Little auks buffer the impact of current Arctic climate change

David Grémillet, Jorg Welcker, Nina J. Karnovsky, Wojciech Walkusz, Hall Margaret, Jérôme Fort, Zachary Brown, John R Speakman, Ann M.A. Harding

HAL Id: hal-01100441
https://hal.science/hal-01100441

Submitted on 19 Mar 2015

Little auks buffer the impact of current Arctic climate change

David Grémillet,[1,2] Jorg Welcker,[3] Nina J. Karnovsky,[4] Wojciech Walkusz,[5,6] Margaret E. Hall,[7] Jérôme Fort,[8] Zachary W. Brown,[4] John R. Speakman,[9] Ann M.A. Harding,[10]

[1] Centre d'Ecologie Fonctionnelle et Evolutive, UMR5175, CNRS-INEE, 1919 route de Mende, 34293 Montpellier Cedex 5, France. E-mail: david.gremillet@cefe.cnrs.fr
[2] Percy FitzPatrick Institute, DST/NRF Centre of Excellence, University of Cape Town, Rondebosch 7701, South Africa
[3] Norwegian Polar Institute, Fram Centre, 9296 Tromsø, Norway. Email: welcker@npolar.no
[4] Pomona College, Department of Biology, 175 W. Sixth Street, Claremont, CA 91771 USA. Email: Nina.Karnovsky@pomona.edu
[5] Institute of Oceanology, Polish Academy of Sciences, Powstańców Warszawy 55, 81-712 Sopot, Poland. Email: walwo@iopan.gda.pl
[6] Freshwater Institute, Fisheries and Oceans, 501 University Crescent, Winnipeg, MB, R3T 2N6, Canada
[7] BirdWatch Ireland, Unit 20 Block D, Bullford Business Campus, Kilcoole, Co. Wicklow, Ireland. Email: hall_m_e@yahoo.co.uk
[8] National Environmental Research Institute, Department of Arctic Environment, Frederiksborgvej 399, 4000 Roskilde, Denmark. Email: fort.jerome@gmail.com
[9] School of Biological Sciences, University of Aberdeen, Tillydrone Avenue, Aberdeen AB24 2TZ, Scotland, UK. Email: j.speakman@abdn.ac.uk
[10] Alaska Pacific University, Environmental Science Department, 4101 University Drive, Anchorage, AK 99508, USA. Email: aharding@usgs.gov

Running title: **Arctic seabirds and climate change**

Keywords: Behavioural plasticity, Envelope models, Global warming, North Atlantic, Pelagic food web, Zooplankton.

Author for correspondence:
David Grémillet. Centre d'Ecologie Fonctionnelle et Evolutive, UMR5175, CNRS-INEE, 1919 route de Mende, 34293 Montpellier Cedex 5, France.
E-mail: david.gremillet@cefe.cnrs.fr

1

Abstract:

Climate models predict a multi-degree warming of the North Atlantic in the 21st century. A research priority is to understand the impact of such changes upon marine organisms. With 40-80 million individuals, planktivorous little auks (*Alle alle*) are an essential component of pelagic food webs in this region that are potentially highly susceptible to climatic effects. Using an integrative study of their behaviour, physiology and fitness at three study sites, we evaluated the impact of ocean warming on little auks across the Greenland Sea in 2005-2007. Contrary to our hypothesis, the birds responded to a wide range of sea surface temperatures via plasticity of their foraging behaviour, allowing them to maintain their fitness levels unchanged. Predicted effects of climate change are significantly attenuated by such plasticity, confounding attempts to forecast future impacts of climate change by envelope models.

Introduction:

The earth's climate is warming, and this trend is amplified in Polar regions (Serreze *et al*. 2007; Graversen *et al*. 2008). Recent investigations confirm significant ocean warming in the Arctic sector of the North Atlantic (Polyakov *et al*. 2005; Walczowski & Piechura 2006; Dmitrenko *et al*. 2008), and predict further increase of sea surface temperatures (SST) in this region across the 21st century (Karnovsky *et al*. 2010). One current challenge is to investigate the impact of these rapid changes upon organisms, food webs, and biogeochemical cycles (Beaugrand *et al*. 2010). In this study, we tested the hypothesis that warmer surface water conditions in the North Atlantic impact the morphology, physiology, and behaviour of little auks (*Alle alle*), as well as their fitness (reproductive output and survival).

The little auk is a particularly well-suited study species in the context of climate change because it is an important component of the Arctic food web, and is likely to be significantly affected by changing sea temperatures. Little auks are the most numerous seabird in the North

2

Atlantic (with a population estimated to be 40-80 million individuals, Stempniewicz 2001), and consume up to 24% of local plankton production (Karnovsky & Hunt 2002). They mainly feed on copepods, which are strongly affected by climate change, with a marked tendency for temperate, smaller-sized species to spread northwards (Beaugrand *et al*. 2009). Moreover, little auk field metabolic rate is 70% higher than predicted by body mass, and they have very limited capacity to store fat. Consequently they are predicted to be particularly sensitive to altered feeding conditions (Harding *et al*. 2009a).

Here we used a natural experiment across the Greenland Sea to mimic forecasted ocean warming of the North Atlantic (Fig.1). This framework follows Wernberg *et al*. (2010), who successfully used synoptic, regional differences in sea-surface temperature to simulate forthcoming ocean warming and test the response of marine organisms to climate change. Such design also allowed further investigations, such as testing the evolutionary response of plants to climate change (Etterson & Shaw 2001), and complies with Brown *et al*. (2011). In our study system, recent work showed a very strong link between summer SST within the foraging areas of little auks, species composition of local zooplankton communities, and the dietary preferences of the birds (Karnovsky *et al*. 2010), whereby colder water contained more larger copepods, which were also preferentially fed upon by little auks (Karnovsky *et al*. 2010). Conversely, birds had to feed on smaller, less profitable copepod species in warmer water. Comparing the ecophysiology of little auks from different colonies subject to contrasting SST regimes at one moment in time therefore allowed us to simulate the effect that increasing water temperatures might have on this Arctic species across the 21st century. Using this rationale we tested the hypothesis that higher summer SST would result in diminished little auk fitness, with the predictions that higher SST would modify little auk diet, foraging effort, provisioning rates, breeding success and adult survival.

Material and methods:

The study took place during the little auk breeding season (July) in 2005, 2006 and 2007 at Kap Höegh, East Greenland (70°43'N, 22°38'W, hereafter KH), Hornsund, West Spitsbergen (77°00'N, 15°22'E, hereafter HS), and Kongsfjorden, West Spitsbergen (79°01'N, 12°25'E, hereafter KF), respectively. Yet not all variables listed below were collected at all sites in all years (see Table 1 for details).

