relationships between seabirds and marine ecosystems, the diets of adults and chicks should be analyzed throughout the whole breeding season, including the egg-formation and incubation periods.

Sampling of stomach contents by the non-lethal water offloading technique has been done in many species of penguins and procellariiforms that transport food in their stomachs (Wilson 1984, Bost et al. 1994, Cherel et al. 1996), but few studies have been done with alcids that transport food in their bills (Wilson et al. 2004). The stable isotope ratio of blood plasma and egg yolk also provides information on the average trophic level of a bird's diet over a few days to 1 wk, while these tissues were formed (several days before sampling for blood plasma and the egg-formation period for egg yolk), without digestion biases (Hobson 1993, 1995, Hobson & Clark 1993, Hobson et al. 1994, Forero & Hobson 2003). Therefore, integrating information on the stomach contents of adults, stable isotope ratios of blood plasma or that of egg yolk, and bill-loads for chicks should be useful for monitoring the diets of both adults and chicks throughout the breeding season.

In the Sea of Japan, the seasonal northern expansion of the Tsushima Warm Current (Naganuma 2000, Nakata & Tanaka 2002) is believed to have a strong influence on the marine ecosystem during spring and summer. Along the coast of Hokkaido, sea surface temperature (SST) rises from 3°C to 20°C over 4 mo (March to August). As a result, the marine food web changes drastically. For example, a phytoplankton bloom occurs in early spring (Tameishi et al. 1999). In March and April, swarms of spawning euphausiids form at the sea surface when the SST increases to 4°C, and disperse when the SST further increases to 8°C (Hanamura et al. 1989). The distribution of warm-water-preferring Japanese anchovy *Engraulis japonicus* is also affected by the northward expansion of the warm water (Nagasawa & Torisawa 1991). This area therefore provides a suitable system in which to examine the influences of marine food web changes, induced by physical oceanographic changes, on the diets of marine top predators.

The rhinoceros auklet *Cerorhinca monocerata* is a medium-sized (480 to 620 g) alcid that breeds in temperate waters in the North Pacific (Gaston & Jones 1998). It feeds on various pelagic fish species (Thayer & Sydeman 2007). About 291 000 pairs breed on Teuri Island in the northern part of the Sea of Japan (Osa & Watanuki 2002).

The diets of rhinoceros auklet chicks have been repeatedly monitored on Teuri island (Watanuki 1987, Takahashi et al. 2001, Deguchi et al. 2004). It is known that rhinoceros auklets bring back Japanese sandlance *Ammodytes personatus* and Japan Sea greenling *Pleurogrammus azonus* to their chicks early in the chick-rearing period, and then change their prey to Japanese anchovy, which are large and energy-rich, hence important for chicks, in the middle of chick rearing (Takahashi et al. 2001). The timing of arrival of anchovies in the surrounding waters may thus determine chick growth and fledging success of rhinoceros auklets on Teuri Island (Takahashi et al. 2001, Deguchi et al. 2004). However, the diets of adult auklets throughout the breeding season, including the egg-formation and incubation periods, are unknown. Diet during the chick-rearing period could differ between adults and chicks, as suggested by a previous study (Davoren & Burger 1999). Understanding the mechanisms of the short-term seasonal changes in their diet throughout the breeding season could help to clarify the trophic effects of local physical oceanographic changes on seabird breeding.

To investigate the diet of adults and chicks throughout the breeding season of 2004 and 2005, with different seasonal patterns of the Tsushima Current, we analyzed the stomach contents of adults collected by water off-loading; by using the stable isotope ratios (δ^{15}N, δ^{13}C) of adult blood plasma and of egg yolks; and by investigating chick diet as bill-loads. We predicted that adults would feed themselves on small prey species, including euphausiids that are presumably easier to acquire, and that they would switch chick diets from sandlance and greenling to anchovy, which are large and nutritious prey for chicks, when they became available during the summer due to an intrusion of the warm Tsushima Current. The degree and timing of the northern expansion of warm water, which can vary both seasonally and inter-annually, may induce seasonal and inter-annual changes in the local marine food web and influence the prey selection of rhinoceros auklets, a marine top predator.

MATERIALS AND METHODS

Field work. The field work was carried out between late April and late July of 2004 and 2005 on Teuri Island (44° 25′ N, 142° 19′ E), 28 km off Haboro, northern Hokkaido. The rhinoceros auklets breed on the grassy shoulder slopes of the cliffs along the northwest side of the island. Rhinoceros auklets make burrows more than 1 m deep in the soil, lay eggs in early April, incubate until mid-May, and bring back food for chicks from mid-May to late July (Watanuki 1987). Adults change incubation duties almost every night and bring back bill-loads of food for chicks every night (Gaston & Jones 1998, Takahashi et al. 1999).

Every 2 or 3 d, between 19:30 and 21:30 h, 3 to 4 adults coming back to the nesting sites near the Akaiwa lighthouse were captured by hand or with nets. Those having apparent brood patches or those bringing bill-loads were captured to minimize the possibility of capturing non-breeders. Blood and stomach contents were sampled during the incubation period. After chick hatching, bill-loads were also sampled in addition to blood and stomach contents. In this study, the breeding season was separated into the incubation (30 April to 18 May in 2004, 20 April to 12 May in 2005), early chick-rearing (30 May to 2 June in 2004, 23 May to 9 June in 2005), and late chick-rearing (3 June to 20 July in 2004, 11 June to 19 July in 2005) periods.

In 2004 and 2005, 92 and 145 birds were captured, respectively. About 50 ml warm (ca. 35°C) water was introduced into the proventriculus of these birds using a funnel with a 13 mm diameter, 50 cm length elastic tube. The water and stomach contents were flushed into a bucket by gently pushing the belly of the birds. The procedure was repeated at most 3 times until the offloaded water became clear. About 1 ml of blood was sampled from the brachial vein of 24 and 67 birds in 2004 and 2005, respectively, using a heparinized syringe. The blood was kept in 1.5 ml microtubes and brought back to the field station in a cooler box with ice. It was centrifuged at 2000 × *g* for 10 min to separate blood cells and plasma. Blood samples were kept at –30°C. During the chick-rearing period, bill-loads were sampled, identified, and measured at the station, then kept at –30°C.

Ten eggs of rhinoceros auklets were collected from their nests on 20 April 2005, during the egg-laying season. Egg yolks were separated and then kept at –30°C.

Analyses of stomach contents and bill-loads. Stomach samples were drained using 0.33 mm mesh filter in the field station and preserved in 70% 2-propanol. Prey was identified to the lowest taxon level possible using reference vertebrae of fish and identification guides (Nakabo 1993, Chihara & Murano 1997). Among 92 and 145 stomach samples, 81 and 86 samples contained identifiable items in 2004 and 2005, respectively. By referring to the size of vertebrae, 0-year-old (0+) sandlance were separated from >1-year-old (>1+) sandlance. The total length of euphausiids in the stomach contents was measured if possible.

Bill-loads were collected from 62 and 82 adults in 2004 and 2005, respectively. Each prey item was identified to species, and its fork length (fish) or mantle length (squid) and body mass were measured. Sandlance >110 mm in fork length were classified as age >1+ class and those <110 mm were the 0+ age class, and Japan sea greenling <180 mm were classified as the 0+ age class (Takahashi et al. 2001, Ishikawa & Watanuki 2002). Anchovies were all >130 mm and mature so we did not classify the anchovies into age classes.

Analyses of stable isotope ratios. The $\delta^{15}N$ and $\delta^{13}C$ of blood plasma (samples in 2004 and 2005), egg yolk (sampled only in 2005), and those of potential prey including the euphausiid *Thaysanoessa inermis*, squid Coleoides, 0+ and >1+ sandlance *Ammodytes personatus*, and 0+ Japan Sea greenling *Pleurogrammus azonus* were measured following Hobson (1993). Euphausiids were sampled by bongo net (0.33 mm mesh aperture, 60 cm mouth diameter) in the surrounding water on 10 May 2003 by the RV 'Tankai Maru' (National Fisheries Research Institute, Fisheries Research Agency). Other prey items were collected from bill-loads in 2004 and 2005.

Blood plasma and egg yolks were dried at 60°C in an electric oven for 24 h, then ground to a powder. Euphausiids, 0+ sandlance, >1+ sandlance, 0+ greenling, anchovy, and squid were minced, dried, and ground similarly. Lipids were extracted from prey tissues using a chloroform:methanol (2:1) solvent rinse and then dried at 60°C for 24 h to remove any residual solvent. Extraction of lipids was not necessary for blood samples because the lipid component in blood is generally low (Deuel 1955). Samples were kept at –30°C before stable isotope analyses.

Stable carbon and nitrogen compositions of the samples were determined using a mass spectrometer (MAT 252, Finnigan MAT) coupled online via a Finnigan ConFlo II interface with an elemental analyzer (EA 1110, ThermoQuest). Subsamples (1 mg) of homogenized materials were loaded into tin cups and combusted at 1000°C. The resultant CO_2 and N_2 gases were then analyzed. Pee Dee Belemnite (PDB) collected in South Carolina, USA, and atmospheric N_2 were used as standards following Hobson (1993). Stable isotope concentrations were expressed in δ notation as parts per thousand according to the following equation:

$$\delta^{15}N \text{ or } \delta^{13}C = [(R_{\text{sample}}/R_{\text{standard}}) \times 1] \times 1000 \qquad (1)$$

where R = the corresponding ratio $^{13}C/^{12}C$ or $^{15}N/^{14}N$. R_{standard} for ^{13}C and ^{15}N is that for PDB and atmospheric N_2 standard, respectively. Calcium or sodium carbonate for $\delta^{13}C$ and high-purity N_2 gas for $\delta^{15}N$ were also used as working standards during isotope measurements. The analytical precision (±SD) of these measurements is estimated to be ±0.1‰ for carbon and ±0.3‰ for nitrogen.

Stable isotope enrichment factor in plasma and egg yolk. We estimated the trophic level of adult rhinoceros auklets assuming that the enrichment factor in adults was the same as that in chicks. To determine the enrichment factor of carbon and nitrogen in the blood plasma in chicks, we collected 3 eggs and hatched these in an incubator (P-008A, Syowa Furanki), and then fed chicks with 60 g >1+ sandlance every day until fledging (45 to 50 d old). Blood samples were collected at 40 d of age. δ^{13}C and δ^{15}N were –18.7‰ and 13.7‰ for blood plasma and –17.4‰ and 10.9‰ for diet, respectively. Therefore, enrichment factors were –1.3‰ and 2.8‰ for δ^{13}C and δ^{15}N, respectively.

Enrichment factors differ among different types of bird tissues (Hobson & Clark 1992a,b, Hobson 1995). To allow the comparison of analyses of several types of bird tissue, stable isotope ratios in each tissue were modified by the enrichment factor of their tissues (e.g. Hobson et al. 1994). Thus, to compare stable isotope ratios in blood plasma and egg yolk, stable isotope ratios in egg yolk (x) were adjusted using the enrichment factor of blood plasma (y) and that of egg yolk (z) (adjusted value: egg yolk = $x - z + y$). The enrichment factor for egg yolk in rhinoceros auklets was unknown, so we used the average enrichment factor in lipid-free egg yolk of 6 avian species (δ^{13}C: 0.1‰, δ^{15}N: 3.4‰; Hobson 1995).

Sea surface temperature. As the local SSTs around the northern Sea of Japan, we used the daily SSTs based on satellite data (AVHRR sensor on the NOAA satellite and AMSR-E sensor on the AQUA satellite, analyzed by the Japan Meteorological Agency, available in the NEAR-GOOS database, JODC: http://near-goos1.jodc.go.jp/index.html). Daily SSTs at the southern edge of the foraging range of rhinoceros auklets (western Shiribeshi rigion), that around Teuri Island (northern Rumoi region), and that at the northern edge of the foraging range of auklets (Soya region), and mean daily SSTs (satellite data) in the area shown in Fig. 5A–C, were obtained from the Hakodate Marine Observatory (www.data.kishou.go.jp/kaiyou/db/hakodate/finesstHK/finesstHK.html).

Statistics. The daily patterns of prey occurrence during the chick-rearing period were compared between 2 age classes, chicks and adults, using the Kolmogorov-Smirnov test for each prey item. The occurrence of 0+ sandlance, >1+ sandlance, greenling, and anchovy between the stomach contents and bill-loads during the chick-rearing period was compared by a chi-squared test. The δ^{15}N and δ^{13}C were compared among seasons (egg-formation period: adjusted value of egg yolk, incubation period: blood plasma, early chick-rearing and late chick-rearing period: blood plasma) and years using 1-way analysis of variance (ANOVA) with Scheffé's post hoc test.

We defined the date of the prey switching as the date when 50% of the auklets brought and fed on anchovy. To determine the date of prey switching, we used logistic regression analyses. Each bill-load and stomach was assigned to 'anchovy' (1) if it contained anchovy or 'non-anchovy' (0) if it did not (Fig. 1). The same analysis to define the date of prey switching was also conducted for euphausiids, assigned as 'euphausiid' (1) or 'non-euphausiid' (0) (Fig. 1). Among all bill-loads, 95.8% consisted of a single prey species and 4.2% consisted of 2 prey fish species. Among all stomachs, 91.1% contained only a single prey species. Thus bill-loads and stomach contents were easily assigned to anchovy and non-anchovy or euphausiid and non-euphausiid. For these analyses, the dates of sampling were calculated from 1 April. The date of prey switching was calculated from the regression equations. StatView (ver. 5.0, SAS) was used for all statistical analyses.

RESULTS

Seasonal changes of adult and chick diets

Adult auklets fed on euphausiids only during the incubation period in both 2004 and 2005. In 2004, *Thysanoessa longipes* (no measurable individual was included) were found in stomach contents, and in 2005, *T. inermis* (32 to 35 mm in total length, n = 8) were found. During the early chick-rearing period, adults fed themselves on various fish species (squids, 0+ sandlance, >1+ sandlance, 0+ Japan Sea greenling) and then switched to anchovy (Table 1). In bill-loads for chicks, squids (6.7 ± 2.9 g, 89.5 ± 19.1 mm), 0+ sandlance (0.7 ± 0.5 g, 59.3 ± 8.6 mm), 0+ Japan Sea greenling (7.3 ± 4.9 g, 97.9 ± 21.6 mm), and anchovy (23.8 ± 4.8 g, 137.7 ± 6.8 mm) were found both in 2004 and 2005 (Table 1).

