

Matches and mismatches: ocean climate, prey

INTRODUCTION

A critical issue in ecology, especially in an age of rapidly changing climate, concerns how environmental variability influences ecosystem processes. In recent years, the match-mismatch hypothesis has been invoked frequently as a mechanism linking climatic variation to trophic perturbations across a range of ecosystem types (Visser et al. 1998, Anderson & Piatt 1999, Platt et al. 2003, Drever & Clark 2007). The central tenet of the match-mismatch hypothesis is that predators breed more successfully in years in which

the most energetically demanding phase of their breeding cycle overlaps extensively (i.e. 'matches') with the seasonal peak in prey availability. In the marine environment, where the match-mismatch hypothesis has its roots (Cushing 1990), climatic changes are asymmetrically altering the phenologies of species at different trophic levels, causing an increase in the frequency and severity of mismatching between predators and their prey (Edwards & Richardson 2004). Because many mid- to high-trophic-level marine predators, including many species of seabirds, rely heavily on one or a few prey species while breeding

(Reid et al. 2006), strong temporal matching between their breeding period and the annual peak in the availability of key prey species can be vital to successful population processes (Regehr & Montevecchi 1997, Durant et al. 2003, Suryan et al. 2006).

At Triangle Island (British Columbia, Canada), previous research showed that in cold, phenologically late years, when compared with warm, phenologically early years, offspring of the seabird Cassin's auklet *Ptychoramphus aleuticus* grew more quickly on diets that remained richer in the copepod *Neocalanus cristatus* until later in the season (Bertram et al. 2001, Hedd et al. 2002). Invoking the match-mismatch hypothesis, these authors proposed that the relationship was causal: in cold, late years, the period of maximal biomass of late-stage copepodites in surface waters begins late and ends late, matching well with the birds' energetically demanding chick-provisioning period

nestling diets until later in the season in cold ocean years compared to warm ocean years. This is expected because the seasonal cycle of *Neocalanus* spp. is prolonged and delayed in cold conditions (Mackas et al. 1998, Tadokoro et al. 2005, Mackas et al. 2007), creating greater temporal overlap between the auklets' chick-provisioning period and the period during which this prey item is available to them in near-surface waters. Because *N. cristatus* persists longer in diets in colder years, then (P2) it will also be more prevalent overall in diets in colder years.

This variation in diet is predicted to have 2 effects on Cassin's auklet offspring. First, (P3) they will have greater mass at fledging in years in which *Neocalanus cristatus* is more persistent and prevalent in their diets. This is expected because the copepod is a high-quality prey item, being conspicuous, lipid-rich and spatially predictable for foraging parents. In addition, (P4) the seasonal decline in fledging masses will be less marked in years in which *N. cristatus* persists longer in diets, because even late-hatched nestlings will receive this prey item in considerable quantities. I also consider variation in the proportion of offspring that survive the period between hatching and fledging, predicting that as with fledging masses, (P5) there will be a positive relationship between the overall representation of *N. cristatus* in nestling diets and the proportion that survive; and finally, that (P6) the seasonal decline in the proportion that survive will be less pronounced in years in which *N. cristatus* persists longer in diets.

MATERIALS AND METHODS

Study area. The study was conducted at Triangle Island, British Columbia, Canada (50° 52' N, 129° 05' W), in each year from 1996 to 2006.

Field methods. About 80 nest sites (the birds use earthen burrows) were examined at 5 d intervals to monitor the timing and success of Cassin's auklet breeding in each year. Nest checks began in late March or early April, just prior to the start of laying, in all years except 2000 and 2001, when they began in mid-April, at the mid-laying stage. When an egg was first found, the burrow was left undisturbed for 35 d, then again inspected at 5 d intervals until a hatchling was found. When first found, hatchling wing length (± 1 mm, using a wing bar) and mass (± 1 g, using a 50 g spring scale) were measured. Hatching dates, thus nestling ages, were estimated using a calibration of wing length against age for known-aged nestlings based on measurements made previously at Triangle Island (Hedd et al. 2002). Nestlings were then measured and weighed at Ages 5, 10, 25 and 35 d, and then every 2 d until they disappeared. They were consid-

ered to have fledged successfully if they survived at least 35 d and were not later found dead in the burrow. Fledging mass was taken to be the last mass recorded prior to the chick's disappearance (nestling Cassin's auklets leave the burrow to begin an independent life at sea at an average age of 40 to 45 d).