Sea-surface temperatures

We estimated mean SST for the month of July (the little auk chick-rearing period) each year for an area of approximately 4000 km^2 adjacent to each colony using satellite data provided by EUMETSAT Ocean and Sea Ice Satellite Application Facility (OSI SAF; see Welcker *et al*. 2009a). The size of this sampling area was chosen so as to fully enclose little auk core foraging areas at sea, as determined from at-sea direct observations and recordings of foraging trip durations (Karnovsky *et al*. 2010, Welcker *et al*. 2009a). Mean July SST was calculated by averaging daily means based on all data points available within the selected areas.

Diet

Prey items caught by adults breeding at all colonies and brought back to their chicks were collected and identified following Harding *et al*. (2009a). Briefly, breeding little auks were caught in noose carpets at the colony, and zooplankton that they collected at sea were scooped out of their gular pouch. Individual plankton meals were stored in 4% borax-buffered formaldehyde solution, and examined under a stereomicroscope. Prey items were identified to species level wherever possible, and remaining taxa were identified to the lowest possible taxonomical level. *Calanus* species were identified according to Kwaśniewski *et al*. (2003).

Abundant taxa were enumerated from subsamples while large and rare individuals from different taxa were counted for the whole diet sample.

Foraging effort

We determined foraging parameters of little auks in 2007 at the three study sites using time-depth-recorders (TDR). The TDRs used were Cefas G5 Data Storage Tags (CTL, Lowestoft, UK), with 8 MB of memory, which were cylindrical in shape with a rounded tip to minimize water resistance. The TDRs weighed 2.7 g in air, or 1.6% of the average initial mass of experimental birds. These devices have no measurable impact on little auk energy consumption (Harding *et al*. 2009a). We programmed the TDRs to record temperature and pressure every 5 seconds for up to 5 days. When the birds dove below 1.5 meters, temperature and pressure readings were made every 0.2 seconds for the duration of the dive. TDRs were attached ventrally using Loctite® glue to adult little auks raising chicks 1-18 days old. Birds were caught either by hand in accessible nest crevices, or using noose carpets on rock surfaces. Handling lasted less than 10 minutes in all cases and data loggers were deployed for a maximum of 5 days. Recorded data were analyzed following Harding *et al*. (2009a) so as to extract (1) foraging trip durations (2) total flight time per foraging trip (3) total number of dives per 24h (4) the proportion of time (%) spent underwater per 24h.

Chick feeding rates

To estimate chick feeding rates at KH and HS breeding adults were individually-marked with colour rings and/or picric acid, and their nest sites were observed non-stop for 24-48h periods, allowing exact recording of nest visits. In addition to direct observations, miniature radio-transmitters (Holohil Systems Ltd., Carp, Canada; and Biotrack Ctd., Dorset, UK) attached to

breeding adults were also used to determine chick feeding rates at KF (see Welcker *et al.* 2009b for details).

Daily Energy Expenditure (DEE)

DEE (in kJ day^{-1}) of little auks breeding at KH and KF was estimated using the Doubly-Labelled Water technique (DLW), following Welcker *et al.* (2009b) and the single sample method. Breeding adults caught at the nest and/or on the colony were weighed, given a intra-peritoneal injection of DLW, colour-marked, and released immediately. A single blood sample was drawn upon recapture, within 24-72h. Isotopic dosages, laboratory analyses, and DEE calculations followed Speakman (1997) and were conducted as detailed in Welcker *et al.* (2009b).

Breeding performance

Little auks raise a single chick in an underground nest crevice. During chick-rearing, each studied nest was monitored every three days. Chick growth rates and fledging mass were only recorded at KH and HS using a Pesola balance (precision ± 2.0 g) because nests were out of reach at KF, and only the presence/absence of the chick was determined using light-scopes (Moritex Europe ltd., Cambridge, UK). Fledging mass was the last measurement taken prior to a chick's departure from the colony, and only chicks that had reached 20d when they disappeared from the nest were considered fledged (Harding *et al.* 2004). Fledging age and maximum fledging success (defined as the number of chicks fledged or reaching 20d/ number hatched) were calculated for a subsample of nests at each of the three colonies.

Adult body condition and survival

For all adults caught at the three colonies we recorded body mass, headbill length and wing length, and these measurements were used to calculate an index of body condition (body mass corrected for structural size) as detailed in Harding *et al*. (2011). Adult survival rates of birds from KH and KF were determined using a Capture-Mark-Recapture analysis. Briefly, at KH breeding adults (n=147) were caught in 2005 and individually marked with combinations of three colour rings and one metal ring. At KF, 299 birds were caught in 2006 and an additional 110 individuals in 2007, and marked in a similar way. Subsequent resighting sessions were conducted annually during the breeding season until 2009, with a minimum of 6 days per year and site. We used Cormack-Jolly-Seber (CJS) models implemented in the program MARK (White & Bunrham 1999) to estimate yearly survival rates. With our data we were unable to separate mortality from permanent emigration; therefore estimated survival rates reflect apparent survival rather than true survival (however, for simplicity, we refer to 'survival rates' in this paper). We fitted two sets of CJS models: (I) using the combined data from KH and KF to estimate yearly survival from 2006/07 to 2008/09 and to test for between-colony differences, and (II) using KH data only to estimate yearly survival in 2005/06 for which no data was available for KF.

We assessed the goodness-of-fit of the global model allowing for time and colony specific survival (denoted as Φ) and resighting probabilities (denoted as p) using the program U-CARE (Choquet *et al*. 2009). This model clearly did not fit the data ($\chi^2_4 = 31.55$, p < 0.001). Inspection of the component tests revealed that rejection of the CJS model was mainly based on test 2.CT, indicating strong resighting heterogeneity (trap-happiness) especially in KF birds. We accounted for trap dependence by estimating different resighting probabilities for individuals that were seen versus not seen the previous year (Pradel 1993), denoted as 'h' in our models. The resulting model $\{\Phi_{c*t}, p_{c*t*h}\}$, where c is colony and t is time (year), fitted the data well ($\chi^2_2 = 0.72$, p = 0.70) and was used as the starting point for model selection based on

the Akaike information criterion adjusted for small sample size (AICc; Anderson & Burnham 1999). The goodness-of-fit test for the second dataset (KH only) indicated that the CJS model fitted these data well ($\chi^2_3 = 2.13$, $p = 0.55$), thus the model $\{\Phi_t, p_t\}$ was used as a starting point for this analysis. All possible models allowing survival probabilities to vary with time and/or colony and/or SST (including additive models) were examined. To account for model selection uncertainty we report survival estimates ± SE based on model averaging (Burnham & Anderson 2002; See Table 3).

