UNIVERSITÉ DU QUÉBEC

CLIMATE VARIATION, ARTHROPOD ABUNDANCE AND BREEDING

PHENOLOGY OF TWO SHOREBIRD SPECIES BREEDING IN THE HIGH ARCTIC

RAPPORT DE RECHERCHE

PRÉSENTÉ À

L'UNIVERSITÉ DU QUÉBEC À RIMOUSKI

Comme exigence partielle

du programme de

Maîtrise en gestion de la faune et de ses habitats

PAR

MAUDE PICOTIN

DÉCEMBRE, 2007

REMERCIEMENTS

Merci à tous ceux qui ont travaillé pour que je puisse faire la maîtrise professionnelle;

Merci à Joël pour m'avoir guidée, dirigée, aidée tout au long de mon D.E.S.S. et de ma maîtrise;

Merci à Laura, Maude, Benoît, Nicolas, Valérie, Ludovic et Robert pour le travail sur le terrain et dans le labo;

Merci à Laura aussi pour son aide, sa disponibilité et sa générosité, à Ludovic pour m'avoir aidée à m'y retrouver avec les arthropodes, à Manon pour m'avoir aidée à m'y retrouver avec les régressions, et à Alain pour son aide avec les statistiques;

Merci à ma famille, maman, papa, Marie-Eve, grand-maman, sans le soutien moral, affectif et financier de qui je n'aurais pu poursuivre des études graduées;

Merci enfin à Daniel, pour avoir accepté de ne me voir qu'une fin de semaine sur deux pendant quatre sessions, pour ses encouragements, son aide, et tout son amour.

RÉSUMÉ

Les changements climatiques n'affectent pas tous les niveaux de la chaîne trophique de la même manière. Il est donc important de comprendre les interactions entre ces différents niveaux afin d'être plus à même d'anticiper les effets et conséquences du réchauffement climatique. Dans les environnements sujets à une forte saisonnalité, tel l'Arctique, il est d'autant plus important pour les oiseaux de synchroniser le moment de leur reproduction avec la courte période d'abondance de ressources alimentaires. La date optimale d'éclosion survient généralement légèrement avant le pic de disponibilité de nourriture, maximisant le taux de croissance des oisillons. Les oiseaux migrant sur de longues distances peuvent être particulièrement vulnérables à une perte de synchronie, qui peut mener à un déclin de population. Nous avons étudié la relation entre les variations climatiques, des ressources alimentaires (arthropodes) et la phénologie de la reproduction de deux espèces de bécasseaux, le bécasseau à croupion blanc (*Calidris fuscicollis*) et le bécasseau de Baird (*Calidris bairdii*). Ces deux espèces effectuent de longues migrations et se reproduisent en Arctique. Nous avons suivi la reproduction des oiseaux, échantillonné leur ressource alimentaire (arthropodes terrestres de surface) et enregistré les conditions climatiques (température et couverture neigeuse) durant les saisons estivales 2005 et 2006 à l'île Bylot (Nunavut, Canada). La date médiane d'éclosion des deux espèces précédait le pic d'abondance d'arthropodes de quelques jours, qui lui-même suivait ou précédait légèrement le pic de température journalière estivale. Nous avons étudié les changements de température durant les différentes périodes du cycle de reproduction des bécasseaux sur l'île Bylot au cours des 5 dernières décennies. Nous avons trouvé une diminution significative de la température moyenne de l'air durant l'été de 1950 à 1972 (-0,6°C par décennie) suivie d'une augmentation significative entre 1973 et 2006 (0,4°C par décennie). Les hausses de températures les plus prononcées sont survenues durant la période précédant la reproduction des bécasseaux et durant la période d'élevage des oisillons (environ 0,7°C par décennie). Les températures enregistrées récemment sont similaires à celles observées il y a plus de 50 ans. Les deux espèces à l'étude avaient tendance à se reproduire légèrement plus tôt en 2005 et 2006 qu'en 1954 (date médiane d'éclosion 2 à 9 jours plus hâtive). En général, nos résultats suggèrent que les espèces de limicoles les plus communes se reproduisant sur l'île Bylot réussissent jusqu'à maintenant à suivre adéquatement les changements climatiques récents (i.e. la phénologie de leur reproduction est bien synchronisée avec les changements saisonniers de la disponibilité d'arthropodes). Nous concluons qu'il est peu probable que la perte de synchronie soit un facteur affectant négativement les populations de ces espèces migrants sur de longues distances et se reproduisant dans l'est du Haut Arctique.