During the chick-rearing period, there were no significant differences in the occurrence of 0+ sandlance, greenling, and anchovy between adult and chick diets (χ^2-test: 2004, χ^2 = 0.30, p = 0.86; 2005, χ^2 = 3.30, p = 0.19, Table 1). The daily patterns of the occurrence of prey items in adult and chick diets also did not differ significantly (Table 2).

Among stomach samples of parents that provided bill-load samples, 61 contained identifiable prey items both in 2004 and 2005. Most stomach samples and bill-loads comprised a single prey species. One of 62 bill-loads and 4 of 61 stomach samples contained more than 2 prey species in 2004, and 5 of 82 bill-loads and 3 of 61 stomach samples contained more than 2 prey species in

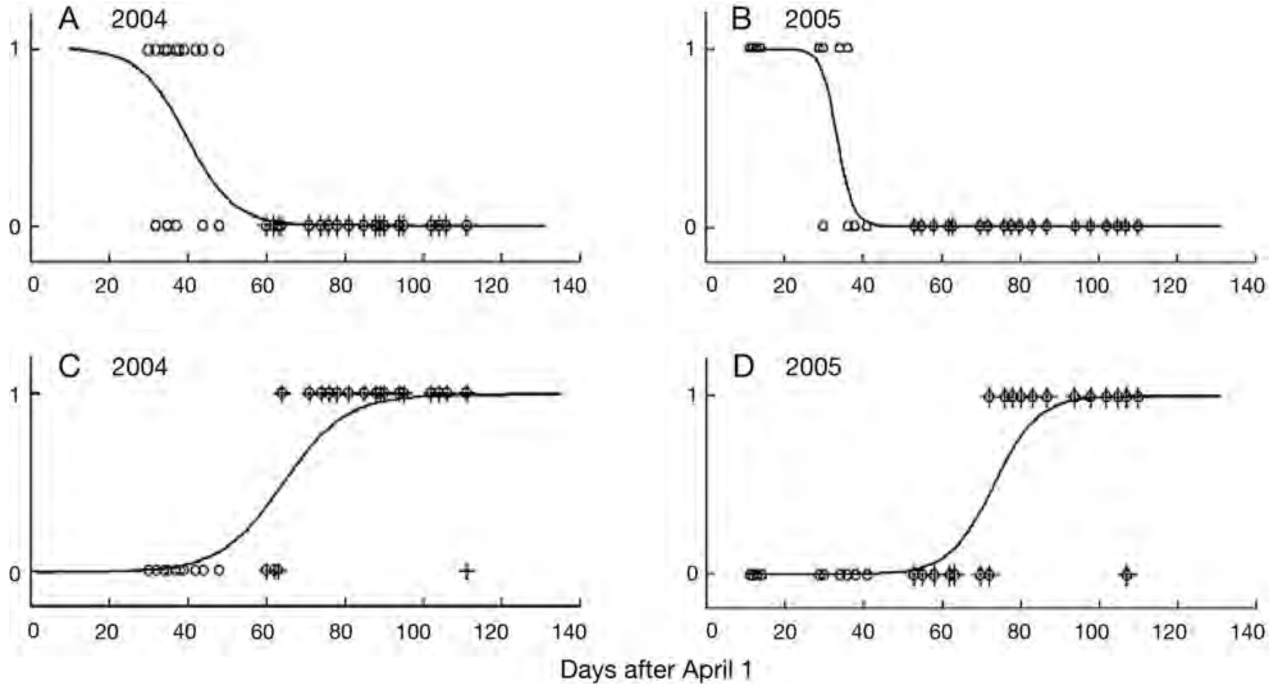

Fig. 1. *Cerorhinca monocerata.* Seasonal change in the occurrence of euphausiids and anchovy from stomachs and bill-loads of auklets in 2004 and 2005. Date of sampling was calculated from 1 April. (A,B) Occurrence of euphausiids (designated as 1) and that of non-euphausiids (designated as 0) in stomachs (○) and bill-loads (+) . (C,D) Occurrence of anchovy (1) and that of non-anchovy (0) in stomachs (○) and bill-loads (+). Logistic regressions are all significant and are shown as thin lines

2005. In 58 of 61 birds, bill-loads and their stomach samples contained the same prey species, both in 2004 and 2005, indicating that parents fed themselves on the same prey as they provided for their chicks.

As seasonal patterns in the occurrence of prey types in bill-loads and stomachs were quite similar, these were combined to determine the timing of prey switching. During the incubation period, parents switched from euphausiids to non-enphausiids on Day 33 (3 May) in 2004 and Day 39 (9 May) in 2005 (Fig. 1). During the chick-rearing period, parents switched prey to anchovy on Day 65 (4 June) in 2004 and on Day 75 (14 June) in 2005 (Fig. 1). The duration between the time when anchovy first appeared in bill-loads and the time when 50% of parents brought back anchovy was only 8 d in 2004 and 10 d in 2005 (Fig. 1).

Table 1. *Cerorhinca monocerata*. Percentage occurrence of each prey item found in adult stomachs and bill loads for chicks in 2004 and 2005

Stage	Euphausiid		0+ Sandlance		>1+ Sandlance		Greenling		Squid		Anchovy		Sample size	
	Bill load	Stomach	Bill load	Stomach	Bill load	Stomach	Bill load	Stomach	Bill load	Stomach	Bill load	Stomach	Bill load	Stomach
2004														
Incubation	–	61.9	–	19.0	–	9.5	–	14.3	–	14.3	–	0.0	–	21
Early chick rearing	0.0	0.0	87.5	87.5	0.0	0.0	12.5	25.0	12.5	37.5	0.0	0.0	8	8
Late chick rearing	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	94.4	100.0	54	53
2005														
Incubation	–	64.0	–	4.0	–	24.0	–	4.0	–	12.0	–	0.0	–	25
Early chick rearing	0.0	0.0	25.7	22.2	0.0	11.1	71.4	66.7	2.9	11.1	0.0	0.0	35	18
Late chick rearing	0.0	0.0	6.4	4.7	0.0	0.0	0.0	0.0	0.0	2.3	93.6	95.3	47	43

Table 2. Results of a Kolmogorov-Smirnov test with the daily patterns of prey occurrence between 2 age categories during the chick-rearing period. There were no significant differences in the daily patterns of prey occurrence between the age categories

	2004		2005	
	D	p	*D*	p
Greenling	0.05	>0.99	0.22	0.77
0+ sandlance	0.00	>0.99	0.17	0.96
Anchovy	0.05	>0.99	0.11	>0.99

Stable isotope ratio in adult blood plasma

Stable isotope ratios changed seasonally. Blood plasma δ^{15}N was greater in the late chick-rearing period than in the incubation period in 2004 (Fig. 2, ANOVA: $F_{1,19} = 16.6$, $p < 0.01$). Sample size in the early chick-rearing period in 2004 was too small (n = 3) for statistical analysis. Similarly, blood plasma δ^{15}N was greater in the early and late chick-rearing period than the incubation period and the adjusted δ^{15}N of egg yolk in 2005 (Fig. 2, ANOVA with Scheffé's test: $F_{3,73} = 81.6$, $p < 0.01$). In 2004, blood plasma δ^{13}C did not differ between the incubation and the late chick-rearing periods (Fig. 2, ANOVA: $F_{1,19} = 0.28$, $p = 0.61$). In 2005, blood plasma δ^{13}C during the incubation and early chick-rearing periods was higher than in the egg-formation and late chick-rearing periods (Fig. 2, ANOVA with Scheffé's test: $F_{3,73} = 60.3$, $p < 0.01$).

There were inter-annual differences in the stable isotope ratios. Although blood plasma δ^{15}N did not differ between 2004 and 2005 (Fig. 2, ANOVA: incubation period, $F_{1,35} = 5.64$, $p = 0.34$, late chick-rearing period, $F_{1,33} = 0.47$, $p = 0.53$), blood plasma δ^{15}C was higher in 2005 than 2004 (Fig. 2, ANOVA: incubation period, $F_{1,35} = 11.55$, $p < 0.05$, late chick-rearing period, $F_{1,33} = 10.15$, $p < 0.05$).

DISCUSSION

Diet as determined by stomach contents, stable isotope ratios, and bill-loads

Diet information based on stomach contents are often biased due to rapid digestion of soft-bodied prey (e.g. crustaceans, Bradstreet 1980) and the long retention of hard body parts (e.g. squid beaks, Wilson et al. 1985). Extrapolated from the retention time in the black guillemot *Cepphus grylle* and Atlantic puffin *Fratercula arctica* (2.7 to 3.8 h, Hilton et al. 2000), the stomach contents of the rhinoceros auklets collected on their arrival in the evening may reflect the food ingested about 3 to 4 h before sunset. In general, euphausiids and fish make diurnal vertical migrations to depths of between 30 and 100 m (Beamish 1965, Scott & Scott 1988, Iguchi & Ikeda 2004), and hence they may only be available during a limited time of the day for rhinoceros auklets, which have a maximum dive depth of 52 to 57 m (Kato et al. 2003, Kuroki et al. 2003). Thus, prey found in the stomach samples can be biased.

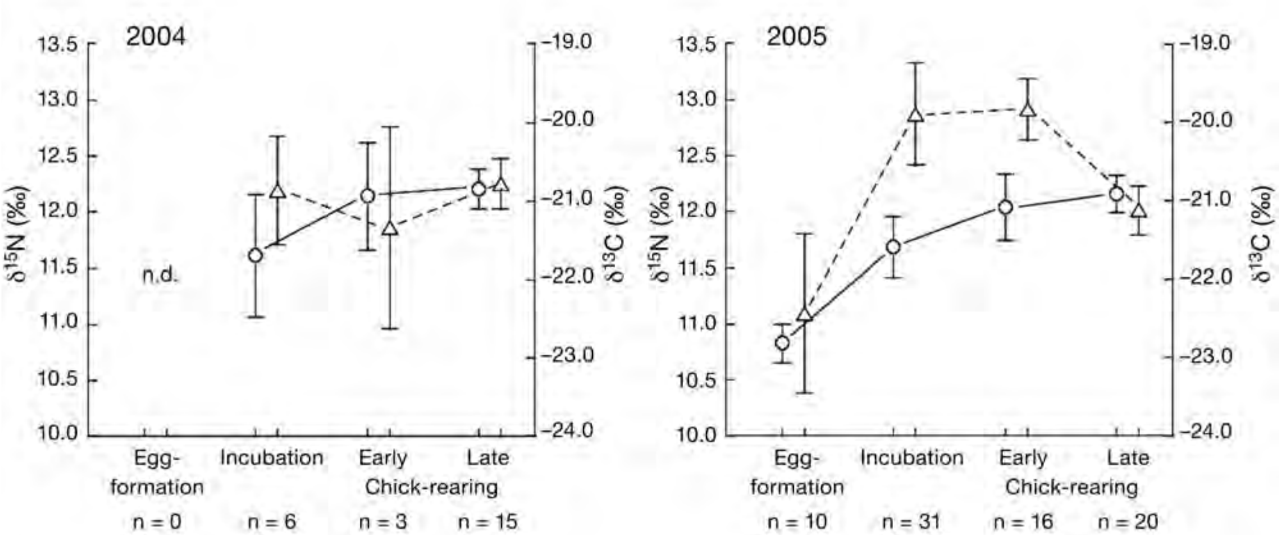

Fig. 2. *Cerorhinca monocerata.* Changes in the blood plasma δ^{15}N (○) and δ^{13}C (△) between incubation period, early chick-rearing period, and late chick-rearing period in 2004 and 2005. Data are means ± 1 SD. Sample sizes (number of birds) are shown below the *x*-axis. δ^{15}N (○) and δ^{13}C (△) in the egg-formation period (egg yolk, x) in 2005 were adjusted by the enrichment factor of blood plasma (y) and that of egg yolk (z) (adjusted value; egg yolk = $x - z + y$) to compare to the stable isotope ratio of blood plasma in other periods

When the enrichment factor for blood plasma (–1.3‰ and 2.8‰ for δ^{13}C and δ^{15}N, this study) and that for egg yolk (0.1‰ and 3.4‰ for δ^{13}C and δ^{15}N, Hobson 1995) were subtracted from the measured stable isotope values, blood plasma stable isotope values reflected the prey species found in the stomach contents (Fig. 3). Low δ^{15}N in the egg yolk in 2004 indicated that rhinoceros auklets had fed mainly on euphausiids during the egg-formation period (Figs. 2 & 3). The δ^{15}N of blood plasma was lower during the incubation period, when the adults fed on fish and euphausiids, than during the chick-rearing period, when they fed only on fish (Fig. 2). The adjusted blood plasma stable isotope values (Fig. 3) appeared to be close to those of 0+ sandlance in early chick rearing, and close to the mean value of 0+ sandlance and anchovy in late chick rearing in 2004. In 2005, stable isotope values were between the values of 0+ sandlance and 0+ greenling during early chick rearing and closest to that of anchovy during late chick rearing.

The δ^{13}C values of 0+ sandlance and 0+ greenling were higher in 2005 than in 2004 (Fig. 3). This explains the higher blood plasma levels of δ^{13}C in 2005 than 2004. For example, in the Bering Sea, inter-annual variations of δ^{13}C in the marine food web were found in the late 1990s (Schell et al. 1998, Brodeur et al. 2002). These changes in δ^{13}C in the Bering Sea may be caused by changes in the pattern of primary production, especially coccolithophore blooms with high δ^{13}C ratios (Napp & Hunt 2001, Stockwell et al. 2001), as suggested by Brodeur et al. (2002). No data on the patterns of primary production in our region were available, although the inter-annual difference in patterns of primary production (possibly not by coccolithophore blooms in our region) may be the cause of the inter-annual difference in δ^{13}C in auklets and prey species. The overall agreement of the prey composition, as estimated by stomach sampling and blood stable isotope ratios, thus suggests that the stomach samples were not particularly biased on average, and thus can be useful in assessing adult diet.