Further statistical analyses

Differences in SST between years and sites were assessed using ANOVA. We used least squares linear regressions to test whether variation in our response variables across the different colonies and different years was related to differences in SST (Wernberg *et al*. 2010). This was done to assess the effect of SST on foraging effort (foraging trip duration, flight time, number of dives and time underwater per foraging trip), chick feeding rates and chick growth (peak mass, fledging mass and fledging age), daily energy expenditure and adult body condition. Data were log-transformed where necessary.

To examine the effect of SST on diet composition we used a two-pronged approach. To account for the fact that these data contained many zeros (prey item not present in a sample) which cannot be accommodated with simple data transformations, we first fitted a generalized linear model with binomial errors to test whether SST affected the probability of a diet item (*Calanus hyperboreus*, *C. glacialis*, and *C. finmarchicus*) to occur in a sample. In a second step we then tested whether the proportion of these items in the diet was related to SST, excluding all zeros. Data were arcsin-transformed for this analysis.

Similarly, we used a generalized linear model with binomial error to assess the effect of SST on fledging success. All statistical analyses were performed using R 12.2 (R Development Core Team 2010). Averages (X) are provided ± standard deviation.

Results:

We studied birds at three different localities in 2005-2007 (Fig. 1), where they foraged for zooplankton in surface waters (<40m). SST in foraging areas off the three study sites differed substantially ($F_{2,121} = 96.25$, $p < 0.001$) and this difference was consistent across years ($F_{2,121} = 2.03$, $p = 0.136$). SST was lowest around Kap Höegh ($X = 0.39\pm0.29°C$), intermediate around Hornsund ($X = 1.81\pm0.18°C$), and highest around Kongsfjorden ($X = 4.51\pm1.06°C$). Cold areas of the Greenland Sea favor larger copepods (*Calanus hyperboreus,* 7-8 mm long), and warmer areas favor smaller copepods (*C. Glacialis,* 3-5 mm long and *C. Finmarchicus* 2-4 mm long; Karnovsky *et al*. 2010). Studying food loads brought back to the colonies by breeding parents, we found that little auks fed primarily on copepods (68 − 97%). Diet was adjusted according to local copepod availability, with birds preferentially feeding on larger copepods in the colder water off Greenland (Table 2; Fig. 2A) and on smaller copepods in warmer water off Spitsbergen (Table 2; Fig. 2B and 2C). Birds also nearly doubled their foraging trip duration between colder and warmer water, and nearly tripled their foraging flight time (Table 2, Fig. 3A and 3B). However, the number of dives per foraging trip and time spent underwater per foraging trip was not significantly correlated with SST (Table 2, Fig.3C and 3D). This indicates that copepod swarms were similarly profitable once the birds were underwater, however, little auks breeding near warmer waters had to spend more time on the wing to reach them. Despite enhanced foraging activity over warmer water, little auk daily energy expenditures estimated by the doubly-labelled water method were unaffected by SST (Table2). We speculate that little auks might buffer higher foraging costs by reducing

their energetic investment into other activities, for instance by decreasing patrolling flight over the breeding site outside their actual foraging trips (a common and energetically costly behaviour in this species).

Crucially, plasticity in foraging behaviour allowed birds to balance their energy budgets, and to maintain chick provisioning rates across the SST range (Table 2). Chick growth curves were consequently similar when parents foraged in cold and warm water (Fig. 4A). In warmer water, chicks tended to reach higher peak mass and to fledge later (Table 2; but note the very low regression coefficients for both relationships: 0.048 and 0.040, respectively), yet the essential parameters of fledging mass and fledging success were unaffected by SST across the three study sites (Table 2). Further, there was no effect of SST on the body condition index of breeding little auks (Table 2; Fig. 4B), nor on adult survival (Table 3; Fig. 4C). There was nonetheless substantial inter-annual variability in adult survival especially at KH, strongly suggesting that this variable might also be driven by events occurring outside of the breeding season (see Lee *et al*. 2007).

Discussion:

Using our comparative framework across the Greenland Sea, we reject the hypothesis of a general impact of current Arctic Ocean warming on the fitness of the highly abundant, ecologically important little auk. During our study, the overall SST differential measured across study sites was >5°C. In oceanographic terms, this is a major difference, which is predicted to cause vast changes in zooplankton community composition (Beaugrand *et al*. 2009). Such a ΔSST is close to the maximum change of 7°C predicted for the North Atlantic in the 21st century (Karnovsky *et al*. 2010). We therefore consider this ΔSST and our study design adequate to test the impact of ocean warming on little auk ecophysiology.

One potential limitation of our study design is that we studied birds of the same species exposed to contrasted environmental conditions, however, these birds attended breeding colonies hundreds of km apart. There is therefore the possibility that observed patterns are not due to species-specific plasticity, but to micro-evolution of distinct groups within a meta-population. However, a study conducted in North Atlantic *alcidae* (the seabird family including little auks) demonstrated that distant breeding populations of the same species are genetically highly homogeneous, strongly suggesting intense genetic mixing, even between the most distant breeding sites (Riffaut *et al.* 2005). Furthermore, recent population genetic analyses of little auks breeding across the North Atlantic also show very high genetic mixing among populations (Wojczulanis-Jakubas *et al.* In prep.). It is therefore reasonable to assume that birds from our three study sites belong to the same population, with similar potential for ecophysiological plasticity.

Moreover, our analyses focused on the impact of ocean surface warming, which is in line with the major research objectives of the inter-governmental panel on the impact of climate change (IPCC, working group II) for their forthcoming 2014 assessment report. However, a series of other biotic and abiotic environmental variables may potentially affect the ecophysiology and fitness of seabirds such as little auks (e.g. wind and air temperature, competition, see Fort *et al.* 2009), and might explain the wide numerical range recorded for some variables, such as breeding success (61-98%) or annual adult survival (61-92%; Fig.6). Furthermore, some results specific to the Hornsund (HS) site which deviate from the general, significant trends presented in Fig 3C and 3D suggest the existence of locally different functional relationships between SST and seabird foraging parameters. These aspects deserve further investigation, yet there is compelling evidence that water temperature is the single most important environmental parameter within oceanic ecosystems, and that its rapid increase is currently

triggering a complete reorganisation of the plankton community upon which little auks feed in the North Atlantic (Beaugrand *et al*. 2009; 2010).