Approximately 10 provisioning adults were captured for diet sampling while returning to the colony in darkness using pheasant nets erected between 2 large poles. Sampling occurred at 10 d intervals beginning on 18 May (28 May in the very late 2005 season), and ending on 27 June (5 sessions in total per year, except 2005 when there were 4). This 6 wk interval corresponds well with the provisioning period of pairs that laid by the median laying date in most years. Occasionally, sampling sessions needed to be delayed by 1 to 3 d due to inclement weather, or they spanned 2 or 3 consecutive nights until ~10 samples were obtained. Adult auklets carry zooplankton to their young in a sublingual pouch. Upon capture, we massaged the adults' pouches to induce them to regurgitate their food loads through a funnel into a small, preweighed, screw-top plastic bottle, later filled with buffered formalin.

Laboratory methods. Regurgitated samples were transferred to stacked sieves and rinsed repeatedly with water to remove preservative. Individual items present in subsamples were identified to the lowest possible taxonomic level (usually species, especially for common items), enumerated, blotted dry, and weighed on an electronic balance. As in other recent studies of Cassin's auklet diet from the northeast Pacific (Abraham & Sydeman 2004, Adams et al. 2004), prey species were identified and enumerated by M. Galbraith, Institute of Ocean Sciences, Sidney, British Columbia. In statistical analyses, each individual food load was treated as an independent and equal sample, regardless of its mass or completeness. In all analyses, I used measures based on wet biomass of prey items in food loads.

Statistical approach. First, I examined factors that affected the percentage biomass of auklet nestling diets comprised of *Neocalanus cristatus*. As predictor variables, I used Year (1–11), Sampling session within the year (a surrogate for date; 1–5), and their Interaction. The match-mismatch hypothesis predicts that the representation of *N. cristatus* in diets will vary among years, being more prevalent in colder years (P2); and that there will be a Year \times Sampling session interaction, with the prey item more persistent in colder years (P1).

Second, I examined factors that affected post-hatching offspring survival and fledging masses. In these analyses, I considered only offspring that hatched by 25 May (73% of the entire sample) because diets

through most of the developmental periods of these earlier offspring were well covered by the sampling scheme. As predictor variables, I used Year, Hatching date, and their interaction. Again, the match-mismatch hypothesis predicts that both the proportion that survive to fledge and fledging masses will vary among years, with higher survival rates and heavier fledging masses in years with more

meaningful support (Table 3). Thus, fledging masses varied among years, and tended to decline with hatching date. However, the lack of interaction between year and hatching date indicates that the rate of decline differed little among years. The latter result is not consistent with predictions of the match-mismatch hypothesis.

The annual mean fledging mass was greater in years in which monthly mean sea surface temperatures were lower, and in years in which diets included more *Neocalanus cristatus* (Fig. 4). As predicted by the match-

mismatch hypothesis, the most parsimonious model for explaining interannual variation in Cassin's auklet fledging mass was simply the proportion of *N. cristatus* in diets, regardless of the month (Table 4).

In the logistic analysis to explain variation in Cassin's auklet nestling survival ($n = 413$), the model including year and hatching date was best supported, and had good predictive power ($R^2 = 0.35$). The model including the Year \times Hatching date interaction also received support ($\Delta AIC_c < 2.0$), although it received less than half the weight of the best-supported model (Table 5). Thus, offspring survival varied among years, and tended to decline with later hatching but with only a weak tendency for the rate of seasonal decline in survival to vary among years.

Annual offspring survival was higher in years in which the monthly mean sea surface temperature was lower, and in years in which the annual mean percentage biomass of *Neocalanus cristatus* in individual food

fledge (P5), and they fledged at heavier masses (P3), in years in which *N. cristatus* made up a greater proportion of their diets. The direct effect of diet on offspring survival and growth, itself a direct consequence of spring ocean climate, outweighed any indirect influence of sea surface temperature.

Only 2 of the model's predictions were not strongly supported. Fledging masses did not decline more steeply with later hatching in warmer than in colder years (P4), and there was only a weak tendency for survival to do so (P6). Experiments on several seabird spe-

cues that predict feeding conditions later in the season (Frederiksen et al. 2004). However, energetics studies indicate that avian laying dates can be constrained by unfavourable feeding conditions (Stevenson & Bryant 2000). In seabirds, for example, carry-over effects from late winter and spring feeding conditions can affect the timing of laying (Daunt et al. 2006, Durant et al. 2006, Guinet et al. 2006). It is possible then that relatively poor feeding conditions in warm, unproductive years cause the auklets to lay too late (Ainley et al. 1990).