Differences in adult and chick diets provide a potential impediment to assessing the relationship between oceanographic change and seabird breeding status. Adults of thick-billed murres *Uria lomvia*, common murres *U. aalge*, black guillemot, rhinoceros auklets in Canada, roseate terns *Sterna dougallii*, and Arctic terns *S. paradisaea* feed on smaller and lower quality prey that are easy to collect for their own consumption, but feed chicks with large, high quality prey (Gaston & Nettleship 1981, Davoren & Burger 1999, Ramos 2000, Butler & Buckley 2002, Hatch 2002, Wilson et al. 2004). However, we found that the differences in prey species for adults and chicks were not significant in rhinoceros auklets on Teuri Island. These differences, i.e. whether the diet of adults and chicks are similar, may reflect regional differences in prey availability or differences in how fish are carried in the bill. Single-prey loaders, such as murres and terns, bring back a single prey item in their bill on each trip, whereas multiple-prey loaders such as puffins and rhinoceros auklets bring back multiple prey items per trip. Prey selection might be more

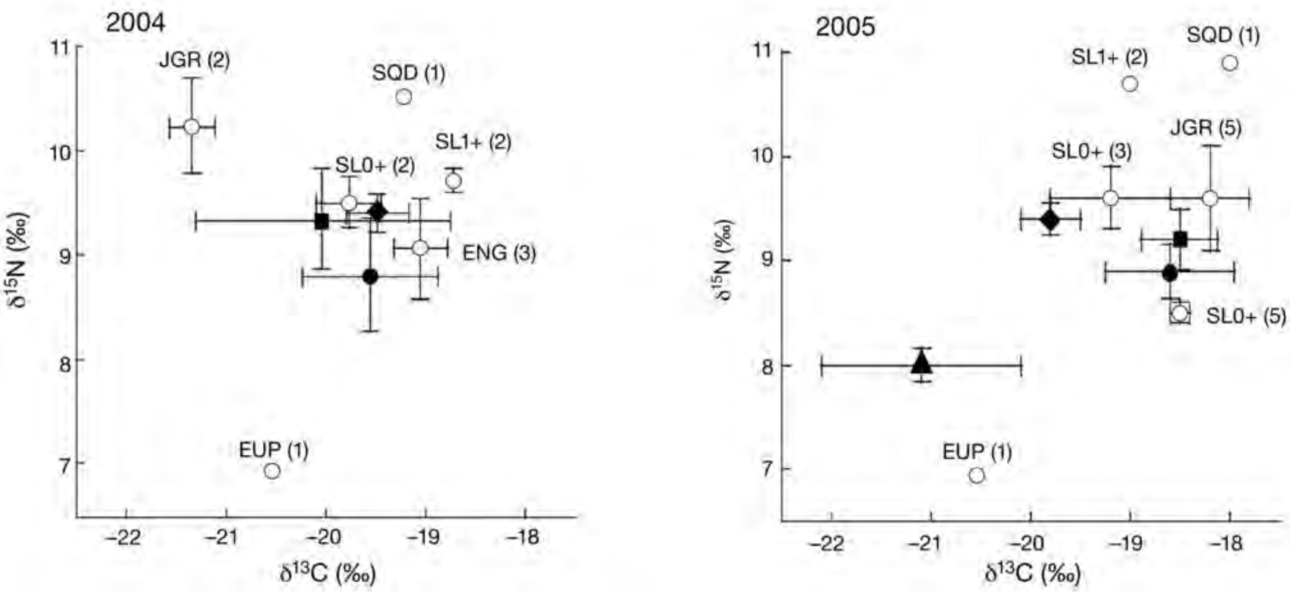

Fig. 3. Adjusted δ^{15}N and δ^{13}C of egg yolk (▲) and those of blood plasma during incubation (●), early chick-rearing (■), and late chick-rearing period (◆) in 2004 and 2005. Stable isotope ratios of prey (SL0+: 0+ sandlance, SL1+: >1+ sandlance, JGR: greenling, SQD: squid, ENG: anchovy) collected in 2004 and 2005 are also shown (○). Euphausiids (EUP) were collected only in 2003, and their stable isotope ratios are shown in both panels. Data are means ±1 SD. Sample sizes are on the symbols

sensitive in single-prey loaders, since adults must select 1 large fish to maximize their food load (Wilson et al. 2004). Although the reasons remain unknown, the diets of adults and chicks of rhinoceros auklets in our region showed similar seasonal and inter-annual changes, and presumably reflect the strong influence of marine environmental change.

Seasonal and inter-annual changes in diet and the marine environment

Only a single study to date has reported euphausiids in the stomachs of adult rhinoceros auklets during the non-breeding season (Ainley & Sanger 1979). Our study is the first to demonstrate that 'piscivorous' rhinoceros auklets may feed on substantial quantities of euphausiids during the early breeding season, i.e. during the egg-formation and incubation periods. This finding was similar to the result that tufted puffin *Fratercula cirrhata*, a closely related 'piscivorous' seabird, forages for a lower trophic diet before chick hatching (Williams et al. 2008). Diets during egg formation and incubation may determine the timing of breeding, clutch size, or egg quality and parental body condition in seabirds (Chastel et al. 1995, Oro et al. 1996, Barbraud & Chastel 1999, Gasparini et al. 2007), and consequently affect reproductive success. Sorenson et al. (2009) reported that Cassin's auklet *Ptychoramphus aleuticus* laid larger eggs earlier and had higher fledging success in years when females fed on lower trophic level crustaceans than in years when females fed on higher trophic level fish. One of the possible benefits to seabirds of eating crustaceans such as euphausiids might be the intake of carotenoids. Carotenoids are widely used by animals as red and yellow pigments (Møller et al. 2000), but are also hypothesized to enhance antioxidant activity and immune function (Chew 1996, Blount et al. 2002). Euphausiids contain large quantities of carotenoids (Fisher et al. 1955) that accumulate in seabird eggs through trophic effects (Blount et al. 2002). Our study suggests that euphausiids, which are lower trophic level crustaceans and highly seasonal in the northern Sea of Japan, could be an important factor in the breeding performance of rhinoceros auklets. Thus, the dynamics of euphausiid stocks and whether the birds time their egg-laying to match euphausiid blooms appear to have a critical effect on seabird populations.

We predicted that parents would select euphausiids, perhaps the prey easiest to collect, not only during egg formation and incubation, but also during chick rearing, for themselves. However, in this study, during the incubation period, rhinoceros auklets switched their prey from euphausiids to fish and did not feed on euphausiids during the chick-rearing period. In the Arctic, sub-Arctic, and Antarctic regions, euphausiids are available at the sea surface throughout the summer, coinciding with the seabird breeding season (e.g. Coyle & Cooney 1993, Everson 2000, Coyle 2005). In the Bering Sea, many seabirds forage for euphausiids during the summer (Gaston & Jones 1998, Brooke 2004, Hunt et al. 2008). On the other hand, in the temperate regions such as the sea around Japan, including the study area, euphausiids are available at the sea surface for only a short period in the early spring, since they descend to deep, cool water when the surface water temperature increases in the summer (Endo 1984, Hanamura et al. 1989, Iguchi & Ikeda 2004). The euphausiids *Thysanoessa longipes* and *T. inermis*, the main prey of auklets in the early spring in this study, are found at the sea surface (less than 30 m deep) in the northern part of the Sea of Japan only in March and April (Hanamura et al. 1989, Iguchi & Ikeda 2004). In the waters around Teuri Island, *T. inermis* forms dense spawning swarms at the sea surface in the early spring, and then descends to deeper water (>100 m) in the summer when the SST rises to over 8°C in May (Hanamura et al. 1989), becoming unavailable to rhinoceros auklets. Seasonal changes in SST during early spring around the colony in 2004 and 2005 were consistent with the timing of the auklet diet switching: the shift from euphausiid to non-euphausiid prey coincided with the date that SSTs in the auklets' foraging range rose above 8°C, i.e. Days 40 to 55 (10 to 25 May) (Figs. 1, 4 & 5). In addition, euphausiid species differed between 2004 and 2005. In 2004, all identifiable euphausiids were *T. longipes*. In contrast, in 2005, all euphausiids were *T. inermis*. This latter species is the dominant spawning swarm-forming euphausiid around Teuri Island in March to April (Hanamura et al. 1989) and hence is fed on by many species of seabird (e.g. black-tailed gull *Larus crassirostris*, Tomita et al. 2009). However, in 2004, the total catch of *T. inermis* in commercial fisheries around Teuri Island was less than 20% of that in normal years (N. Tomita unpubl.), suggesting a shortage *of T. inermis*. We believe that *T. longipes* might have been fed on by auklets during the egg-formation and incubation periods as an alternative prey, due to a shortage of *T. inermis*, the ordinarily dominant euphausiid, during 2004.

During the chick-rearing period, adult auklets fed themselves and their chicks 0+ sandlance and 0+ greenling for the first couple of weeks, and then switched to anchovy. The Japan sea greenling is a cold-water fish inhabiting the Sea of Japan off Hokkaido. It spawns around Rishiri Island, Rebun Island, and Musashi Bank (60 to 90 km north of Teuri Island) in winter, after which 0+ greenling move to the Okhotsk Sea in June when the SST rises (Shimazaki & Kyushin

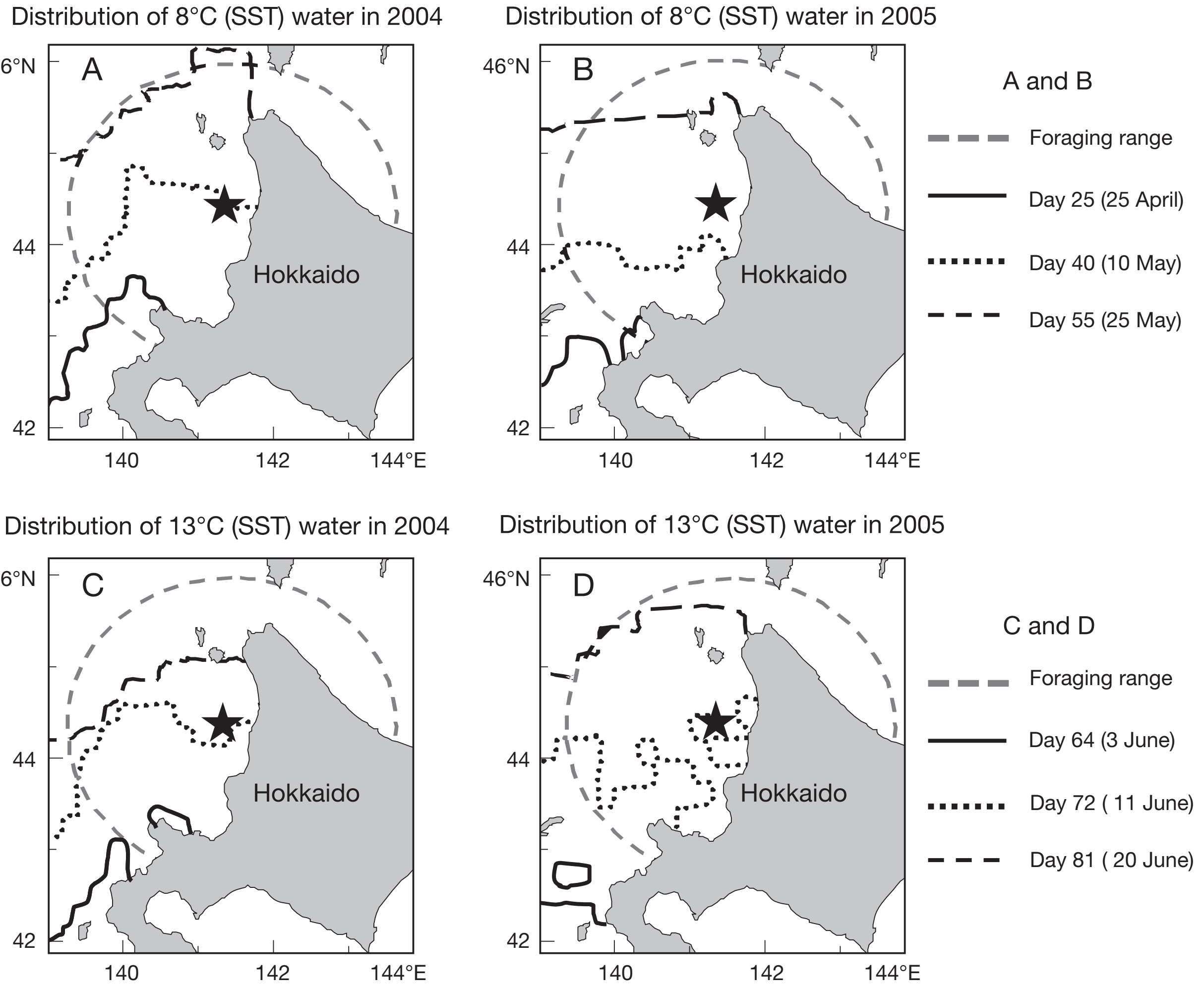

Fig. 4. Northward expansion of the distribution of 8°C and 13°C SST. (A,B) Boundary of the 8°C water on Day 25 (25 April, the day euphausiids mainly appeared in stomachs of auklets both in 2004 and 2005; solid line), on Day 40 (10 May, approximate timing of diet switching from euphausiids to other fish species in 2004 and 2005; dotted line), and Day 55 (25 May, dashed line) in 2004 and 2005. (C,D) Boundary of the 13°C water on Day 64 (3 June, the day anchovy first appeared in bill loads in 2004; solid line), on Day 72 (11 June, the day anchovy first appeared in bill loads in 2005; dotted line), and Day 81 (20 June, broken line) in 2004 and 2005. Data, analyzed by the Japan Meteorological Agency, were obtained from the NEAR-GOOS data base, JODC: http://near-goos1.jodc.go.jp/index.html. Broken gray circle shows the potential maximum foraging range of rhinoceros auklets (164 km; Kato et al. 2003). ★: Teuri Island