Beyond these caveats, our findings are important for a better understanding of the short-term plastic responses of marine polar organisms to rapid ocean warming, for studies modelling the ecological impact of current and future Arctic climate change, and for the design of ecological monitoring of a warming Arctic (Grémillet & Charmantier 2010). In particular, our study is among the first to assess the capacity of a marine predator to buffer the consequences of climate change. Our conclusions are coherent with those of recent investigations which stress that behavioural plasticity is the primary mechanism by which animals deal with the consequences of climate change (Bradshaw & Holzapfel 2006; Charmantier *et al*. 2008; Kearney *et al*. 2009). Thus far, a wide range of studies have identified correlations between climate variables, the distribution, phenology, and dynamics of wild populations (Parmesan & Yohe 2003). Such evidence has played a key role in demonstrating the ecological consequences of ongoing climate change, and these correlations have been used to design climate envelope models to forecast future trends (Sommer *et al*. 2010). Behavioural plasticity demonstrated here significantly attenuates the impact of anticipated climatic effects undermining the ability of envelope models to realistically mirror future trends. Our data therefore underline recent criticism of such models (Morin & Thuiller 2009), and support the proposed development of mechanistic models as an alternative (Buckley *et al*. 2010). These novel tools are powerful and can be better validated, yet they require vast amounts of information relative to the functional ecology of the species concerned. In this context, our detailed study of the ecophysiology of little auks facing the consequences of climate change is a crucial step towards developing mechanistic models of the impact of climate change upon marine organisms (Fort *et al*. 2009).

During the study period, little auks maintained their fitness despite contrasting ocean surface temperatures and copepod availability across the Greenland Sea. This indicates that they are successful at dealing with the impact of current climate change in the Arctic. However, recent experiments and modelling strongly suggest that little auks function close to their maximum foraging capabilities, and will not cope with further degradation of their feeding conditions (Karnovsky *et al*. 2010). Indeed, breeding little auks for which flight costs had been artificially augmented had significantly lower body masses, and fledged considerably lighter chicks (Harding *et al*. 2009b). Consequently, we argue that even if little auks seem currently able to buffer the consequences of climate change in the North Atlantic, such abilities will not extend indefinitely. Following rapid North Atlantic warming, the 5°C isotherm will soon reach the East Greenland coast at 70°N and West Spitsbergen at 80°N. This will not only exclude large *C. Hyperboreus* copepods whose thermal preferendum lies between -2° and +4°C (Karnovsky et al. 2010), but may also favour 'southern invaders,' such as *Metridia lucens*, which are currently absent from the area. It remains to be tested whether little auks will manage to efficiently feed upon these organisms, an adaptation which will require morphological (bill shape), physiological (digestion) and behavioural plasticity. Understanding the limits of such plasticity is essential for the mechanistic modelling of climate effects on little auks and other organisms to achieve its potential.

References:

Anderson, D.R. & Burnham, K.P. (1999). General strategies for the analysis of ringing data. *Bird Study* 46, S261-270.

Beaugrand, G., Edwards, M. & Legendre, L. (2010). Marine biodiversity, ecosystem functioning, and carbon cycles. *Proc. Natl. Acad. Sci. USA* 107, 10120-10124.

Beaugrand, G., Luczak, C. & Edwards, M. (2009). Rapid biogeographical plankton shifts in the North Atlantic Ocean. *Glob. Change Biol.* 15, 1790-1803.

Bradshaw, W.E. & Holzapfel, C.M. (2006). Evolutionary response to rapid climate change. *Science* 312, 1477–1478.

Brown, C.J., Schoeman, D.S., Sydeman, W.J., Brander, K., Buckley, L., Burrows, M., Duarte, C.M., Moore, P.J., Pandolfi, J.M., Poloczanska, E., Venables, W. & Richardson, A.J. (2010). Quantitative approaches in climate change ecology. *Global Change Biol.* (in press).

Buckley, L.B., Urban, M.C., Angilletta, M.J., Crozier, L.G., Rissler, L.J. & Sears, M.W. (2010). Can mechanism inform species' distribution models? *Ecol. Lett.* 13, 1041-1054.

Burnham, K.P. & Anderson, D.R. (2002). *Model Selection and Multimodel Inference: A Practical Information-Theoretical Approach.* 2nd ed. Springer Verlag, New York.

Charmantier, A., McCleery, R.H., Cole, L.R., Perrins, C., Kruuk, L.E.B. & Sheldon, B.C. (2008) Adaptive phenotypic plasticity in response to climate change in a wild bird population. *Science*, 320, 800–803.

Choquet, R., Lebreton, J.-D., Gimenez, O., Reboulet, A.-M. & Pradel, R.(2009). U-CARE : Utilities for performing goodness of fit tests and manipulating capture-recapture data. *Ecography* 32, 1071-1074.

Dmitrenko, I.A., Polyakov, I.V., Kirillov, S.A., Timokhov, L.A., Frolov, I.E., Sokolov, V.T., Simmons, H.L., Ivanov, V.V. & Walsh, D. (2008). Toward a warmer Arctic Ocean: Spreading of the early 21st century Atlantic Water warm anomaly along the Eurasian Basin margins. *J. Geophys. Res.* 113, C05023.

Etterson, J.R. & Shaw, R.G. (2001). Constraint to Adaptive Evolution in response to Climate Change. *Science* 294: 151-154.

Fort, J., Porter, W.P. & Grémillet, D. (2009). Thermodynamic modelling predicts energetic bottleneck for seabirds wintering in the northwest Atlantic. *J. Exp. Biol*. 212, 2483-2490.

Grémillet, D. & Charmantier A. (2010) Shifts in phenotypic plasticity constrain the value of seabirds as ecological indicators of marine ecosystems. *Ecol. Appl*. 20, 1498-1503.

Graversen, R.G., Mauritsen, T., Tjernström, M., Källen, E. & Svensson, G. (2008). Vertical structure of recent Arctic warming. *Nature* 451, 53-56.

Harding, A.M.A., Van Pelt, T.I., Lifjeld, J.T.& Mehlum, F. (2004). Sex differences in little auk *Alle alle* parental care: transition from biparental to paternal-only care. *Ibis* 146, 642-651.

Harding, A.M.A., Egevang, C., Walkusz, W., Merkel, F., Blanc, S. & Grémillet, D. (2009a). Estimating prey capture rates of a planktivorous seabird, the little auk (*Alle alle*), using diet, diving behaviour, and energy consumption. *Polar Biol*. 32, 785-796.

Harding A.M.A., Kitaysky A.S., Hall, M.E., Welcker, J., Karnovsky, N.J., Talbot, S.L., Hamer, K.C. & Grémillet D. (2009b). Flexibility in the parental effort of an Arctic-breeding seabird. *Funct. Ecol.* 23: 348-358.