In terrestrial birds, individuals expend more energy while foraging to provision nestlings when temporally mismatched with their prey base (Thomas et al. 2001). Functionally, then, the increased energetic demand on provisioning adults, combined with offspring receiving less of the lipid-rich copepods, could largely explain the reduced breeding success of Cassin's auklets in mismatch years. Prey species might also be less lipid-rich in warmer, less productive years as they themselves experience poor feeding conditions, with consequences for their predators (Wanless et al. 2005). While most auklet nestlings are fed at least once on most nights (Hedd et al. 2002), they might fare better when *Neocalanus cristatus* dominates diets because while this species is available, both parents are able to provision daily due to its spatial predictability. Notably, there was no suggestion that food loads containing *N. cristatus* were simply heavier than loads comprised of other species.

While temporal matching with the copepods' life cycle appeared to be critical for successful breeding by Cassin's auklets in this system, recent empirical and theoretical assessments of the match-mismatch hypothesis also consider how variation in prey abundance influences seasonal trophic interactions (Gotceitas et al. 1996, Durant et al. 2007). In particular, greater prey abundance could potentially override temporal mismatches between predator and prey. Even in a classic match-mismatch study system, modelling suggested that prey abundance can be more important than temporal matching for the Atlantic puffin *Fratercula arctica* feeding on herring *Clupea harengus* in Norway (Durant et al. 2005).

Mackas et al. (2001) found a positive association between the magnitude of the annual *Neocalanus* copepod biomass peak and the intensity of summer upwelling off southern British Columbia. Thus, we can expect these copepods to be more abundant in surface waters in years of colder ocean temperatures and stronger primary production. That tendency is evident when comparing the 1996–1998 period (which was warm and unproductive, with negative copepod biomass anomalies) against the 1999–2002 period (cold and productive, with positive copepod biomass anomalies).

However, through the warm 2003–2005 period, biomass anomalies were similar in magnitude and direction to those in the cold 1999–2002 period (Mackas et al. 2007); yet *N. cristatus* became scarce in Cassin's auklet diets early (in mid-June) as it had in 1996–1998. This difference suggests that the timing, rather than the magnitude, of the biomass peak is the more important determinant of the persistence of these copepods in auklet diets at Triangle Island. The fact that the prey item was similarly abundant (~50% of total biomass) in diets from mid-May until early June during both the cold and the 2 warm periods further supports this idea. In this auklet-copepod system compared to the puffin-herring system (Durant et al. 2005), both predator and prey tend to be closer trophically to primary production. While available in near-surface waters, the copepods may be superabundant relative to the birds' harvest in any year.

To summarize, Cassin's auklets at Triangle Island bred less successfully, with reduced offspring survival rates and fledging masses, in years with warmer ocean temperatures. As hypothesized previously (Bertram et al. 2001), results of the present study indicate that strong temporal mismatching with one specific prey species, the copepod *Neocalanus cristatus*, largely drove the poor breeding success in warm years. This study adds to a growing body of evidence showing that climate-driven phenological mismatches can dramatically alter trophic interactions, and that these disruptions have the potential to affect demographic processes in the predator (Both et al. 2006). This could be especially true in marine systems, in which temporal mismatching between trophic levels is both frequent and widespread (Anderson & Piatt 1999, Edwards & Richardson 2004). As the oceans continue to warm (IPCC 2007), we can expect the associated changes in the functioning of marine ecosystems to have considerable consequences.

Acknowledgements. Thanks to the many field workers who helped to collect data. Thanks also to D. Bertram for initiating the study, and to M. Court, J. Higham, C. Smith, R. Ydenberg and the Canadian Coast Guard for top-notch logistical support. M. Galbraith, Institute of Ocean Sciences, Sidney, deserves special thanks for enumerating prey items in the Cassin's auklet 'gurge' samples. The research was conducted under a Scientific Permit from the Canadian Wildlife Service and an Animal Care Permit from Simon Fraser University. Funding was provided by the *Nestucca* Oil Spill Trust Fund, the Climate Change Action Fund, the World Wildlife Fund Canada, the Science Horizons, Migratory Bird, and Birds Oiled at Sea programs of Environment Canada, the Natural Sciences and Engineering Research Council of Canada (grants to F. Cooke), and the Centre for Wildlife Ecology. Finally, I thank D. Esler and B. Smith for statistical advice, and D. Bertram, D. Mackas and B. Smith for constructive reviews of the draft manuscript.

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*Editorial responsibility: Rory Wilson,
Swansea, UK*

*Submitted: February 11, 2008; Accepted: June 10, 2008
Proofs received from author(s): September 5, 2008*