1982, Nagasawa & Torisawa 1991). 0+ sandlance are heavily harvested by commercial fisheries in April to June around the shore areas in Hokkaido, including Teuri Island (Nagasawa & Torisawa 1991). Sandlance move shorter distances than greenling, although they also move to northern areas when the SST rises in summer (Department of Fisheries and Forestry in Hokkaido 2004). Therefore, as the SST increases during the chick-rearing period (Figs. 4 & 5), the availability of those fish species may decrease. In contrast, in the coastal area of Hokkaido, the anchovy is a warm-water species that appears in water with an SST of 12 to 15°C (Mihara 1998). The availability of anchovy may therefore increase with the seasonal increase in SST around Teuri Island. The maximum potential foraging range of rhinoceros auklets breeding on Teuri Island can be assumed to be 164 km from Teuri Island (Kato et al. 2003, see Fig. 4). The timing of prey switching to anchovy in 2004 and 2005 was consistent with the time that the 13°C SST water arrived at the southern edge of their maximum foraging range (Figs. 4 & 5). Furthermore, the timing of the switch to anchovy differed between the 2 years, i.e. Day 65 (4 June) in 2004 and Day 75 (14 June) in 2005, 10 d later in 2005 than 2004. The strength of the Tsushima Current in the Sea of Japan (monthly anomalous flow rate of Tsushima Current in the Japan Sea coast off Maizuru, central Sea of Japan) during May to June was approximately 57%

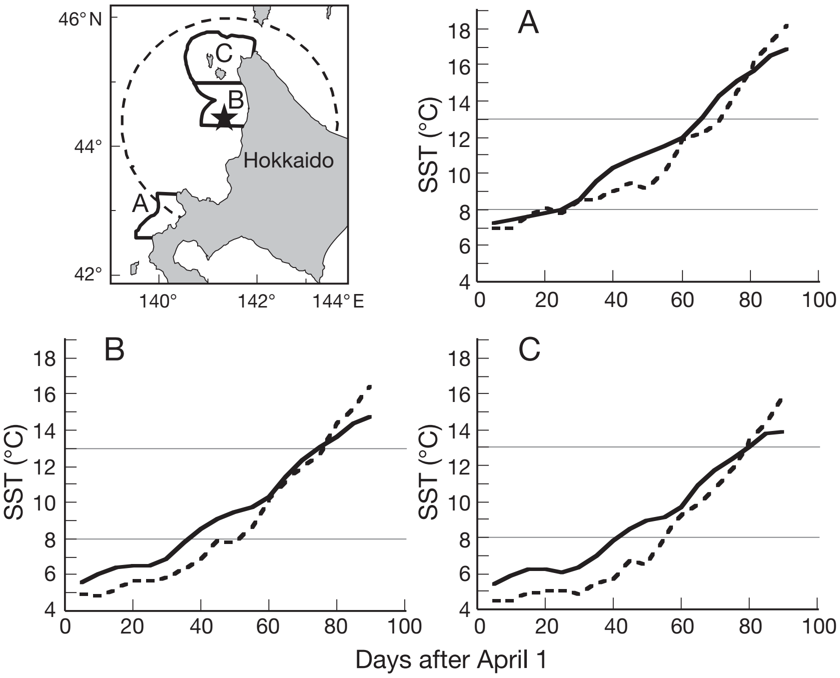

Fig. 5. Daily changes of SSTs (A) at the southern edge of the foraging range of rhinoceros auklets (western Shiribeshi region), (B) around Teuri Island (northern Rumoi region), and (C) at the northern edge of the foraging range of auklets (Soya region), and mean daily SSTs (satellite) in the area shown in the map. Data in (A), (B) and (C) were obtained from the Hakodate Marine Observatory (www.data.kishou.go.jp/kaiyou/db/hakodate/finesstHK/finesstHK.html). Sampling date was calculated from 1 April. Solid (dotted) line shows SSTs in 2004 (2005). Thin horizontal lines show the SSTs 8°C (indicator of euphausiid dispersal) and 13°C (indicator of anchovy arrival). ★: Teuri Island

stronger in 2004 than 2005 (Japan Meteorological Agency: www.data.kishou.go.jp). The cooler SST in 2005, compared to that in 2004, during the breeding season (Fig. 5) also indicates a stronger flow rate of the Tsushima Current during 2004. This would be the reason for the annual differences of the timing of auklets switching prey to anchovy. Anchovy is the most energy-rich diet for auklet chicks in this region (Takahashi et al. 2001), therefore the auklets switched their diet for both themselves and their chicks when anchovies became available around their colony. Further, parents may switch their prey to anchovy as quickly as possible, since anchovy is a highly nutritious diet for their chicks (Takahashi et al. 2001). In this study, parents switched to anchovy (0 to >50% occurrence) within only 8 d in 2004 and within 10 d in 2005 (Fig. 1). These switching speeds were faster than the intrusion speed of the Tsushima Current, which was extrapolated from daily changes in SST within the foraging range of auklets (Fig. 5). Parents may actively focus their foraging efforts in areas where anchovies are first available when they arrive within the maximum foraging range of the auklets.

In conclusion, quick switching in adult diets from euphausiids to fish species and then in both adult and chick diets to anchovy was consistent with the seasonal and inter-annual changes in the arrival of warm water. The current-related rapid change in the local marine food web structure appears to induce drastic changes in the trophic condition of the rhinoceros auklet and forces an active response with respect to foraging behavior and prey selection; it might consequently affect the breeding output of auklets. Hence, this study also suggests the potential usefulness of using the prey switching of rhinoceros auklets, a highly mobile marine top predator, as a sensitive indicator of local marine environmental change. Furthermore, our study is the first to shed light on the diet during the egg-formation and egg-laying periods, among the most important periods that determine breeding output, in rhinoceros auklets, which in turn helps to understand the interactions between population dynamics of marine top predators and local and global-scale oceanographic changes.

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Defining spring transition: regional indices for the California Current System

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ABSTRACT: While the physical and ecological importance of the spring transition in the California Current System (CCS) is well recognized, there is no widely agreed upon metric for tracking the phenomenon. Most metrics reflect oceanographic events of the northern CCS; few pertain to southern regions. Our goal was to compare 2 commonly used methods for identifying spring transition in the CCS that use data on wind-driven upwelling and coastal sea levels to 2 newly developed methods that use data on sea levels as well as satellite-derived sea-surface temperatures (SSTs). More specifically, we assessed whether methods typically used in northern regions of the CCS could be applied to other regions. To demonstrate the biological implications of those methods, we evaluated relationships between timing of spring transition and recruitment of 2 groundfish species, Pacific ocean perch *Sebastes alutus* and sablefish *Anoplopoma fimbria*. Our results suggest that while dramatic changes in wind-derived upwelling and coastal sea levels consistently indicate spring transition in the northern CCS, this is not the case for central and southern regions. In those regions, spring transition may be better represented by the rate of change in sea levels and/or changes in spatial patterns of SSTs. Only metrics based on wind-driven upwelling and sea levels were related to groundfish recruitment; when transitions in upwelling winds and sea levels were delayed, recruitment tended to be poor. We advise caution when identifying dates of spring transition and applying them to analyses of ecological phenomena; a combination of several methods may be required to reveal the multidimensional physical and biological changes that occur during that transition.

KEY WORDS: Spring transition · California Current · Bakun upwelling · Sea levels · Sea-surface temperatures · Groundfish recruitment

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INTRODUCTION

The transition from winter to spring ocean conditions over the shelf and slope portions of the California Current System (CCS) is characterized by a shift in circulation, stratification, and biological habitat. The Aleutian low-pressure system weakens and is displaced northward by the North Pacific high-pressure cell (Strub et al. 1987, Strub & James 1988, Schwing et al. 2006), regional winds and alongshore currents shift from predominantly northward to southward (Huyer et al. 1979), coastal sea level drops, nutrients are upwelled to the euphotic zone (Huyer et al. 1979), primary productivity increases (Lynn et al. 2003, Thomas & Brickley 2006), and winter zooplankton communities over the shelf are replaced by spring/summer communities (Peterson & Keister 2003, Hooff & Peterson 2006; Fig. 1). Delays in spring transition have also been associated with poor survival of higher trophic-level organisms, such as coho salmon (Logerwell et al. 2003), fewer colonizations of new habitat by the common murre *Uria aalga* (Zador et al. 2009), and reduced reproductive success of mussels, rockyshore barnacles (Barth et al. 2007), groundfish (e.g. Pacific ocean perch; Holt & Punt in press), and seabirds (e.g. the planktivorous auklet *Ptychoramphus aleuticus*; Sydeman et al. 2006). While the physical and ecological importance of the spring transition has been embraced by many, there is no widely agreed upon metric for tracking the phenomenon (Kosro et al. 2006).

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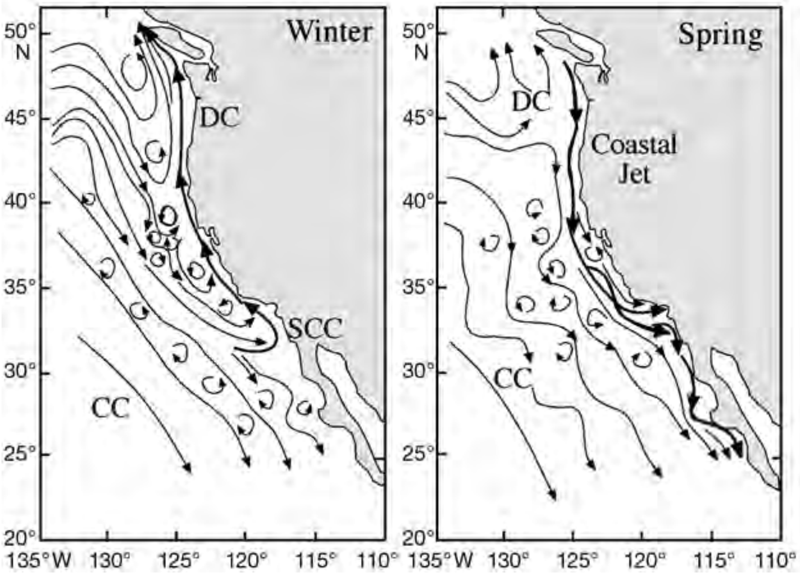

Fig. 1. Seasonal variation of large-scale and coastal currents in the California Current System (adapted with permission from Hickey & Royer 2001, originally from Strub & James 2000). CC: California Current, DC: Davidson Current, SCC: Southern California Countercurrent

Most indices of spring transition date reflect physical and biological phenomena of the northern CCS; few pertain to southern regions. The switch from downwelling-favorable winter winds to upwelling-favorable spring/summer winds is the most commonly used metric (Schwing et al. 1996, 2006, Barth et al. 2007). Closely related to wind-driven upwelling is the timing of the persistent drop in coastal sea level (also driven by local and remote wind stress) from high levels characteristic of warm, winter, downwelled waters, to lower levels characteristic of cool, spring/summer, upwelled waters (Strub et al. 1987, Bilbao 1999, Kosro et al. 2006). Other metrics include the timing of a reversal in current direction off Vancouver Island (Thomson & Ware 1996), changes in the cross-shore pressure gradients indicating the development of a spring equatorward jet (Lynn et al. 2003), variations in the spatial structure of sea-surface temperatures (SSTs) from isotherms primarily perpendicular to the coast in winter, to isotherms parallel to the coast in summer (Lynn et al. 2003), increases in chlorophyll *a* concentrations (Lynn et al. 2003), and shifts in zooplankton species composition from species found predominantly in southern regions (in winter) to those found in northern regions (in summer; Peterson & Keister 2003, Hooff & Peterson 2006). Although biological responses of physical spring transition have been documented off central California (e.g. phytoplankton; Lynn et al. 2003), the timing of the transition is not well documented for that region.

Our first goal was to compare 2 commonly used methods for identifying spring transition in the CCS that use data on wind-driven upwelling and coastal sea levels to 2 newly developed methods that use data on sea levels as well as satellite-derived SSTs, and more specifically, to assess whether methods typically used in northern regions of the CCS can be applied to central and southern regions (from Cape Mendocino, California, to the US–Mexico border). Second, to investigate the biological relevance of those time series of spring transition, we examined the relationships between spring transition and larval abundance (age-0) of 2 west coast groundfish species (sablefish *Anoplopoma fimbria* and Pacific ocean perch *Sebastes alutus*). We chose those species because previous evidence suggests that the timing of spring transition affects their recruitment (Schirripa & Colbert 2006, Holt & Punt in press). In addition, they are of management interest due to the contribution of sablefish to the commercial west coast groundfish catch (Schirripa 2007) and the designation of Pacific ocean perch as 'overfished' (Hamel 2007a). Furthermore, both stocks are currently assessed by the Pacific Fisheries Management Council and so estimates of age-specific abundances exist (Hamel 2007b, Schirripa 2007). In fact, the assessment of sablefish currently uses information on oceanographic conditions to inform estimates of recruitment and may benefit from improved characterization of the timing of favorable conditions.

We chose to investigate recruitment for those species because most hypotheses about environmental effects on groundfish pertain to early life-history stages (i.e. mortality prior to recruitment) when age-class strength is typically determined (Bakun 1996). In particular, the 2 most compelling hypotheses about mechanisms relating spring transition to recruitment of groundfish are the timing of prey availability for larvae during the critical period early in life, and the timing of favorable current conditions to transport groundfish larvae to preferred habitat (e.g. for sablefish, see Schirripa & Colbert 2006).

MATERIALS AND METHODS

Data. To identify dates of spring transition, we compiled coast-wide data on oceanographic conditions from 3 sources: Bakun upwelling wind indices, coastal sea levels, and *in situ* and satellite-measured SST fields. Bakun upwelling indices were derived from the daily average of wind-driven cross-shore transport computed from surface atmospheric pressure gradients generated from atmospheric models (Environmental Research Division of the Pacific Fisheries Environmental Laboratory, available online at: www.pfeg.noaa.gov/, for 1967 to 2007). Although satellite-derived wind data exist for recent years (after 1999; Pickett & Schwing 2006), those time series are too short to test hypotheses about groundfish recruitment. We analyzed northern, central, and southern regions of the CCS separately because dates of spring transition (and environmental variables that determine them) tend to be coherent at spatial scales corresponding to the size of those regions (Strub et al. 1987). In particular, Strub et al. (1987) found positive covariation in the timing of the spring transition at alongshore scales of 500 to 2000 km driven predominantly by large-scale wind stress (at alongshore scales of ~1500 km). In addition, the lines between regions (at Cape Mendocino, 40.0° N, and Point Conception, California, 34.5° N) are well-recognized boundaries in physical and biological oceanographic conditions, although additional boundaries north of Cape Mendocino have also been documented (Huyer et al. 2005, Venegas et al. 2008). Furthermore, we compared dates of spring transition with recruitment time series for groundfish stocks, which are typically resolved at relatively large, regional (or sometimes, coast-wide) scales, requiring information on environmental conditions at similarly large scales. Bakun indices were averaged over coastal stations within regions (6 stations in total).