ABSTRACT

Climate change does not affect all levels of the food web in the same way. It is therefore important to understand the interactions between different components of the food chain and investigate their responses to temperature changes in order to anticipate consequences of global warming. In environments characterised by strong seasonality, such as the arctic tundra, it is critical for breeding birds to synchronize their timing of breeding with the short period of high food abundance. Optimal hatch date usually occurs slightly before the peak in food availability and maximises chick growth rate. Lack of synchrony can lead to population decline and long distance migrants can be particularly vulnerable to a mismatch. We studied the relationship between climatic conditions, seasonal variation in food resources and breeding phenology of two long-distance migrants, the White-rumped Sandpiper (*Calidris fuscicollis*) and the Baird's Sandpiper (*Calidris bairdii*), breeding in the High Arctic. We monitored bird reproduction, sampled their food (surface-active and low- flying terrestrial arthropods) and monitored climatic conditions (temperature and snow cover) during the summer 2005 and 2006 on Bylot Island (Nunavut, Canada). The median hatching dates for the two species were a few days before the peak in arthropod abundance, which in turn was slightly after or before the summer peak in air temperature. We investigated changes in air temperatures from the Bylot Island area during the different phases of the shorebirds breeding cycle over the last 5 decades. We found a significant decline in summer mean air temperature from 1950 to 1972 (-0.6°C per decade) followed by a significant increase from 1973 to 2006 (0.4°C per decade). The temperature increase was more pronounced during the pre-breeding and brood-rearing periods (about 0.7°C per decade). Recently recorded temperatures were similar to those observed over 50 years ago. The two study species tended to breed slightly earlier in 2005/2006 compared to 1954 (median hatch dates being 2 to 9 days earlier). Overall, our results suggest the most common sandpipers breeding on Bylot Island are, so far, adequately tracking recent climate warming (i.e., their breeding phenology is well synchronised with seasonal changes in arthropod availability). We conclude that a mismatch is an unlikely factor negatively affecting populations of these long-distance migrants breeding in the eastern High Arctic.

TABLE DES MATIÈRES

LISTE DES TABLEAUX

LISTE DES FIGURES

LISTE DES ANNEXES

INTRODUCTION

Over the last 6 decades, the mean annual temperature in Canada has increased by 0.9°C (Environnement Canada 2007). An important aspect of climate change is its inconsistency (Houghton 2004); its rate varies with time and its magnitude is not constant throughout the planet (Walther *et al.* 2002; Strode 2003). The magnitude of warming in the Arctic over the last decades has been approximately twice as high as the global rate (Anisimov *et al.* 2007).

Many studies have demonstrated advancement in the phenology of plants, insects and birds following global warming (Hughes 2000; McCarty 2001; Peñuelas and Filella 2001; Walther *et al.* 2002; Pearce-Higgins *et al.* 2005). However, climate change does not affect all levels of the food web the same way. While the phenology of plants and arthropods is known to be strongly dependent on local abiotic environmental factors (e.g., temperature, moisture, snow cover, photoperiod; Hodkinson *et al.* 1996; Thórhallsdóttir 1998; Molau *et al.* 2005), the phenology of migrating birds is, however, affected by a combination of biotic and abiotic factors acting along their entire migratory route (e.g., photoperiod, ambient temperature, food supply; Gwinner 1996; Strode 2003; Visser *et al.* 2004; Meltofte *et al.* 2007).

In order to maximize their breeding success, birds have to match their timing of reproduction with the peak in food abundance. Optimal hatching date is generally a few days before food peak (Dias and Blondel 1996; Visser *et al.* 2006). As the phenology of the different components of the food chain is regulated by different variables, climate change can cause a mismatch between the demands of the nestlings and the peak in food supply (Visser *et al.* 1998; Visser *et al.* 2004). Consequences of such a mismatch can include a reduction of juvenile growth and survival rising from a reduction in feeding rates (Sanz *et al.* 2003), an increase in parental foraging costs leading to a decrease in adult survival (Thomas *et al.* 2001) and, ultimately, a decline in bird populations (Visser *et al.* 2004).

In a strongly seasonal environment such as the arctic tundra, seasonal changes in food availability for birds generally show a pronounced peak and is strongly weather dependent (Schekkerman *et al.* 2004). It is therefore particularly critical for arctic birds to match their timing of reproduction with the short period of high food abundance (Berteaux *et al.* 2004). This can be particularly challenging for long-distance migrants that, by not detecting changes occurring on their breeding grounds, could arrive at an improper time to exploit the resources optimally (Sanz *et al.* 2003).

Worldwide, nearly half of the wader populations with known population trend are declining (International Wader Study Group 2003). Many hypotheses explaining this trend have been suggested and tested, notably habitat loss and degradation (Morrison *et al.* 1994;

International Wader Study Group 2003; Thomas *et al.* 2006), increased disturbance from human activities and predators (Morrison *et al.* 1994; Thomas *et al.* 2006), and climatic conditions on the breeding grounds (Morrison *et al.* 1994) and during migration (Thomas *et al.* 2006).