Harding, A.M.A., Welcker J., Steen, H., Hamer, K.C., Kitaysky A.S., Fort, J., Talbot, S.L., Cornick, L.A., Karnovsky, N.J., Gabrielsen, G.W. & Grémillet D. (2011). Adverse foraging conditions may impact body mass and survival of a high Arctic Seabird. *Oecologia* 167: 49-59.

Karnovsky, N.J. & Hunt, G.L. Jr. (2002). Estimation of carbon flux to dovekies (*Alle alle*) in the North Water. *Deep-Sea Res. II* 49, 5117–5130.

Karnovsky, N., Harding, A.M.A., Walkusz, V., Kwaśniewski, S., Goszczko, I., Wiktor, J., Routti, H., Bailey, A., McFadden, L., Brown, Z., Beaugrand, G. & Grémillet, D. (2010). Foraging distributions of little auks (*Alle alle*) across the Greenland Sea: Implications of present and future climate change. *Mar. Ecol. Progr. Ser.* 415, 283-293.

Kearney, M., Shine, R. & Porter, W.P. (2009). The potential for behavioral thermoregulation to buffer ''coldblooded'' animals against climate warming. *Proc. Natl. Acad. Sci. USA* 106, 3835–3840.

Kwaśniewski, S., Hop, H., Falk-Petersen, S.& Pedersen, G. (2003). Distribution of *Calanus* species in Kongsfjorden, a glacial fjord in Svalbard. *J. Plankton Res.* 25, 1–20.

Morin, X. & Thuiller, W. (2009). Comparing niche- and process-based models to reduce prediction uncertainty in species range shifts under climate change. *Ecology* 90, 1301-1313.

Parmesan, C. & Yohe, G. (2003). A globally coherent fingerprint of climate change impacts across natural systems. *Nature* 421, 37-42.

Polyakov, I. V., *et al.* (2005). One more step toward a warmer Arctic. *Geophys. Res. Lett.*, 32, L17605.

Pradel, R. (1993). Flexibility in survival analysis from recapture data: Handling trap-dependence. In: *Marked individuals in the study of bird population* (eds. Lebreton, J.-D. & North, P.M.) Birkhaüser Verlag, Basel, pp. 29-37.

Riffaut, L., McCoy, K.D., Tirard, C., Friesen, V.L. & Boulinier, T. (2005). Population genetics of the common guillemot *Uria aalge* in the North Atlantic: geographic impact of oil spills. *Mar. Ecol. Progr. Ser.* 291, 263-273.

Stempniewicz L (2001). Alle alle Little Auk. The journal of the birds of the western palearctic. BWP Update, vol. 3. Oxford University Press, Oxford, pp 175–201.

Serreze, M.C., Holland, M.M. & Stroeve, J. (2007). Perspectives on the Arctic's shrinking sea ice cover. *Science*, 315, 1533-1536.

Sommer, J.H., Kreft, H., Kier, G., Jetz, W., Mutke, J. & Barthlott, W. (2010). Projected impacts of climate change on regional capacities for global plant species richness. *Proc. Roy. Soc. B*. 277, 2271-2280.

Speakman, J.R. (1997) *Doubly labelled water: theory and practice*. Chapman and Hall, New York.

Walczowski, W. & Piechura, J. (2006). New evidence of warming propagating toward the Arctic Ocean. *Geophys. Res. Lett.,* 33, L12601.

Welcker, J., Harding, A.M.A., Karnovsky, N.J., Steen, H., Strøm, H. & Gabrielsen, G.W. (2009a). Flexibility in the bimodal foraging strategy of a high Arctic alcid, the little auk *Alle alle*. *J. Avian Biol.* 40, 388-399.

Welcker, J., Harding, A.M.A., Kitaysky, A.S., Speakman, J.R. & Gabrielsen, G.W. (2009b). Daily energy expenditure increases in response to low nutritional stress in an Arctic-breeding seabird with no effect on mortality. *Funct. Ecol.* 23, 1081-1090.

Wernberg, T., Thomsen, M.S., Tuya, F., Kendrick, G.A., Staehr, P.A. & Toohey, B.D. (2010). Decreasing resilience of kelp beds along a latitudinal gradient: potential implications of a warmer future. *Ecol. Lett*. 13, 685-694.

White, G. C. & Burnham, K.P. (1999). Program MARK: survival estimation from populations of marked animals. *Bird Study* 46, S120–139.

Wojczulanis-Jakubas, K., Jakubas, D., Harding, A.M.A., Karnovsky, N.J., Steen, H., Strøm, H., Welcker, J., Boertman, D.M., Gavrilo, M., Johnsen, A., Lifjeld J.T. (in prep.) The most numerous Palearctic seabird - little auk constitutes one panmictic population.

Table 1. Summary table of sample sizes for measurements conducted at the different study sites in different years. 'SST' is sea-surface temperature (number of days for which satellite data were available). 'Foraging' is the number of birds equipped with TDRs. 'Chick feeding' is the number of birds for which chick feeding rates were determined. 'FMR' is the number of birds for which field metabolic rate was estimated. 'Reproduction' is the overall number of nests for which breeding parameters were determined, yet growth rates and fledging masses were only determined at KH and HS (see methods). 'Condition' is the total number of adult birds weighed and measured. The survival analysis was conducted up to 2009 and sampling details specific to this aspect are provided in the methods section

|	Kap Höegh (KH)			Hornsund (HS)			Kongsfjorden (KF)	
	2005	2006	2007	2005	2006	2007	2006	2007
SST	18	18	7	31	30	12	13	13
Diet	20	24	22	33	30	23	22	22
Foraging			6			11		7
Chick feeding	18	14	15			13	22	38
FMR	15	12					16	27
Reproduction	31	29	32	10	47	41	29	41
Body condition	78	140	86	38	36	45	352	296

Table 2. Summary of statistical analyses testing the potential link between SST and different seabird parameters. Statistical tests are based on least squares linear regressions except for diet probabilities (probability of a prey item to occur in a diet sample) and breeding success for which a relationship with SST was assessed by generalized linear models with binomial errors. See Methods for details. Significant p-values (p<0.005) are highlighted in bold.