Daily sea level data were extracted from the University of Hawaii Sea Level Database (available at: http://uhslc.soest.hawaii.edu/uhslc/data.html) for Neah Bay, Washington (representing the northern region), San Francisco (representing the central region), and San Diego (representing the southern region), California. Sea levels at a single station in each region were chosen because of evidence for covariation in that metric at large spatial scales (250 to 1300 km; Roach et al. 1989). An inverse barometric correction was applied to sea level data using surface pressures from the NCEP/NCAR Reanalysis Project (available online at: www.cdc.noaa.gov/cdc/reanalysis/reanalysis.shtml, for 1967 to 2007).

Daily Reynolds-AVHRR SST data (1985 to 2006) were extracted from the NOAA National Operational Model Archive & Distribution System covering the region from the coastline to beyond the continental shelf (extending 100 km offshore in the north, increasing to 560 km in the south). The SST data were a blend between coarse-scale *in situ* (Reynolds) and fine-scale satellite (AVHRR) observations and were interpolated over points missing in the satellite record as described by Reynolds et al. (2007).

For Pacific ocean perch, maximum likelihood estimates of annual deviations in recruitment to age-3 (1970 to 2006; deviations from a stock-recruitment model, i.e. reflecting indices of recruitment success independent of spawning stock size) were taken from the most recent stock assessment (Hamel 2007b). Those data were shifted by 3 yr to generate time series of age-0 recruitment (1967 to 2003). Pacific ocean perch has a geographic distribution that spans Cape Blanco in the south to the southern US–Canada border in the north, so we compared time series of recruitment to dates of spring transition for the northern region only. For sablefish, the maximum likelihood estimates of the deviations in recruitment to age-0 (1972 to 2006) were generated from the same model used in the most recent stock assessment (Schirripa 2007) with one difference. In that assessment, an environmental covariate of recruitment, monthly average sea-surface heights from 4 locations off Washington and Oregon were included to improve model fit (i.e. generating time series of recruitment deviations independent of interannual variability in sea-surface height). For our analyses, we used estimates of recruitment deviations that did not include that environmental covariate (M. Schirripa unpublished analyses) since we were interested in testing the relationship between total interannual variation in recruitment and timing of spring transition. Because sablefish are distributed from Baja California in the south to the Gulf of Alaska in the north and the current stock assessment includes survey data from the US–Mexico border to the southern US–Canada border (Schirripa 2007), we compared recruitment time series and dates of spring transition for all 3 regions. Assessments for both species used an age-structured population dynamics model fit to catch and survey indices of abundance and length and age compositions (collected from fishery catches and surveys).

Statistical methods. Dates of spring transition were identified in 4 ways: one method that used Bakun indices (Schwing et al. 2006), another that combined Bakun indices and sea level data (as in Logerwell et al. 2003, adapted from Bilbao 1999, henceforth referred to as the 'Logerwell method'), a modified version of that method that used only sea level data, and one that used spatial patterns in SSTs.

The first method identified timing of spring transition from the start of the wind-driven coastal upwelling season, i.e. the date of minimum cumulative Bakun upwelling index (Schwing et al. 2006, Bograd et al. 2009) averaged over coastal stations within regions.

The Logerwell method uses 2 metrics of ocean conditions: the daily Bakun index averaged over coastal stations within regions and residuals in coastal sea levels from the long-term mean at one location in each region. Both time series were low-pass filtered with a stop frequency of 1/(10 d), using complex demodulation performed in S-plus, to eliminate high frequency variation independent of a seasonal shift. Spring transition was defined as the first date when the Bakun index became positive and sea level residuals became negative, as indicated by the filtered time series. In years when the upwelling and sea-level time series crossed the zero line several times during the spring, the date that best matched the seasonal trends was chosen (as indicated by low-pass filtered time series with a stop frequency of 1/[90 d]).

The third method was a modified version of the Logerwell method with 3 differences. (1) For the modified version, we used only sea level data because they better integrate seasonal shifts in ocean conditions experienced by fish than wind data that were used to generate upwelling indices (Strub et al. 1987). Coastal sea levels on the west coast of the Americas integrate wind forcing and remotely generated, coastally trapped waves (Enfield & Allen 1980), whereas the Bakun upwelling indices are derived from smoothed atmospheric pressure fields and reflect wind-driven coastal upwelling only. (2) We computed sea-level residuals from the 3-yr running mean instead of the long-term mean to better capture seasonal changes in sea levels and remove signals related to interannual changes in mean values. (3) We defined spring transition as the date of steepest negative slope of the filtered time series using a stop frequency of 1/(90 d), since an objective selection of the date of seasonal shift was not possible with the 1/(10 d) filtered time series due to high frequency variation in those data.

We developed a fourth method for identifying dates of spring transition from changes in spatial patterns of SSTs. Although SSTs have been used to characterize the spring transition for specific locations (e.g. off central California, Lynn et al. 2003), those data have not been used to identify coast-wide time series of dates of spring transition. Spatial and temporal patterns in SSTs relate to upwelling of cold water that is characteristic of the spring transition in the north, and in the central region, to the formation of oceanographic features characteristic of spring and summer conditions (Lynn et al. 2003). Because we were interested in the seasonality of spatial patterns in SSTs independent of changes due to solar radiation (i.e. independent of common patterns across the entire region), we removed the mean spatial SST from each daily field to create time series of SST residuals. We examined those SST residuals for the first 240 d of each year because we were only interested in changes that occurred during winter, spring, and summer. Those residuals were then smoothed by computing the 3-d running mean and extracting every third day.

The dominant spatial patterns in residual SST fields were identified for each region using Empirical Orthogonal Function (EOF) analysis (also known as Principal Component Analysis), a multivariate technique that decomposes data series into a linear recombination of multiple orthogonal functions of the original data. The EOFs minimize residual variance in SST residuals and represent the dominant statistical patterns in high-dimensional data (as described by Armstrong 2000). Those functions are selected in descending order of importance (i.e. the first EOF captures the largest portion of variance; subsequent EOFs capture increasingly smaller portions). We identified dates of spring transition from time series of the amplitudes of the first EOF (the first principal component, PC1) because that function explained the largest portion of the variance (61.9, 40.2, and 49.1% for northern, central, and southern regions, respectively) and exhibited spatial patterns characteristic of spring transition. Furthermore, its amplitude (PC1) varied on a seasonal scale. We selected the date of initiation of the seasonally persistent upward slope of smoothed PC1 values (i.e. the date of maximum curvature derived from the second derivative of PC1 values, and low-pass filtered with a stop-frequency of 1/[90 d]) to represent the onset of spring SST conditions. Again, we used the 1/(90 d) filtered time series because objective dates of spring transition could not be identified from the 1/(10 d) filtered data due to high frequency variation.

We further examined latitudinal gradients in Bakun index climatologies and winter-spring differences in SST and wind stress fields to provide insights into the regional patterns of change associated with the spring transition.

To investigate the relationship between dates of spring transition and groundfish recruitment, we fit linear models for both species, Pacific ocean perch and sablefish:

$$\ln(R_{i,t}) = b_{i,0} + b_{i,1} \cdot x_t + \varepsilon_{i,t} \qquad \varepsilon_{i,t} \approx MN(0, \Phi_i) \qquad (1)$$

where $\ln(R_{i,t})$ is the natural logarithm of the recruitment deviation for species i in year t, x_t is the date of spring transition in year t calculated using 1 of the 4 methods described above, $b_{i,0}$ and $b_{i,1}$ are parameters for species i, and $\varepsilon_{i,t}$ are multivariate normally distributed random errors with a variance-covariance matrix Φ_i (dimensioned $t \times t$). Variability in recruitment time series was from natural, biological sources and errors in observations of abundances from surveys and commercial catch. A third source of uncertainty, estimation uncertainty, arose because recruitment deviations were derived from stock assessment models and were not observed directly. Estimation uncertainty was characterized by a variance-covariance matrix of annual recruitment values from the stock assessment model. We included those 3 sources of uncertainty by using multivariate normally distributed errors in Eqn. 1 (ε_i) that included both estimation errors and natural variability combined with observation errors. Following Dichmont et al. (2003), the following objective function was minimized:

$$\ln[\sqrt{Det(\Omega_i + V_i)}] + \frac{1}{2}\sum_{t1}\sum_{t2}(\ln R_{i,t1} - \ln \hat{R}_{i,t1})[(V_i + \Omega_i)^{-1}]_{t1,t2}(\ln R_{i,t2} - \ln \hat{R}_{i,t2}) \qquad (2)$$

where V_i is the variance-covariance matrix of estimates of $\ln(R_i)$ for species i obtained from the stock assessment model that generated those estimates, Ω_i is a matrix with diagonal elements σ^2_ε representing variance associated with natural variability and observation errors, and $\ln\hat{R}_{i,t}$ are expected recruitments (determined from $\ln\hat{R}_{i,t} = b_{i,0} + b_{i,1} \cdot x_t$). Both summations ($t1$ and $t2$) occur over all years in the time series. Therefore, unlike previous studies relating groundfish recruitment to environmental factors (e.g. Schirripa & Colbert 2006), our parameter estimates account for the relative precision of annual recruitment estimates.

We tested whether the linear model was a significantly better fit to the data than a simpler model (e.g. the null model with a y-intercept only) using likelihood-ratio tests, and calculated the Akaike Information Criterion (AIC) value to estimate the gain (or loss) in information content. We then compared results among the 4 methods used to identify dates of spring transition.

RESULTS

Cumulative upwelling

For the northern region of the CCS, the start of the upwelling season (i.e. date of minimum cumulative upwelling after which upwelling was generally positive) usually occurred between March and May. For the central and southern regions it occurred 1 to 3 mo earlier (e.g. Figs. 2a, 3a, & 4a for an example time series from 1999). In fact, in most years, south of 36° N, the start of the upwelling season was identified as 1 January, because winter wind conditions were characterized by weak upwelling rather than downwelling. In those years, the cumulative upwelling index remained positive year round. Seasonally weak or intermittent winter downwelling between 33° and 39° N was reflected in the climatology of Bakun indices for 1948 to 2007, which were positive (indicating upwelling favorable winds) for most months (Fig. 5).

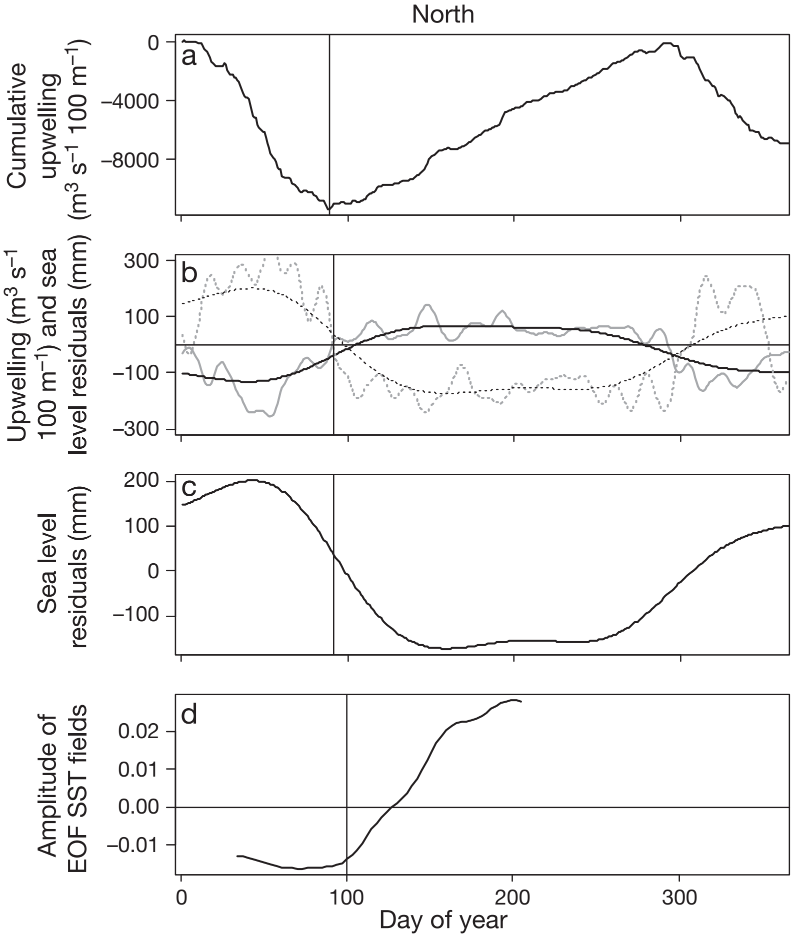

Fig. 2. (a) Cumulative Bakun upwelling indices ($m^3\ s^{-1}$ per 100 m of coastline) for one example year, 1999, in the northern California Current System. (b) Bakun upwelling indices smoothed with a low-pass filter of stop frequency 1/(10 d) (grey solid line) and low-pass filter of stop frequency 1/(90 d) (black solid line), and sea-level residuals from the long-term mean smoothed in the same ways (grey dashed lines for stop frequency of 1/[10 d] and black dashed line for the stop frequency of 1/[90 d]). (c) Sea-level residuals from a 3-yr running mean, smoothed with a low-pass filter of stop-frequency 1/(90 d). (d) Amplitudes of the first EOF of SST fields, smoothed with a low-pass frequency of 1/(90 d). Note, only days of year 1 to 240 were included in the EOF analysis, and smoothing further removed the first and last 40 d of the time series. Vertical lines denote dates of spring transition identified by (a) the method of Schwing et al. (1996) (start of upwelling season), (b) the Logerwell method, (c) the modified Logerwell method, and (d) our method using seasonal trends in SST fields