One additional potential cause of the population decline observed in arctic-breeding waders may rest in the possible asynchrony between the bird breeding phenology and the peak abundance of their food source, arising from their different responses to climate change (Pearce-Higgins *et al.* 2005). Relationships between global warming, bird reproduction and food abundance have been mainly studied with temperate-breeding species (Both and Viser 2001; Sanz *et al.* 2003; Strode 2003; Both, Bijlsma and Visser 2005; Both and Visser 2005). Many studies found similar trends in phenological changes for birds and their food resources, although they do not always occur at the same pace (Visser *et al.* 1998; Pearce-Higgins *et al.* 2005; Visser *et al.* 2006).

The main objective of our study was to link seasonal changes in temperature and arthropod abundance with the timing of reproduction of two shorebird species breeding on Bylot Island in the Canadian High Arctic, the White-rumped Sandpiper (*Calidris fuscicollis*) and the Baird's Sandpiper (*Calidris bairdii*). The study species are long-distance migrants that winter in South America. They are both insectivorous, feeding on a wide variety of arthropods. We tested the hypothesis that recent global warming has lead to

a mismatch between the breeding phenology of these waders and the phenology of arctic arthropods. We investigated temperature changes over the last 5 decades around Bylot Island, and we monitored bird reproduction, seasonal changes in food supply (terrestrial arthropods) and temperature variation during the summer 2005 and 2006 on Bylot Island. Finally, we compared actual bird breeding phenology with data collected on the same species and at the same study site in 1954.

METHODS

Study area and shorebird species

Bylot Island is located north of Baffin Island, Nunavut Territory, Canada, and is part of the Arctic Cordillera (Lepage *et al.* 1998b). Our study was conducted from two camps on the island, the main camp, located in the Qarlikturvik Valley (73° 08' N, 80° 00' W) within Sirmilik National Park on Bylot Island, and a secondary camp located 30 km south of the main camp. Data obtained from both camps were pooled. The study area (approx. 16 km^2) is characterized by a polygon tundra wetland (Ellis and Rochefort 2004) and is located in the Prostrate Shrub zone (accordingly to the bioclimatic zones in the northern Canada, Geological Survey of Canada 2000). The vegetation is mainly dominated by sedges (primarily *Carex aquatilis* var. *strans*, *Eriophorus.scheuchzeri*, and *E. angustifolium*), by grasses (mostly *Dupontia fisheri*, *Arctagrostis latifolium* and *Pleuropogon sabinei*), and by fen mosses (*Drepanocladus* spp. and *Aulocomnium* spp.; Ellis and Rochefort 2004; Gauthier and Tardif 1991).

We studied two shorebird species that are common breeders on Bylot Island, the White-rumped Sandpiper (hereafter White-rumped) and the Baird's Sandpiper (hereafter Baird's). The White-rumped winter in southern South America (South Brazil, Argentina and Chile), reaching Tierra del Fuego and the Falkland Islands and their breeding grounds expand from northern Alaska across Canada to Baffin Island (Piersma *et al.* 1996; Montalti *et al.* 2003). Wintering grounds of Baird's are in Patagonia (south of Chile and Argentina;

Piersma *et al.* 1996). Their breeding grounds are very similar to those of the White-rumped, extending from western Alaska to Baffin Island and northern Greenland (Piersma *et al.* 1996). Both species generally arrive on Bylot Island in late May or very early June (L. McKinnon and J. Bêty unpublished data).

Both species can feed on a wide variety of insects and spiders during the breeding season (Drury 1961; Piersma *et al.* 1996; Montalti *et al.* 2003). When they arrive on the breeding area, they face poor feeding conditions and can supplement their diet with seeds and shoots (Piersma *et al.* 1996). White-rumped feed by deep probing in moss and wet vegetation and eat adult and larvae insects (beetles, craneflies), spiders, small molluscs, crustaceans, leeches, polychaete worms, earthworms and some seeds (Drury 1961; Piersma *et al.* 1996). White-rumped may be considered opportunistic feeders since it forages on different preys depending on area, season and availability (Montalti *et al.* 2003). Baird's mainly feed on surface living insects (Drury 1961). Their diet is primarily composed of insects (chironomids, cranefly larvae and adults, beetles) and spiders (Piersma *et al.* 1996), though they can also eat crustaceans and seeds (Drury 1961).