| Variable	Estimate	SE	t-value	df	p-value	R^2
Diet proportion *C. hyperboreus*	-0.085	0.015	-5.841	117	**<0.0001**	0.226
Diet proportion *C. glacialis*	0.087	0.017	5.267	192	**<0.0001**	0.126
Diet proportion *C. finmarchicus*	0.022	0.004	5.093	186	**<0.0001**	0.122
Diet probability *C. hyperboreus*	-1.298	0.229	-5.677[1]	193	**<0.0001**	
Diet probability *C. glacialis*	2.378	0.938	2.536[1]	193	**0.011**	
Diet probability *C. finmarchicus*	0.354	0.107	3.313[1]	193	**<0.0001**	
Foraging trip duration	0.930	0.264	3.520	22	**0.0019**	0.331
Flight time per foraging trip	0.960	0.142	6.775	22	**<0.0001**	0.661
Dives per foraging trip	-0.552	14.145	-0.039	22	0.97	0.045
Time underwater per trip	0.093	0.195	0.477	22	0.638	0.035
FMR	-4.072	9.657	-0.422	68	0.675	0.003
Chick feeding	-0.004	0.017	0.258	118	0.797	0.0006
Chick peak mass	0.028	0.011	2.454	120	**0.0155**	0.048
Chick fledging age	0.008	0.003	2.873	197	**0.0045**	0.040
Chick fledging mass	0.440	1.160	0.380	120	0.705	0.001
Fledging success	-0.026	0.087	-0.304[1]	339	0.761	
Body condition	0.278	0.146	1.908	1041	0.057	0.003

[1] z-value

Table 3. Survival modelling for adult little auks from Kap Höegh (KH) and Kongsfjorden (KF) in 2006-2009. The five most parcimonous models according to AICc are given out of the possible models allowing survival probabilities to vary with time and/or colony and/or SST that were tested. Φ = apparent (yearly) survival; p = resighting probability; c = colony (KH vs. KF); t = time; h = resighting heterogeneity (h1 extending one year, h2 extending 2 years).