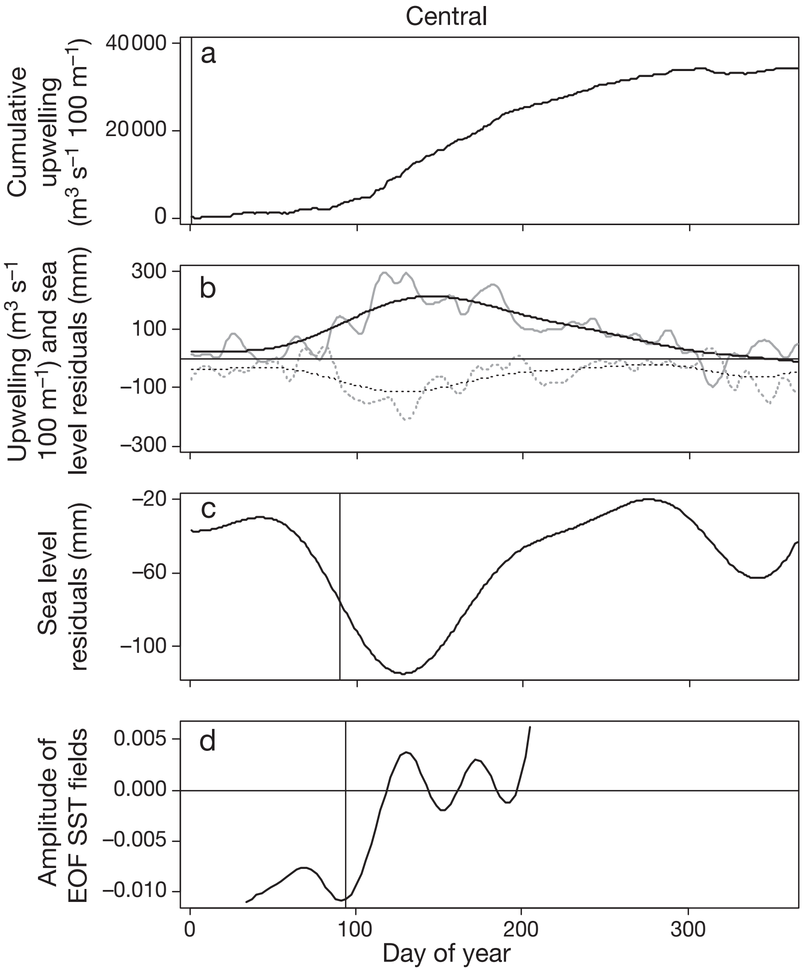

Fig. 3. As in Fig. 2, but for the central region of the California Current System

Logerwell method

When applied to the northern region, the timing of reversal in winds from downwelling favorable to upwelling favorable coincided with a rapid drop in sea levels below their long-term mean (e.g. Fig. 2b). As expected, the dates identified by the Logerwell method were highly correlated with those from the cumulative upwelling method for that region (Fig. 6, top left corner). However, in the central and southern regions, the onset of strong upwelling favorable winds occurred several weeks prior to a gradual decline in sea levels. Similar to the previous method (minimum cumulative upwelling), in some years, dates of spring transition could not be identified with the Logerwell method in the central and southern regions because winds remained upwelling favorable throughout the winter, sea levels remained below their long-term mean, or the dates identified from the 2 metrics were not coincident (e.g. Figs. 3b & 4b).

Modified Logerwell method

In contrast to the Logerwell method, dates of spring transition could be identified using the modified Logerwell method for all 3 regions because that method did not rely on wind-driven upwelling and it employed the date of most rapid decline in sea levels (an event that could be specified for each year) rather than the date of decline below the long-term mean (an event that could not be consistently specified). Rapid declines in sea levels in the southern region tended to occur 10 to 50 d earlier than in the northern and central regions (e.g. Figs. 2c, 3c, & 4c for 1999). The dates of spring transition identified from the modified Logerwell method were only weakly positively correlated with timing of upwelling derived from Bakun indices for the northern and southern regions, and were uncorrelated in the central region (Figs. 6, 7, & 8).

Spatial patterns in SST fields

In our northern CCS region (40.0° to 49° N), the first EOF represented a combination of latitudinal and cross-shore trends in SST residuals. The amplitude of the first EOF (PC1) generally increased from winter to summer each year (e.g. Fig. 9). The spatial patterns in PC1 suggest that nearshore and offshore areas exhibited opposite seasonal trends; nearshore areas were warmer than average during winter and cooler than average in summer (i.e. were negatively correlated with PC1 trends). In contrast, offshore areas (and nearshore around 46° N) exhibited opposite trends, i.e. were positively correlated with PC1 trends. See Fig. 10 for the correlation coefficients of the relationship between the PC1 and SST residuals (which reflect spatial patterns in the first EOF), and the magnitude of the slope of that relationship.

Similarly, for our central region (34.5° to 40.0° N), the first EOF exhibited strong cross-shore patterns (Figs. 9 & 10). In contrast to the northern and central regions, in the south, SST residuals were positively correlated with PC1 values near shore (i.e. SSTs were cooler than average during winter and warmer than average in summer) and negatively correlated offshore.

In the northern region, dates of spring transition identified from SST fields were positively correlated with the timing of the onset of upwelling and dates identified from the Logerwell method (Fig. 6). However, those relationships were either not calculated (Logerwell method) or near zero (upwelling method) in the central and southern regions (Figs. 7 & 8). Relationships between the modified Logerwell dates and those from SST fields were consistently near zero for all regions (Figs. 6, 7, & 8).

The relationships between dates of spring transition and recruitment deviations varied according to species, region, and the method used to identify dates. For sablefish, the models that included spring transition identified from cumulative upwelling and the Logerwell method were significantly better fits to the data than the null models for the northern region ($p = 0.04$ and $p = 0.001$, respectively), and the model based on the modified Logerwell method approached significance ($p = 0.06$; Table 1, Fig. 11). However, this was not the case for the central or southern regions, or the model based on dates identified from SSTs for any region. Indeed, those models had higher AIC values (lower information content) than their null versions. For Pacific ocean perch, only the relationship based on dates of spring transition identified from the Logerwell method approached significance ($p = 0.05$; Table 1, Fig. 12). The remaining 3 models had higher AIC values than their null counterparts, suggesting no gain in information by including dates of spring transition.

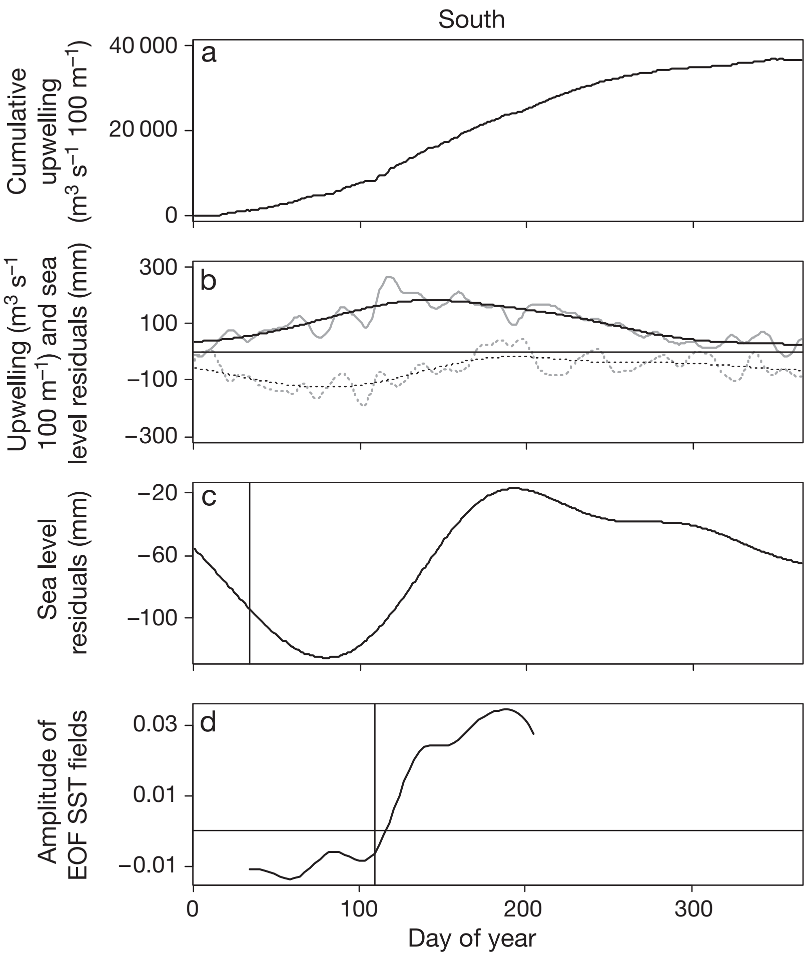

Fig. 4. As in Fig. 2, but for the southern region of the California Current System

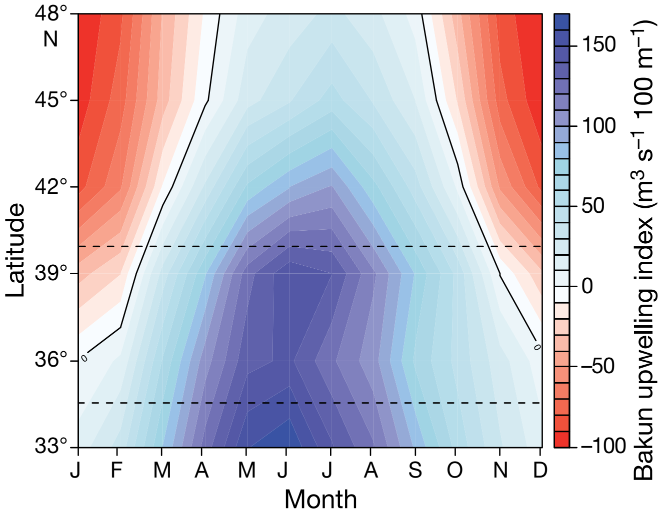

Fig. 5. Hovmöller diagram of monthly average Bakun upwelling index (m^3 s^{-1} per 100 m of shoreline) arranged by latitude on the *y*-axis. The horizontal dashed lines delineate 3 regions of the California Current System: northern, central, and southern

DISCUSSION

Our results suggest that using the Logerwell approach, or the Bakun wind-derived index alone, provides an informative spring transition index in the northern region. However, these metrics may not be appropriate in the central and southern regions because of diminished, intermittent, or absent winter downwelling in those regions. For the central region, for 10 of the 40 years, either smoothed time series of Bakun winds remained positive during the winter or smoothed time series of coastal sea levels remained below their long-term mean. Furthermore, for most years in that region, the timing of onset of upwelling favorable winds differed from the timing of declines in sea levels (e.g. Fig. 3b). For the southern region, the smoothed time series of Bakun winds remained positive for 34 of 40 years. One possible explanation for the

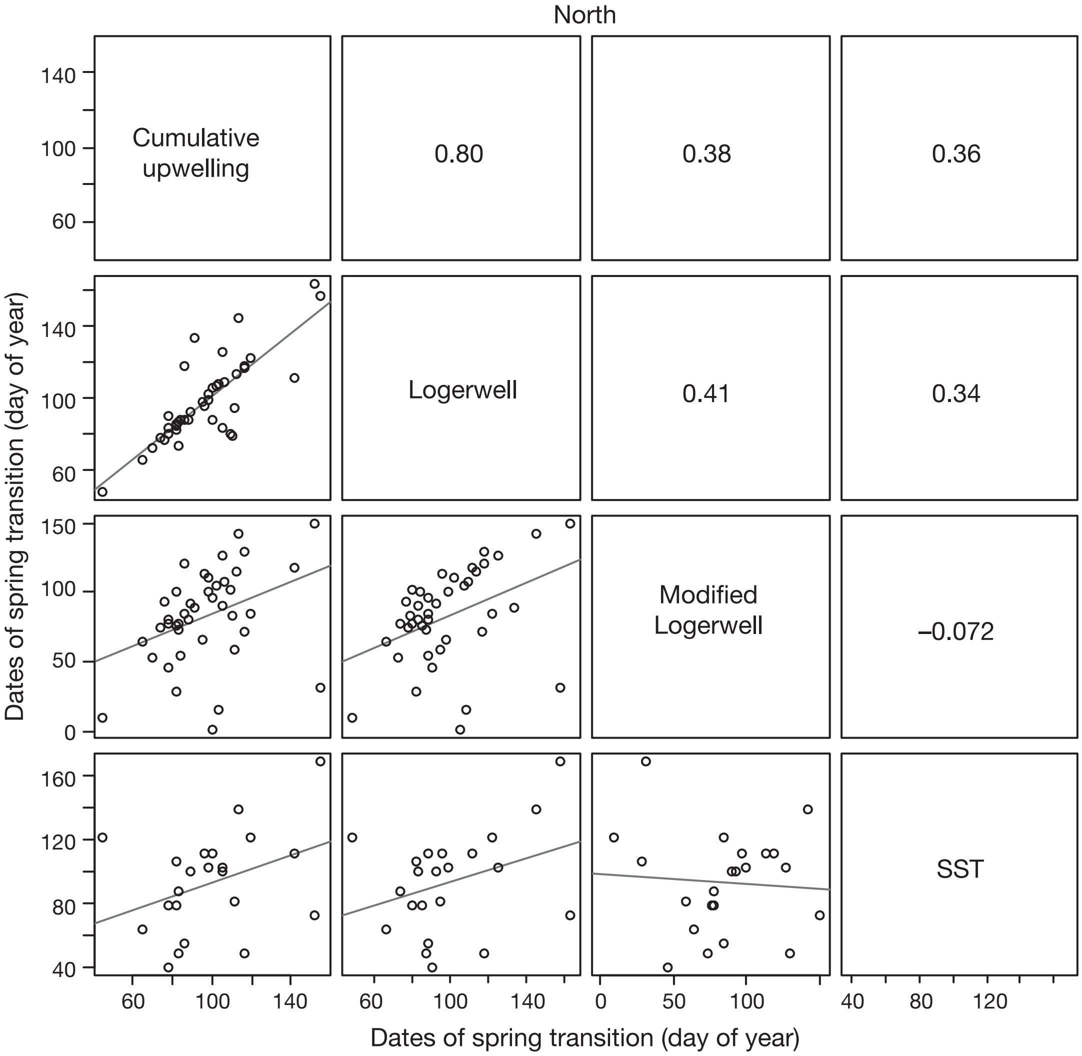

Fig. 6. Correlations between dates of spring transition (day of year) for the northern region of the California Current System identified from 4 methods: the start of the upwelling season (date of minimum cumulative upwelling), the Logerwell method, the modified Logerwell method, and an index of the dominant patterns in SST from EOF analysis that uses the date of maximum curvature in smoothed PC1 values

divergence in the timing of transition among metrics in central and southern regions is strong vertical stratification in the upper ocean during spring. That stratification can negate the impact of wind stress on the upwelling of cold, nutrient-rich water and can confound the relationship between upwelling winds and ecologically-important ocean conditions, as documented in 2005 (Kosro et al. 2006). Another possibility is that remotely forced, coastally trapped waves (Hickey et al. 2006) must be considered in conjunction with local wind forcing to account for seasonal changes in coastal sea levels and SSTs in the southern region (Enfield & Allen 1980). Although sea levels tend to covary at large spatial scales (i.e. exhibiting coherence within regions), Denbo & Allen (1987) found that the magnitude of those fluctuations varied by latitude and were largest several hundreds of kilometers north of maxima in wind stress. Our observations of sea levels at San Francisco and San Diego for the central and southern regions, respectively, may be more closely related to variability in wind stress south of the southern boundary of the respective region than within it. In contrast, sea-level data for the northern region were collected near the northern boundary (Neah Bay) and likely integrate conditions over that region.