Recent and past climatic data

Weather data on Bylot Island were collected by an automated station that recorded weather variables on an hourly basis throughout the years, among which we used air temperature. This complete station was installed in the lowlands (20 m above sea level) in

1993 and has continuously recorded data since March 1994. Since 1995, snowmelt has also been monitored by measuring snow depth at 50 stations along two 250-m transects at 2-day intervals. We thus have summer climatic conditions on Bylot Island from 1994 to 2006. In order to estimate past climatic conditions on Bylot Island, we used data sets from Environment Canada weather stations located at Pond Inlet (72° 40' N, 77° 58' W; data from 1976 to 2006)), Resolute Bay (74° 43' N, 94° 59' W; data from 1950 to 2006) and Clyde River (70° 29' N, 68° 31' W; data from 1950 to 2006) airports (Environnement Canada 2006). We performed regression analyses of Pond Inlet temperatures at against temperatures at Bylot Island (period 1994-2006) to generate an equation allowing us to estimate summer temperatures at Bylot Island from 1976 to 1993. We then performed regression analyses of the temperatures at Resolute Bay and Clyde River against Pond Inlet temperatures (period 1976-2006) to generate estimates of summer temperature at Pond Inlet from 1950 to 1975. Those estimates were then used to assess past summer temperatures on Bylot Island (period 1950-1975). Dates were grouped and analyses were done according to different phases of the shorebird breeding cycle (Table 1).

Arthropod abundance, diversity and biomass

To observe seasonal changes in diversity and abundance of arthropods, modified Malaise traps were used to capture surface active and low-flying arthropods. Traps were composed of a 38 cm x 5 cm x 7 cm plastic pitfall trap filled with glycerine or soapy water above which were set a 50 cm vertical mesh screen and a bottle trap to increase the capture of flying insects. Eight traps in 2005 and ten in 2006 were deployed in both wetland and

mesic tundra, the two dominant foraging habitats used by the study species during the brood rearing period. The traps caught arthropods while they were in movement. Consequently, our trapping results likely reflect a combination of the seasonal changes in abundance and activity of the arthropods. We assumed that such data revealed variation in food availability for shorebirds as movement can increase prey detection probability. The traps were sampled every 2 days from June 19 to July 22 in 2005 and from June 12 to August 1 in 2006. The content of both the top bottle trap and the bottom pitfall trap were pooled and all samples were stored in whirlpaks with 70% ethanol before being sorted and identified to family. To account for different sampling efforts in 2005 and 2006 (8 and 10 traps respectively), total arthropod abundance was divided by the number of trap and thus expressed as number per trap.

Variation in arthropod individual biomass was investigated to better convert number of individual to biomass estimates. Using the specimens collected in 2005, each family was looked at to examine if individuals should be grouped in different size classes based on biomass. To estimate average biomass, subsets were made out of randomly chosen individuals for a given family or from each size class when needed (i.e., high individual variation). Specimens were dried to constant weight at 60°C. The average individual biomass for each family or size class was used to convert arthropods abundance measured collected in 2006 to total biomass measured. Such conversion was precluded for the 2005 samples as arthropods were counted without using any size class.

Shorebird breeding phenology

Active nest searching and subsequent monitoring was conducted for both bird species at the study sites. For each nest, incubation stage, egg measurements and number of eggs and/or young upon hatch was collected and used to estimate laying and hatching dates. Incubation stage was estimated using an egg buoyancy technique (Liebezeit *et al.* 2007). This technique uses the angle and height at which the egg floats in water to determine the proportion of incubation completed. The laying and hatching dates were estimated using 2 different techniques depending on the data available for each nest. A code was assigned to each nest to define how the dates were estimated. A code 1 was assigned to the following situations (estimated precision ± 1 days): 1) hatching date is known and corresponds to the day chicks were found in the nest; 2) hatching date corresponds to the day in between when the eggs were starred and chicks were found in the area of the nest (within 20 m radius); 3) hatching date corresponds to the day in between when the eggs were starred and the nest was found empty (no signs of predation); 4) nests found during the laying period. A code 2 was assigned to any nest where hatching and laying date were estimated using egg buoyancy technique only (estimated precision ± 2 days). For the nests found during incubation, laying date was estimated by subtracting from the observed or estimated hatching date, 21 days of incubation and the clutch size, assuming bird lays 1 egg/day (clutch size typically four eggs).

Data analysis

We performed a two-sided Fisher's exact test to verify if median laying and hatching dates of each bird species obtained with the 2 estimation methods (code 1 and code 2; see above) were different. We also compared breeding data obtained by Drury (1961) in 1954 and those recorded in 2005 and 2006 using the Fisher's exact test. Since we expected that the difference would be towards an earlier phenology in 2005 and 2006 due to recent warming, we performed a right-sided test. In his study, Drury reports observed hatching dates. To account for differences in the hatch date estimation methods between the studies, we adjusted our code 2 hatching dates (i.e., exact hatch date unknown, see above) by adding the average difference between the code 1 (hatching observed) and code 2 estimated dates for each species. We reported the results found with the standardized and un-standardized data. When there were two nests for which the hatch date was the same as the median, we placed one in the "above median" grouping and the other one in the "below median" grouping. When there was only one nest for which the hatch date was the same as the median, it was ignored from the test since we could not put it in one of the two grouping (above median or below median) without introducing a bias. These analyses were performed with SAS 8.2 (SAS Institute Inc., 1999). SYSTAT 11 (SYSTAT Software Inc., 2005) was used to perform regression analysis (predictive equations of weather conditions on Bylot Island; Table 1).