| Φ	p	deviance	# parameter	ΔAICc	AICc weight	Model likelihood
c*t	h2	856.71	9	0	0.424	1
c *t	c +h2	855.59	10	0.909	0.269	0.635
c *t	h1	860.21	8	1.461	0.204	0.482
c *t	c +h1	859.57	9	2.860	0.102	0.239
c *SST	h2	878.70	7	17.93	0.00005	0.0001
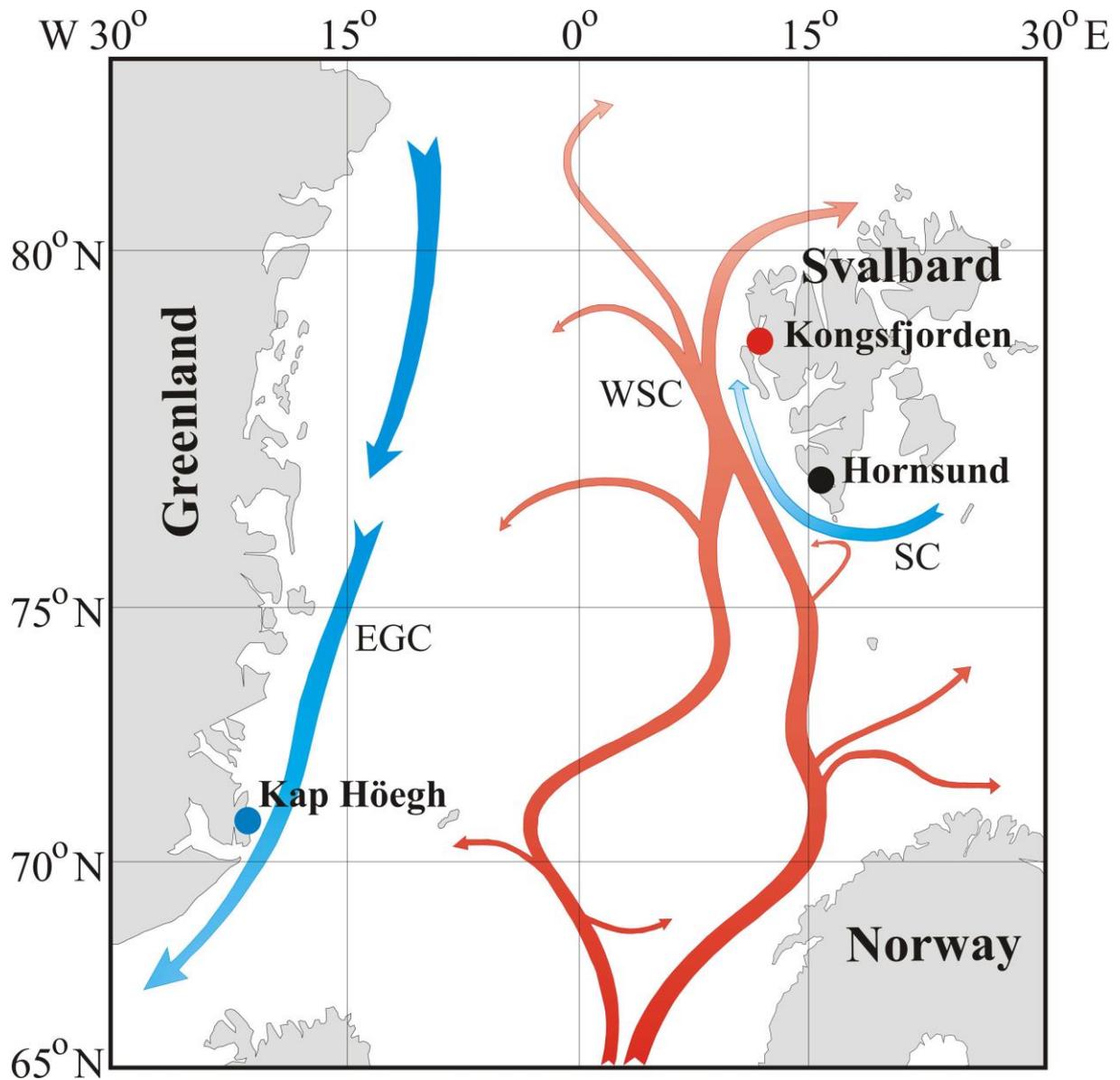
Fig. 1. Position of the three study sites in the Greenland Sea. The East Greenland Current (ECG) maintains cold water conditions off Kap Höegh. Off Hornsund, the cold Sørkapp Current (SC) and the warm West Spitsbergen Current (WSC) provide intermediate water temperature conditions, whereas the WSC forces warmer Atlantic water into the Kongsfjorden area. The northernmost study site is therefore the warmest in terms of sea-surface temperature.
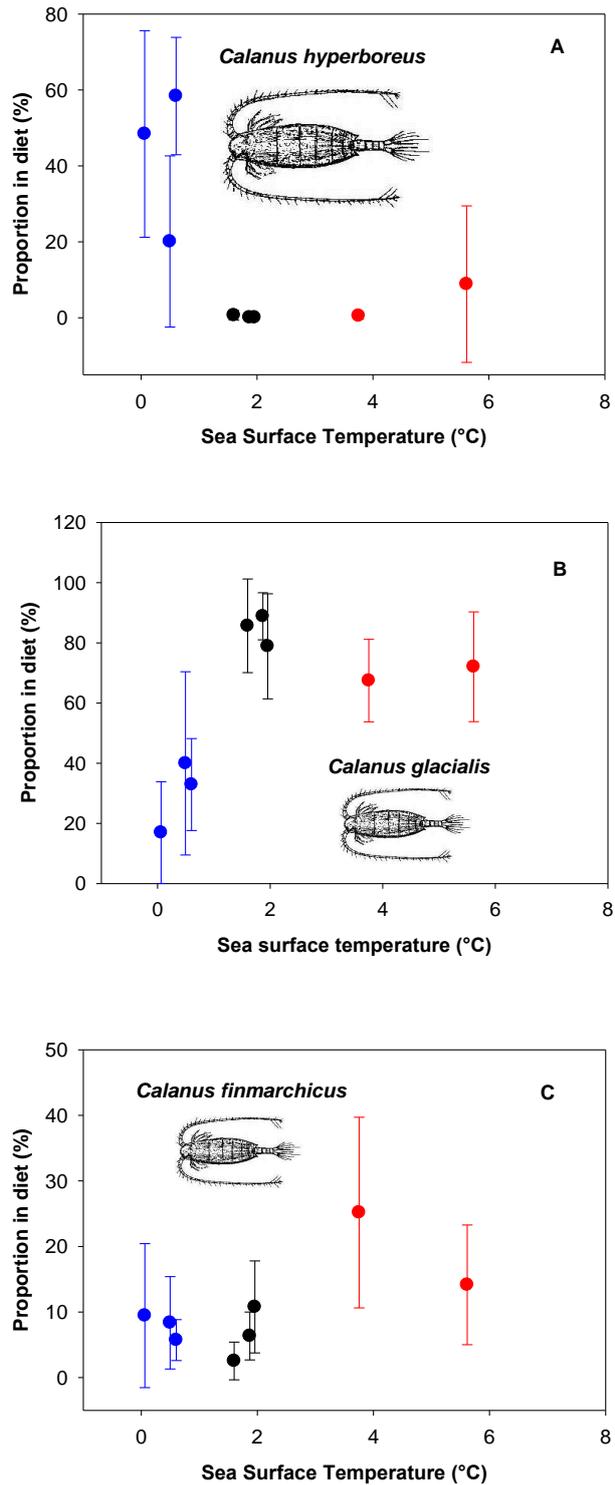
Fig. 2. Little auks feed preferentially on large copepods (*Calanus hyperboreus,* 7-8 mm long) in cold water (Fig. 2A) and on smaller copepods in warmer water (*Calanus glacialis*, 3-5 mm long, Fig. 2B and *Calanus finmarchicus,* 2-4 mm long, Fig. 2C), Kap Höegh in blue, Hornsund in black, and Kongsfjorden in red. See Table 2 for detailed statistics.
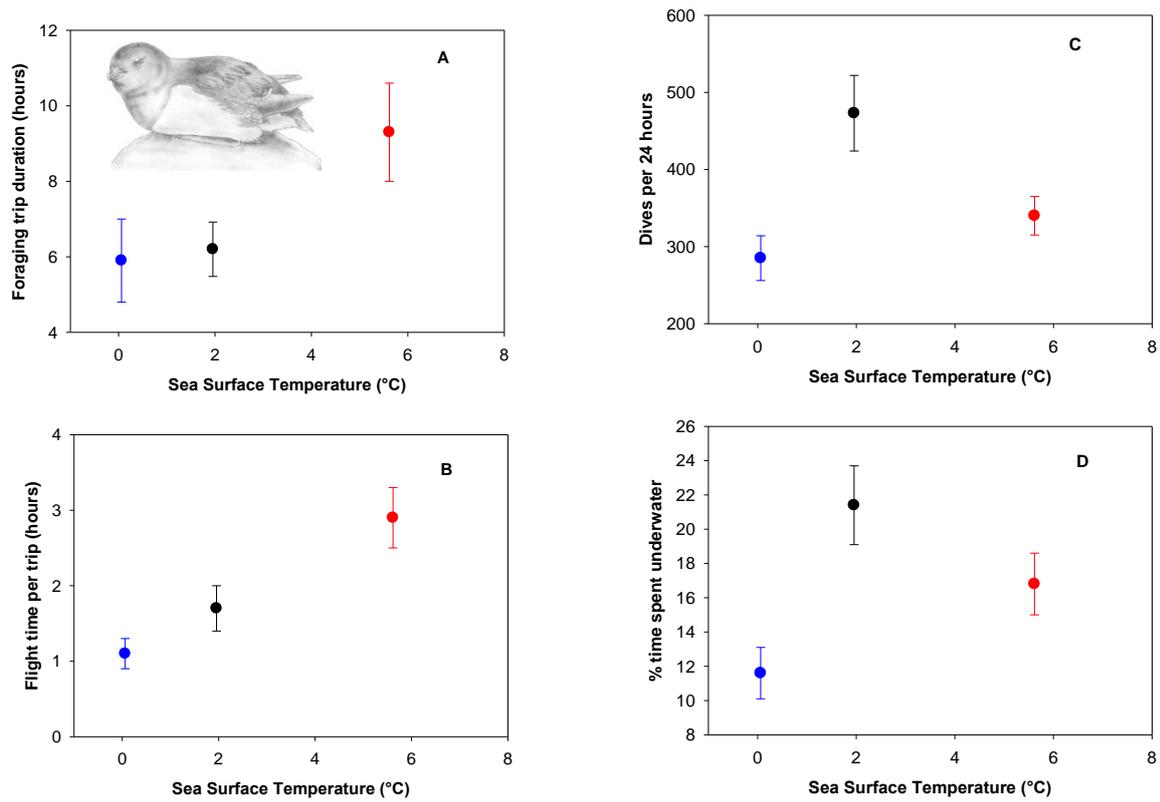