In contrast, we were able to identify dates of spring transition in all 3 regions using our modified version of the Logerwell method. That method had 2 additional advantages. The choice of the date (the date of steepest decline in low-pass filtered time series in sea levels) was more objective than the date chosen using the Logerwell method in years when multiple dates of

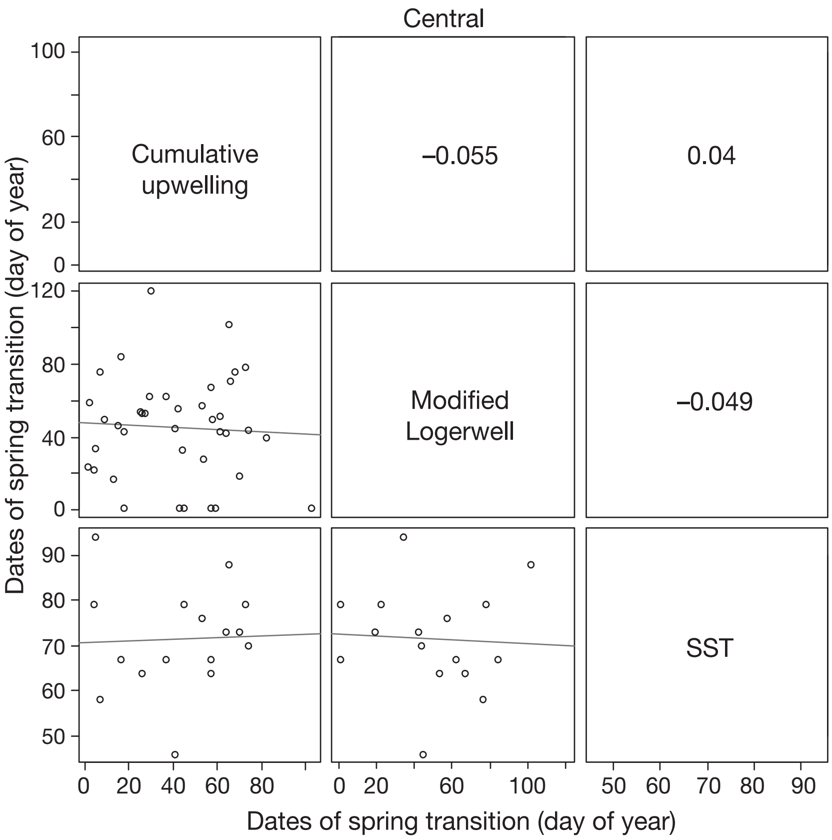

Fig. 7. Correlations between dates of spring transition (day of year) for the central region of the California Current System identified from 3 methods: the start of the upwelling season (date of minimum cumulative upwelling), the modified Logerwell method, and an index of the dominant patterns in SST from EOF analysis that uses the date of maximum curvature of smoothed PC1 values

zero-crossing existed in Bakun winds and sea-level residuals. Furthermore, our method more accurately reflected the timing of seasonal changes in ocean conditions that define the spring transition (date of steepest change) than previous methods that use arbitrary point thresholds (e.g. declines below the long-term mean sea level). However, the ability of our method to detect sudden declines in sea levels was limited by the smoothing of time-series data, which may have excluded high-frequency variation associated with spring transition.

Strong seasonal signals were also evident in our EOF-based indices of SSTs (Fig. 9). In the northern and central regions, differences between spring (April to June) and winter (January to March) SST fields indicate an incursion of cold upwelled water at the coast and/or the presence of remotely forced, coastally trapped waves (see the left panel of Fig. 10). However, the timing of SST changes was weakly (positively) correlated with the start of upwelling in the north only. South of Point Conception, the seasonal trends in SSTs are characterized by a local maximum in warming waters inside the Southern California Bight, a local minimum in warming in a narrow band offshore, and a region of intermediate warming farther offshore (right panel of Fig. 10). The band of minimal seasonal warming is a southeastward extension of the seasonally cooling coastal upwelling waters in the central CCS region. The leading EOF from our analysis of SSTs in the southern region captures these features with an east-west dipole hinging on a line that extends southeastward from Point Conception. Once the regionally averaged seasonal warming is accounted for, the characteristics of the total winter-to-spring SST changes in the 3 regions of the CCS examined here are all consistent with the EOF loadings shown in the right panel of Fig. 10.

Comparison to previous literature

The sequence of seasonal changes in oceanographic variables that we examined generally agree with previous studies. Similar to our results, most studies have found the onset of upwelling favorable winds to either coincide or precede declines in sea level, depending on the region (Strub et al. 1987, Strub & James 1988, Logerwell et al. 2003). In contrast to our findings, Strub et al. (1987) found that seasonal cycles in sea levels lead those of mid-shelf SSTs by 1 to 2 mo across the US west coast (35° to 48° N). The differences in relative timing of SST changes between our results and those of Strub et al. (1987) can be explained in at least 3 ways. First, our measure was of spatial patterns in SSTs (i.e. we used ordination techniques to extract dominant spatial patterns in SST residuals), whereas Strub et al. (1987) used raw SST values. Second, our measure was independent of trends common within regions. In other words, our measure of SST changes was designed to filter out the seasonal trends due to increasing solar radiation that may have been captured by Strub et al. (1987). Third, we chose the date of maximum curvature in smoothed PC1 values as the date of spring transition, which preceded large absolute changes in SSTs described by Strub et al. (1987).

Few studies have examined differences in seasonal patterns in oceanographic conditions across regions in the CCS; most have focused on a single region (usually in the north). In one exception, Strub et al. (1987) found that the seasonal cycle of currents was more dramatic

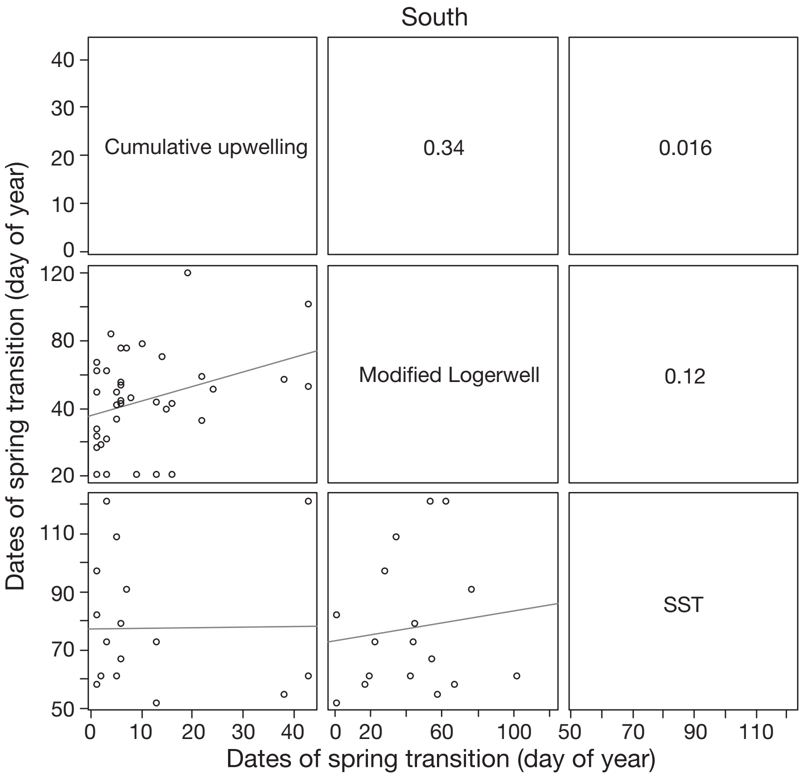

Fig. 8. Correlations between dates of spring transition (day of year) for the southern region of the California Current System (as described in the caption of Fig. 7)

north of 45° N (accounting for 30 to 50% of variance in those currents) compared to the rest of the US west coast. Similar to our results, they found that the magnitude of seasonal cycles in winds and sea levels in the northern CCS exceeded the magnitude in southern regions.

Also similar to our results, south of 35° N, Strub et al. (1987) found that the onset of strong southward winds was followed by a more gradual decline in sea levels than observed in the north. They suggested that those sea-level declines tended to progress northward along the US west coast via coastally trapped waves over a period of 3 to 10 d. We found that declines in sea levels in the north occurred 1 to 4 wk later than in the south, suggesting that, in at least some years, sea levels may be forced by different mechanisms between regions, or the same mechanism (e.g. wind-derived upwelling and poleward propagating coastally-trapped waves) combined withregionally independent atmospheric forcing.

Again similar to our results, Enfield & Allen (1980) found strong correlations between coastal sea levels and wind stress north of San Francisco that were not apparent in the south. They attributed declines in coastal sea levels in the south to forcing by wind stress over the equatorial wave guide (e.g. associated with the Southern Oscillation) modified by annual insolation cycles, rather than local wind stress (which was responsible for declines in sea levels in the north). In another study comparing time series of sea levels across the margins of the Pacific Ocean, Roach et al. (1989) also suggested that sea levels were forced remotely by large-scale disturbances in the southern part of the CCS and locally in the north, as evidenced by higher correlations in sea levels among stations south of 38° N than north of that latitude.

Comparison to other metrics of spring transition

The timing of spring transition derived from other physical and biological indicators of ocean conditions from previous studies were either uncorrelated or pos-

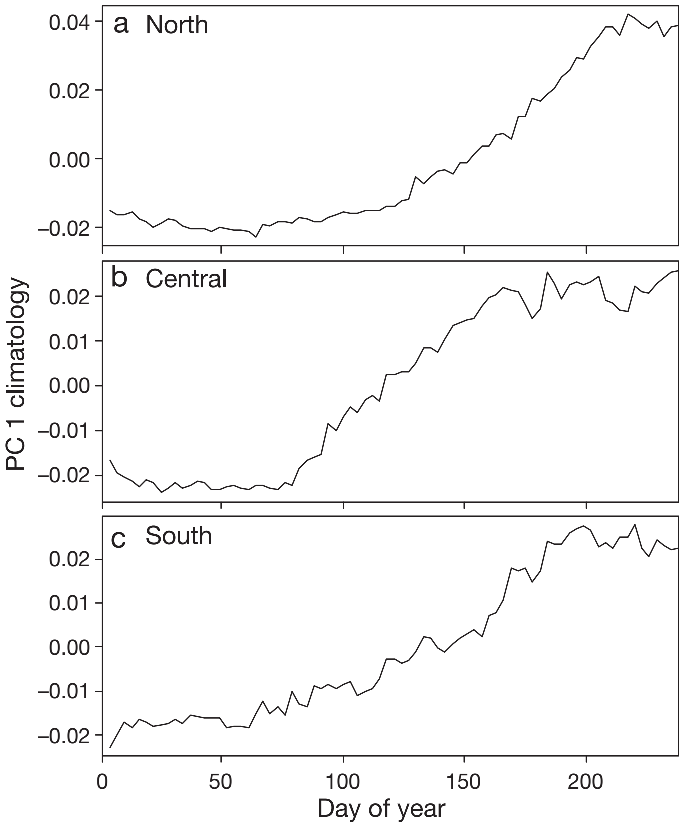

Fig. 9. Climatologies of PC1 values for (a) northern, (b) central, and (c) southern regions of the California Current System for January through August (day of year 1 to 240, 1985 to 2007)

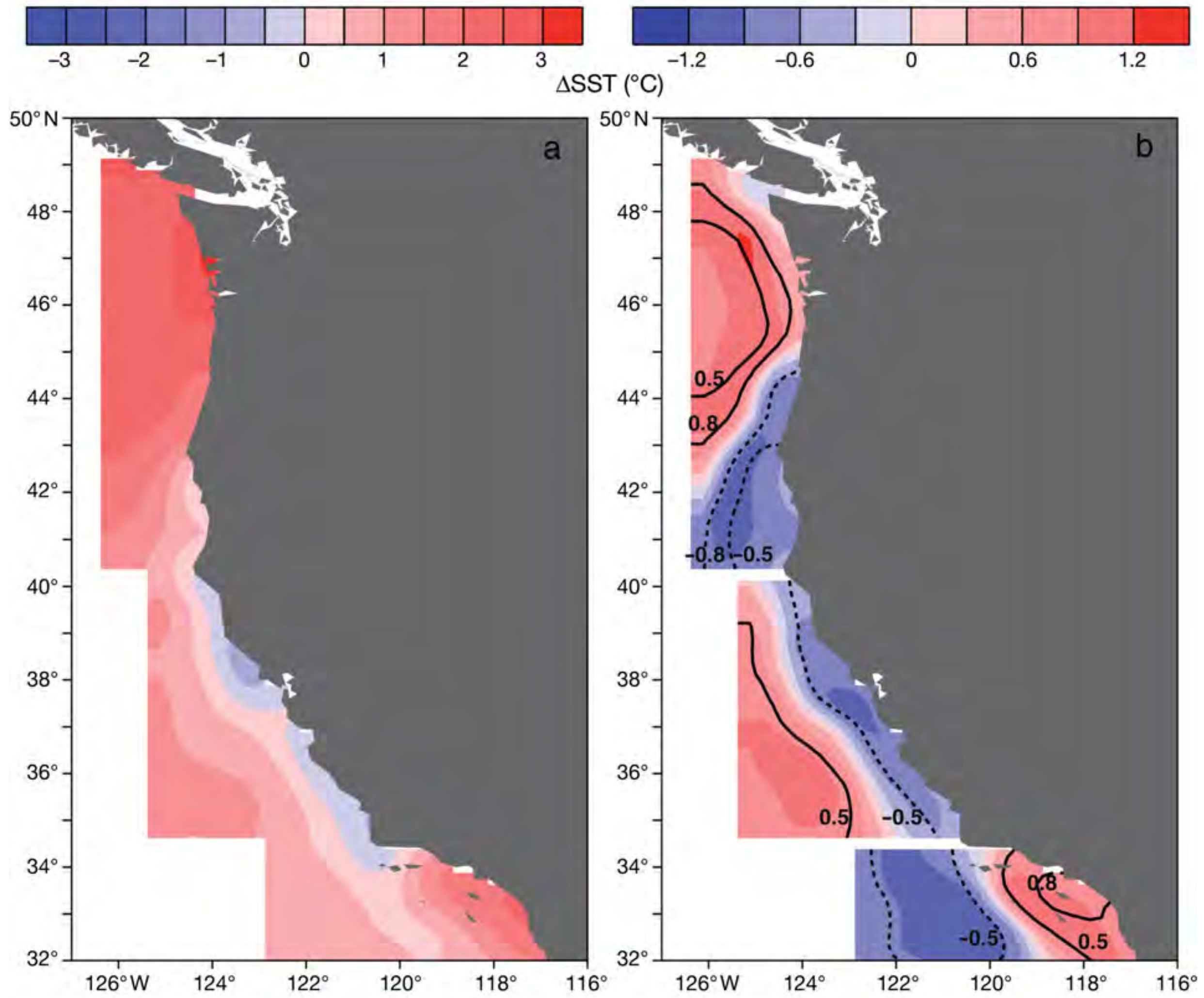

Fig. 10. (a) Change in raw sea-surface temperatures (SSTs) in °C between winter (averaged over January, February, and March) and spring (averaged over April, May, and June) for northern, central, and southern regions of the California Current System. (b) Correlation coefficients between SSTs (residuals from the spatial mean) and the first principal component (PC1) from EOF analysis for each grid point in the northern, central, and southern regions (contours), and slope of the relationship between PC1 (divided by its SD) and SST values for each SST location (colors)