Table 1. Relationships between mean daily air temperatures measured on Bylot Island (BI), and Environment Canada weather stations located in Pond Inlet (PI), from 1976 to 2006, Resolute Bay (RB), from 1950 to 2006, and Clyde River (CR), from 1950 to 2006, following the shorebird breeding cycle. (A) Temperatures estimated at Pond inlet (1950 to 1975) using data from Resolute Bat and Clyde River and (B) temperatures estimated at Bylot Island (1950 to 1993) using known and estimated data at Pond Inlet

(A)

Period	Phase	Date	Equation	N (days)	R^2	P
Spring	Pre-breeding	May 10 to May 31	PI = 0.711 CR + 0.333 RB	601	0.90	< 0.001
Early summer	Laying*	June 1 to June 25	PI = 1.577 + 0.499 CR + 0.458 RB	687	0.67	< 0.001
Mid summer	Hatching**	June 26 to July 25	PI = 3.092 + 0.347 CR + 0.344 RB	833	0.31	< 0.001
Late summer	Brood-rearing	July 26 to August 25	PI = 2.414 + 0.376 CR + 0.414 RB	851	0.38	< 0.001

(B)

Period	Phase	Date	Equation	N (days)	R^2	P
Spring	Pre- breeding	May 10 to May 31	BI = -0.975 + 0.713 PI	221	0.77	< 0.001
Early summer	Laying*	June 1 to June 25	BI = 0.646 + 0.686 PI	251	0.71	< 0.001
Mid summer	Hatching**	June 26 to July 25	BI = 1.369 + 0.700 PI	321	0.56	< 0.001
Late summer	Brood- rearing	July 26 to August 25	BI = 0.770 PI	310	0.76	< 0.001

* Virtually all observed laying dates fall within this period.
** Include all observed hatching dates.

RESULTS

Climate (2005-2006)

We observed similar weather conditions in summer 2005 and 2006 (Table 2). Snowmelt pattern was also similar in both years, reaching 50% snow cover on June 11 and June 13 in 2005 and 2006 respectively.

Table 2. Mean, minimum and maximum daily temperatures for each period in the breeding cycle of the shorebirds in 2005 and 2006

| Breeding period	Year	Mean daily temperature	Minimum daily temperature	Maximum daily temperature
Pre-breeding	2005	-6.56°C	-14.22°C	1.33°C
	2006	-2.40°C	-7.81°C	1.62°C
Laying	2005	2.34°C	-0.29°C	4.43°C
	2006	1.93°C	-0.74°C	5.32°C
Hatching	2005	5.77°C	2.74°C	11.20°C
	2006	5.74°C	2.45°C	11.46°C
Brood-rearing	2005	5.31°C	3.14°C	7.62°C
	2006	6.34°C	2.62°C	10.78°C

Arthropod phenology (2005-2006)

A total of 29 717 arthropods were caught in 2005 (using 8 traps, from 19 June to 22 July) and 43 761 in 2006 (using 10 traps, from 12 June to 1 August; Table 3). Most of the specimens were Dipterans (93.6% in 2005 and 95.0% in 2006), Collembolans (4.6% and 3.1%), Coleopterans (1.2% and 0.3%) and spiders (0.6% and 1.6%). Dipterans and Coleopterans were identified to family. Families for which there were less than 10 individuals captured during the summer (Ephydridae, Heleomyzidae, Rhagionidae and Staphylinidae) were judged non-significant and were not included in the subsequent analyses (i.e., seasonal variations).

We calculated and used mean individual biomass to convert the 2006 abundance measures to total biomass (size class not available in 2005; see Appendix 1). Sphaeroceridae were excluded as we did not estimate individual biomass (no individual captured in 2005). Variations in arthropod abundance and biomass were overall strongly correlated ($r = 0.89$; $P < 0.005$, Figure 1), but the correlation was more pronounced after day 187 ($r = 0.99$; $P < 0.001$), which corresponded to the shorebird hatching period (see below).