Fig. 3. Impact of SST upon little auk foraging trip duration (A), flight time per foraging trip (B), total number of dives per 24h (C) and proportion of time spent underwater (D; see Table 2 for statistical details). Data were recorded in 2007 (Kap Höegh in blue, Hornsund in black, and Kongsfjorden in red) using time-depth recorders deployed between 1.3 and 4.7 days ($X = 3\pm1$), recording between 2-14 foraging trips ($X = 7\pm3$) for each bird.
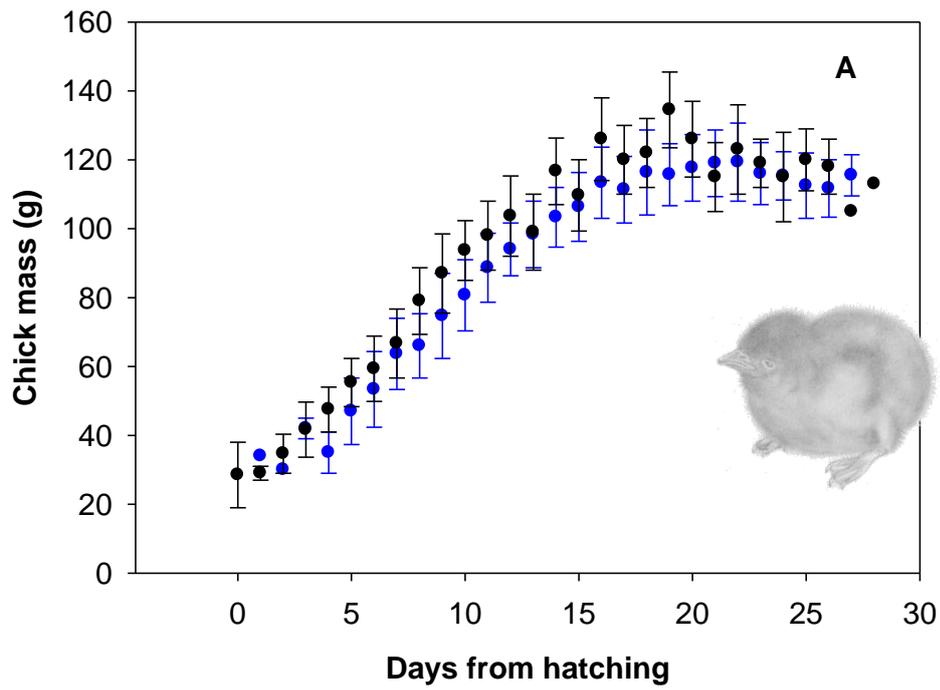
Fig. 4A. Average growth curves of little auk chicks in 2005-2007 at Kap Höegh (colder water, in blue) and Hornsund (warmer water, in black). See Table 2 for detailed statistics.
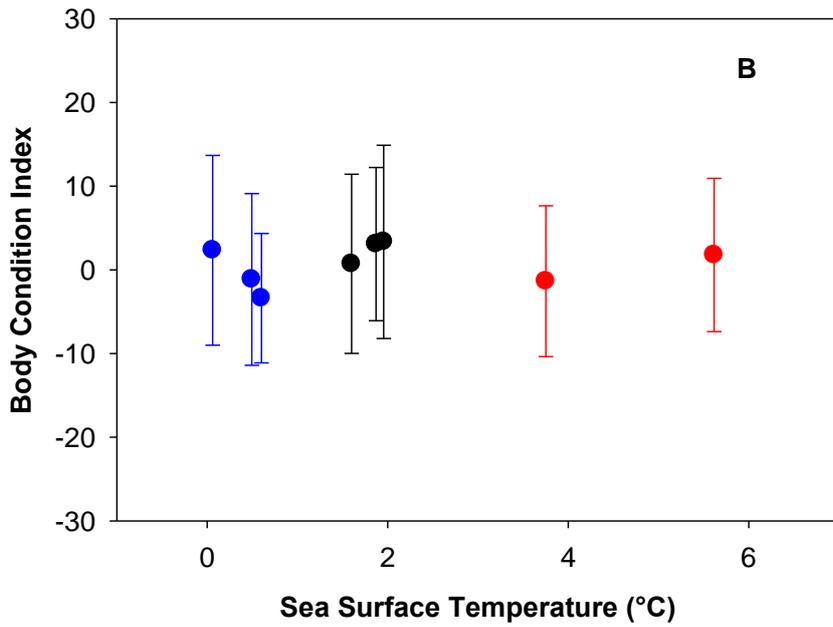
Fig. 4B. No effect of water temperature on the body condition index of adult little auks breeding at three Greenland Sea colonies (Kap Höegh in blue, Hornsund in black, and Kongsfjorden in red) in different years. See Table 2 for detailed statistics.
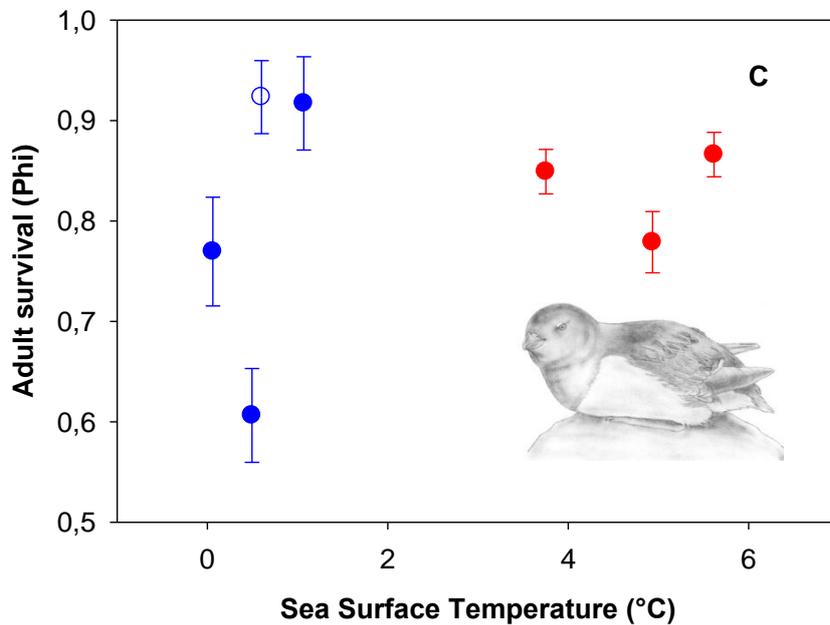
Fig. 4C. No effect of water temperature on the survival rate of adult little auks breeding at two Greenland Sea colonies (Kap Höegh in blue, Kongsfjorden in red) in different years. The best model including SST was 17.9 AICc units less well supported than the best model without an effect of SST. Note substantial annual variation in adult survival at Kap Höegh (open symbol showing 2005 data point). See Table 3 for detailed statistics.