itively correlated with our time series of spring transition. Consistent with the results of Thomson & Ware (1996), we found that dates of spring transition in the vertical shear of currents off Vancouver Island were uncorrelated with dates of spring transition identified from Bakun winds using the Logerwell method in the northern region (r = –0.33, p = 0.53), and the same was true for dates derived from the cumulative upwelling index (r = –0.42, p = 0.40) and the modified Logerwell method (r = –0.45, p = 0.37). These discrepancies can be explained in at least 3 ways. (1) the Bakun upwelling index (used in the cumulative upwelling and both Logerwell methods) is solely based on estimates of local alongshore windstress forcing that causes coastal upwelling, whereas current velocities used by Thomson & Ware (1996) represent integrated oceanic processes more directly. (2) Thomson & Ware's (1996) index of current velocity smoothes out high-frequency wind-induced variation of the upper ocean not related to seasonal shifts, which may be captured by the Bakun upwelling index. (3) Thomson & Ware (1996) examined conditions off Vancouver Island, north of our study region. In addition, the dates derived from SST fields were uncorrelated with those of Thomson & Ware (1996) (r = –0.22, p = 0.67), suggesting that variation in SST is driven by processes other than (or in addition to) coastal currents.

Biological dates of spring transition derived from zooplankton community structure (Peterson 2008) tend to be approximately 1 mo later than dates derived from upwelling indices (Bakun winds and sea level data) perhaps due to a delay in zooplankton response to

Table 1. Summary statistics for linear relationships between dates of spring transition and ln(recruitment deviations) for Pacific ocean perch *Sebastes alutus* and sablefish *Anoplopoma fimbria*. Four methods for identifying dates of spring transition are listed in the third column: the date when the cumulative upwelling is minimized ('Start of upwelling'), the method used by Logerwell et al. (2003) ('Logerwell'), date of steepest change in smoothed sea levels ('Sea level', or modified Logerwell method), and date of seasonal shift in spatial patterns in sea-surface temperatures 'SST'. AIC_c: Akaike Information Criterion for small sample sizes; L ratio: likelihood-ratio test statistic that compares log-likelihoods of the linear and null models, where the null model has an intercept but no slope. p-values are based on a chi-squared distribution of L ratios

Species Region	Method for identifying date of spring transition	No. of years	Null model AIC_c	Linear model					
				b_0	b_1	σ_ε	ΔAIC_c from null model	L ratio	p
Sablefish									
North	Start of upwelling	35	3.8	0.90	−0.00926	0.54	−2.02	4.42	0.036
	Logerwell	35	3.8	1.20	−0.0122	0.50	−7.82	10.22	0.001
	Sea level	35	3.8	0.46	−0.00552	0.55	−1.18	3.58	0.059
	SST	22	12.0	−0.23	0.00134	0.70	2.63	0.07	0.787
Central	Start of upwelling	35	3.8	0.08	−0.00191	0.57	2.15	0.25	0.616
	Sea level	33	−1.1	−0.24	0.0039	0.54	1.86	0.56	0.453
	SST	18	8.0	0.87	−0.0123	0.61	0.47	2.23	0.135
South	Start of upwelling	35	3.8	0.12	−0.0116	0.56	0.69	1.71	0.190
	Sea level	34	3.8	0.20	−0.00409	0.57	1.40	1.02	0.314
	SST	19	8.0	0.57	−0.0078	0.62	1.03	1.67	0.197
Perch									
North	Start of upwelling	37	20.2	0.58	−0.00848	0.62	0.24	2.13	0.144
	Logerwell	37	20.2	0.76	−0.0101	0.60	−1.31	3.69	0.055
	Sea level	37	20.2	0.13	−0.00444	0.63	1.14	1.23	0.267
	SST	22	16.3	−1.10	0.00949	0.65	0.10	2.75	0.098

favorable feeding conditions. Despite differences in average timing, positive correlations between those biological dates and our dates for the northern region (e.g. Logerwell method r = 0.80, p = 0.0004; modified Logerwell method r = 0.74, p = 0.01) suggest that the oceanographic mechanisms associated with spring upwelling and the drop in sea levels may also advect zooplankton species typical of summer conditions (originating from northern regions) into the CCS, replacing species typical of winter conditions (originating from southern regions).

Biological responses to the timing of spring transition

Although persistent changes during spring were evident in all 4 oceanographic time series that we examined, only those related to wind-driven upwelling and sea levels showed significant (negative) relationships with recruitment of Pacific ocean perch or sablefish. Those oceanographic variables reflect upwelling in coastal waters during spring (decreased sea levels and shift from poleward to equatorward winds) and may reflect increases in upwelling-derived productivity important during larval stages of groundfish. However, time series of spring transition derived from spatial-temporal patterns in SST residuals were uncorrelated with recruitment of Pacific ocean perch and sablefish. In contrast to our results for SSTs, Lynn et al. (2003) observed changes in spatial patterns in SSTs concurrent with biological metrics of spring transition. However, they examined fine-scale spatial features in SSTs during spring rather than large-scale spatial trends, and in only a small region off of central California. Furthermore, they used primary productivity, as measured by nearshore vertically integrated fluorescence and beam attenuation coefficients, to demonstrate changes in biological conditions over spring and not higher trophic levels. Our measure of spatial gradients in SST may also be related to biological processes at lower trophic levels, not captured by our metric of groundfish recruitment.

We investigated the relationships between timing of spring transition and groundfish recruitment to demonstrate the biological implications of various methods for identifying timing of spring transition, and not to rigorously test those methods. Our interpretation of those examples is limited for at least 3 reasons. (1) Instead of a single physical driver (e.g. influx of food resources), recruitment may depend on the complex interaction of productivity, currents transporting larvae offshore away from zones of productivity, and distribution of predators. Those factors may be reflected in the different oceanographic variables used to identify spring transition, limiting the application of a single method for detecting that phenomenon. (2) Although both species are assessed as single popula-

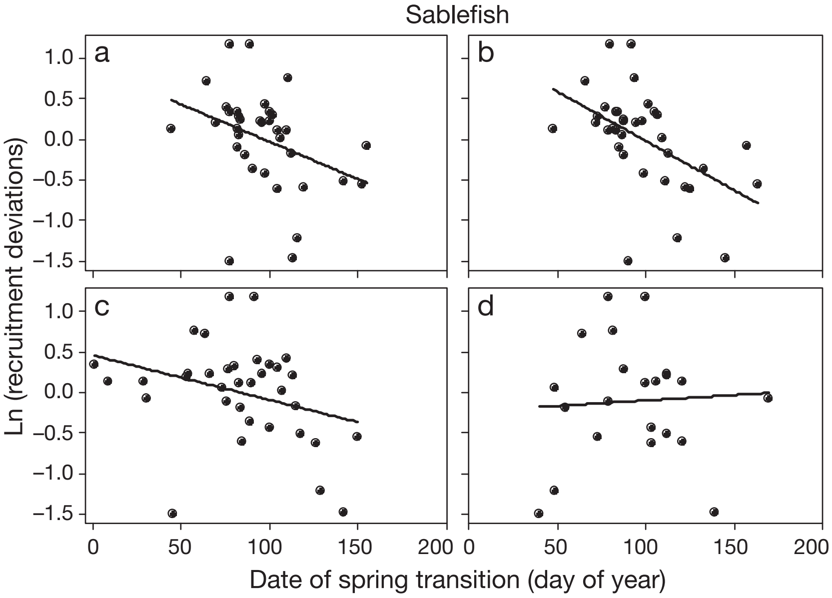

Fig. 11. Relationships between dates of spring transition and ln(recruitment deviations) for sablefish *Anoplopoma fimbria* using 4 methods for identifying spring transition: (a) the date when the cumulative upwelling first becomes positive, (b) the method used by Logerwell et al. (2003), (c) date of the steepest decline in smoothed sea levels, (d) and date of the seasonal shift in spatial patterns in sea-surface temperatures. Note the only difference in ln(recruitment deviations) for each plot is the number of years included. The relationships in plots (a), (b), and (c) were significant (i.e. $p < 0.05$) or approached significance (likelihood-ratio tests, $p = 0.04$, $p = 0.001$, and $p = 0.06$, respectively)

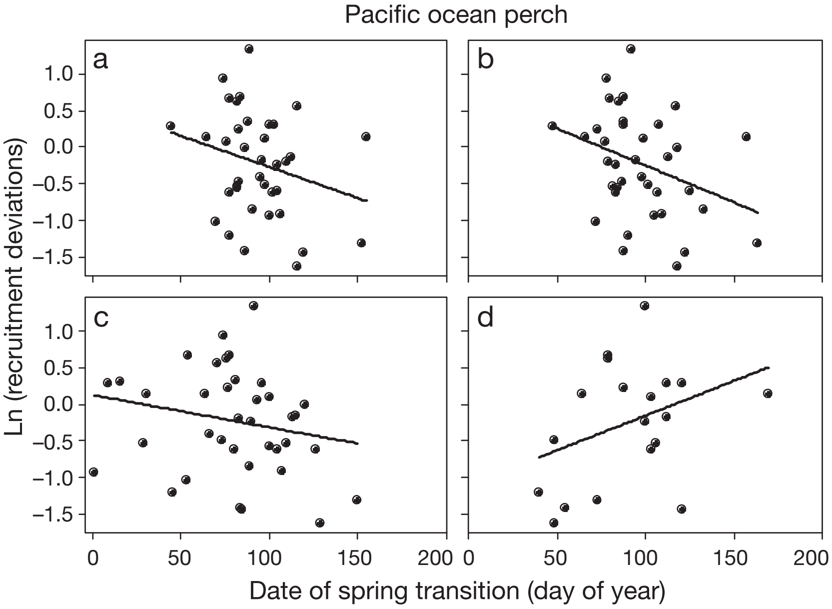

Fig. 12. Relationships between dates of spring transition and ln(recruitment deviations) for Pacific ocean perch *Sebastes alutus*, as described in the caption of Fig. 11. The relationship in plot (b) was marginally significant (likelihood-ratio test $p = 0.05$)

tions, there is some evidence for stock structure within populations (e.g. for sablefish see Schirripa (2007)), and those sub-populations may respond in different ways to delays in spring transition. (3) For Pacific ocean perch, estimates of recruitment include variability in survival experienced over the first 3 yr of life, potentially swamping signals from larval life stages (the first year). Although the timing of spring transition may also influence maternal condition, which may in turn influence recruitment (Sogard et al. 2008), we found no significant relationships between timing of spring transition in the year prior to recruitment and abundance of recruits for either species.

CONCLUSIONS

Spring transition in the CCS is not a single, easily defined phenomenon. We advise caution when identifying dates of spring transition; individual methods for selecting those dates do not capture the complex multidimensional changes that occur. For example, in the southern CCS, dates derived by locally wind-driven upwelling, coastal sea levels, and SSTs differed by 1 to 2 mo of each other, and their time series were not significantly correlated.

The choice of an appropriate method depends on the specific oceanographic conditions relevant for hypotheses being tested (e.g. related to upwelling, temperatures, and/or biological habitat) and the spatial extent of investigation (e.g. regionally-specific or spanning the entire CCS). Metrics related to upwelling may be appropriate when transport constrains the ability of fish larvae to access high quality habitat and/or prey, and metrics derived from spatial patterns in SSTs may be related to other trophic levels (e.g. primary productivity). Instead of developing multiple time series of spring transition that reflect individual physical drivers, multivariate ordination techniques could be used to combine information across metrics (within or among regions). Environmental signals that are common among metrics could be extracted in a series of orthogonal ordination axes. Further studies at large spatial scales, multi-decadal temporal scales, and multiple trophic levels are required to identify metrics that will be relevant to different components of the ecosystem.

Spatially comprehensive metrics of the timing of spring transition (i.e. that include the entire CCS) are warranted given the growing recognition for the ecological importance of this phenomenon and the large spatial scale of physical drivers (and hence biological responses). However, coast-wide metrics of upwelling may not be feasible given region-specific responses to physical drivers (e.g. interactions between coastally trapped waves and local winds). We developed 2 new methods to identify dates of spring transition that use the timing of rapid declines in sea levels and spatial patterns in SSTs, which may be more appropriate than previous methods when comparing northern, central, and southern regions of the CCS. Although not related to recruitment of sablefish or Pacific ocean perch, those methods may be related to other biological phenomena not investigated here. Metrics that span the CCS will be especially relevant with projected changes in the timing of spring transition under global warming scenarios (Snyder et al. 2003).

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