Table 3. Total number of arthropods caught in 2005 and 2006 on Bylot Island. Eight traps were used in 2005 (June 19 to July 22) and 10 traps in 2006 (June 12 to August 1)
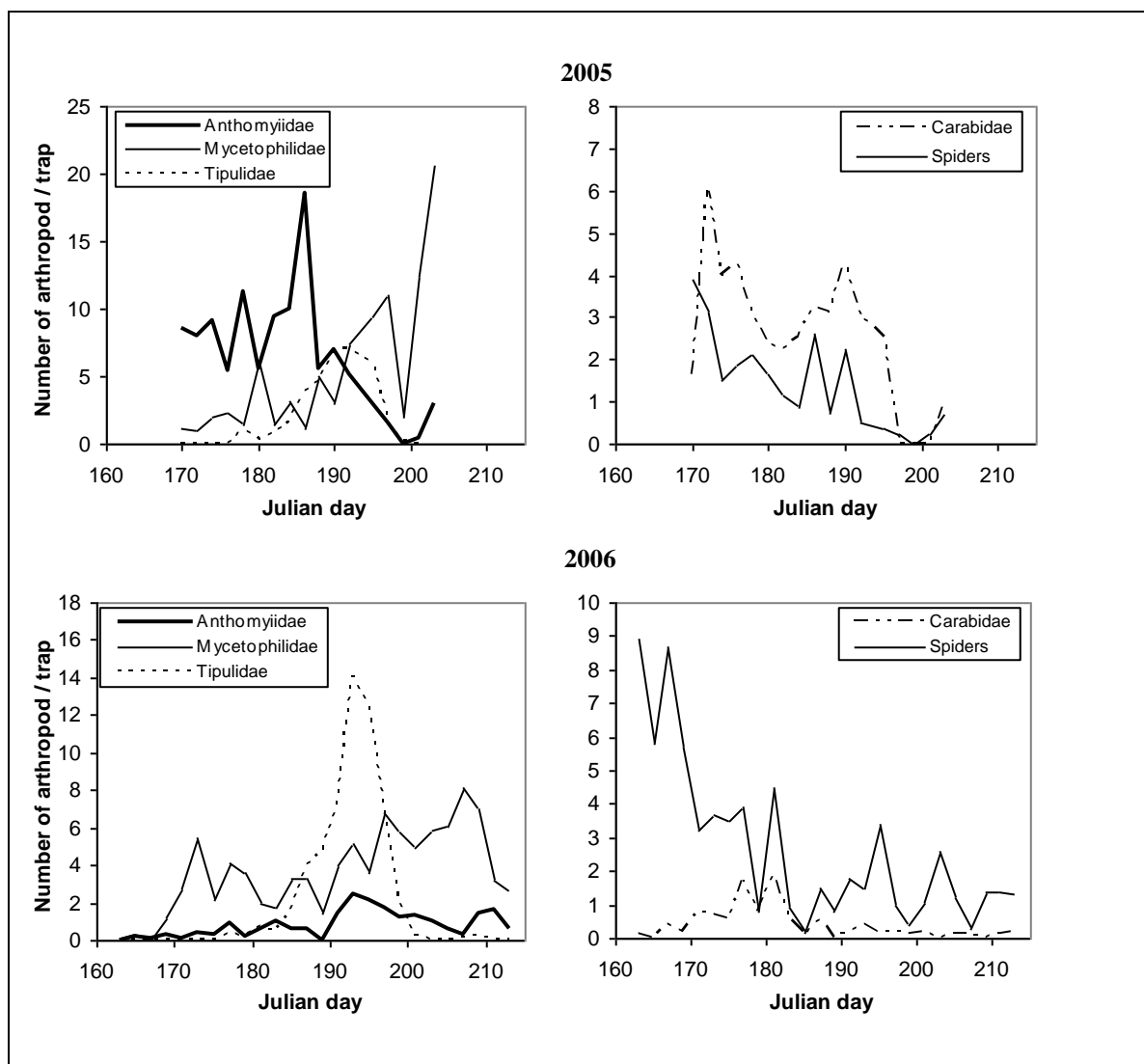
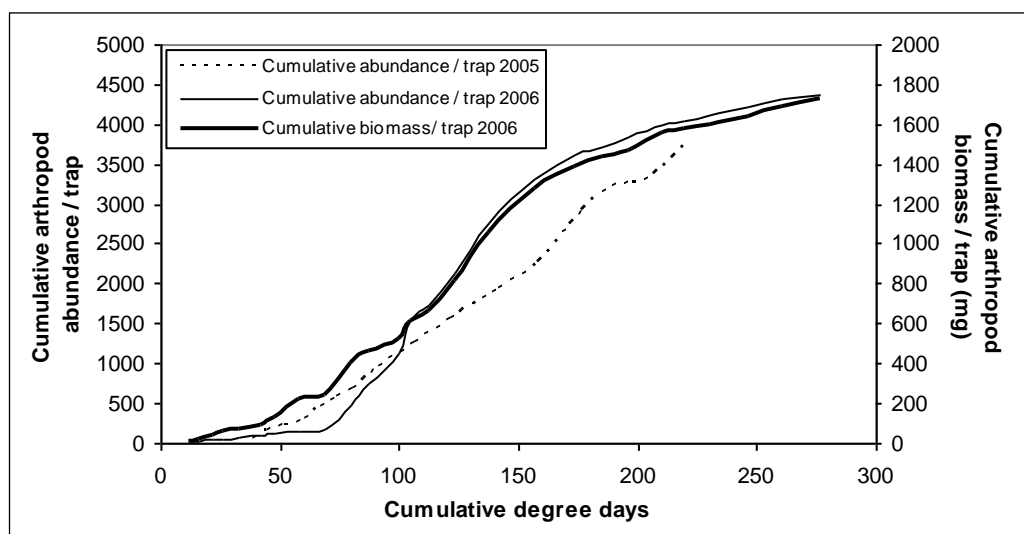| Arthropod	2005	2006	Arthropod	2005	2006
Anthomyiidae	896	212	Rhagionidae	2	0
Cecidomyiidae	265	768	Scathophagidae	96	146
Ceratopogonidae	729	1 146	Sciaridae	2 173	2 288
Chironomidae	15 433	29 020	Sphaeroceridae	0	47
Culicidae	101	127	Syrphidae	80	61
Dolichopodidae	31	603	Tachinidae	27	0
Empididae	763	2 748	Tipulidae	294	549
Ephydridae	4	4	Trichoceridae	76	215
Heleomyzidae	5	5	Carabidae	344	102
Muscidae	5 844	1 677	Curculionidae	22	14
Mycetophilidae	726	946	Staphylinidae	1	0
Phoridae	226	986	Collembolans	1 358	1 371
Piophilidae	30	31	Spiders	191	695
			Total	29 717	43 761
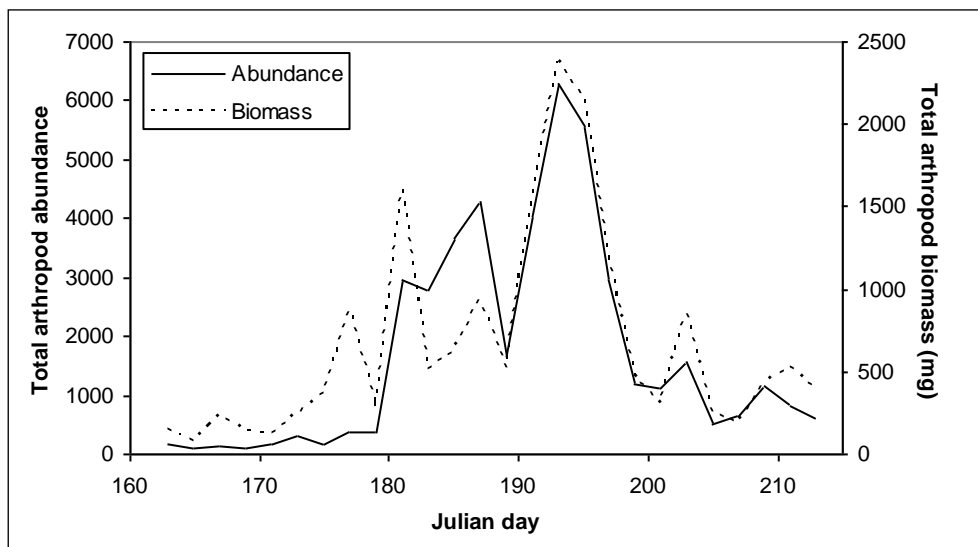
Figure 1. Seasonal variation in arthropod abundance and biomass during summer 2006 on Bylot Island

Arthropods that were previously confirmed as being part of the diet of White-rumped and Baird's were Anthomyiidae, Carabidae, Mycetophilidae, Tipulidae and spiders (Drury 1961; stomach contents, n = 2 for White-rumped and n = 3 for Baird's). Figure 2 shows seasonal variation in abundance of these five specific groups (see Appendix 2 for seasonal variations of all other groups).

We calculated the cumulative degree-days above zero (May 30 to August 1) and found strong logistic association with cumulative arthropod biomass and abundance ($r = 1.00$; $P < 0.0001$; Figure 3).

Figure 2. Seasonal variation in abundance of Anthomyiidae, Carabidae, Mycetophilidae, Tipulidae and spiders in 2005 and 2006

Figure 3. Cumulative summer arthropod abundance (2005 and 2006) and biomass (2006 only) in relation to cumulative degree-days above zero (May 30 to August 1; Julian day 150 to 213)

Shorebird phenology (2005-2006)

We found 36 and 20 nests of White-rumped and Baird's in 2005, and 17 and 29 nests in 2006, respectively. Breeding phenology was estimated for most nests except for those that were depredated before we obtained the information needed to estimate timing of breeding (Table 4). Baird's were the earliest breeders in 2005 and 2006.

Table 4. White-rumped and Baird's Sandpipers breeding phenology on Bylot Island in summer 2005 and 2006

Species	Year	First laying date	First hatching date	Median hatching date	Sample size
White-rumped Sandpiper	2005	158	183	190	27
	2006	161	186	191	17
Baird's Sandpiper	2005	155	180	185	13
	2006	155	177	185	29

* Dates are in Julian days (1 = January 1).

We used two techniques to estimate hatching dates (see methods: observed hatching dates, code 1, or estimation using egg buoyancy technique, code 2). When data on hatching dates were available from both techniques for the same nest, we compared these estimates (Figure 4). The egg buoyancy technique tended to over-estimate hatching date of the Baird's by 1.75 days and under-estimate hatching date of the White-rumped by 0.75 days. We thus used these differences to standardize our estimations of laying and hatching dates (Baird's: adjusted date = code 2 date − 1.75 days; White-rumped: adjusted date = code 2 date + 0.75 day).
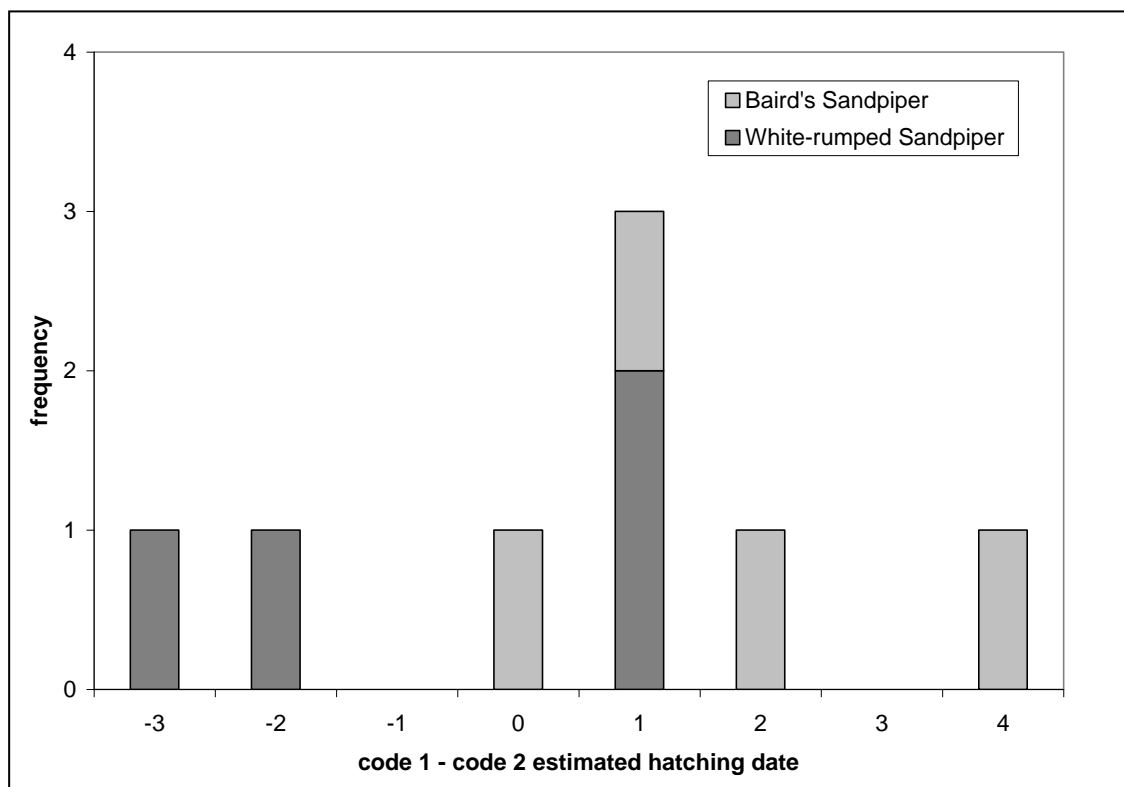
Figure 4. Differences between hatching dates estimated from the observation of starred eggs or nestlings (code 1) and those estimated with the egg buoyancy technique (code 2) for the same nest (Baird's Sandpiper or White-rumped Sandpiper)

The snow cover reached <65% when most Baird's started laying and <40% when most White-rumped laid their first egg (Figure 5). During the laying period, the mean daily temperature did not exceed 3°C in 2005 and 3.3°C in 2006. Mean temperature for the entire hatching period was 7.4°C in 2005 and 6.2°C in 2006 for the White-rumped, and of 6.7°C in 2005 and 5.5°C in 2006 for the Baird's. The peak abundance of arthropods occurred 5

days after the peak in mean daily temperature in 2005 and 3 days before the peak in mean

daily temperature in 2006.
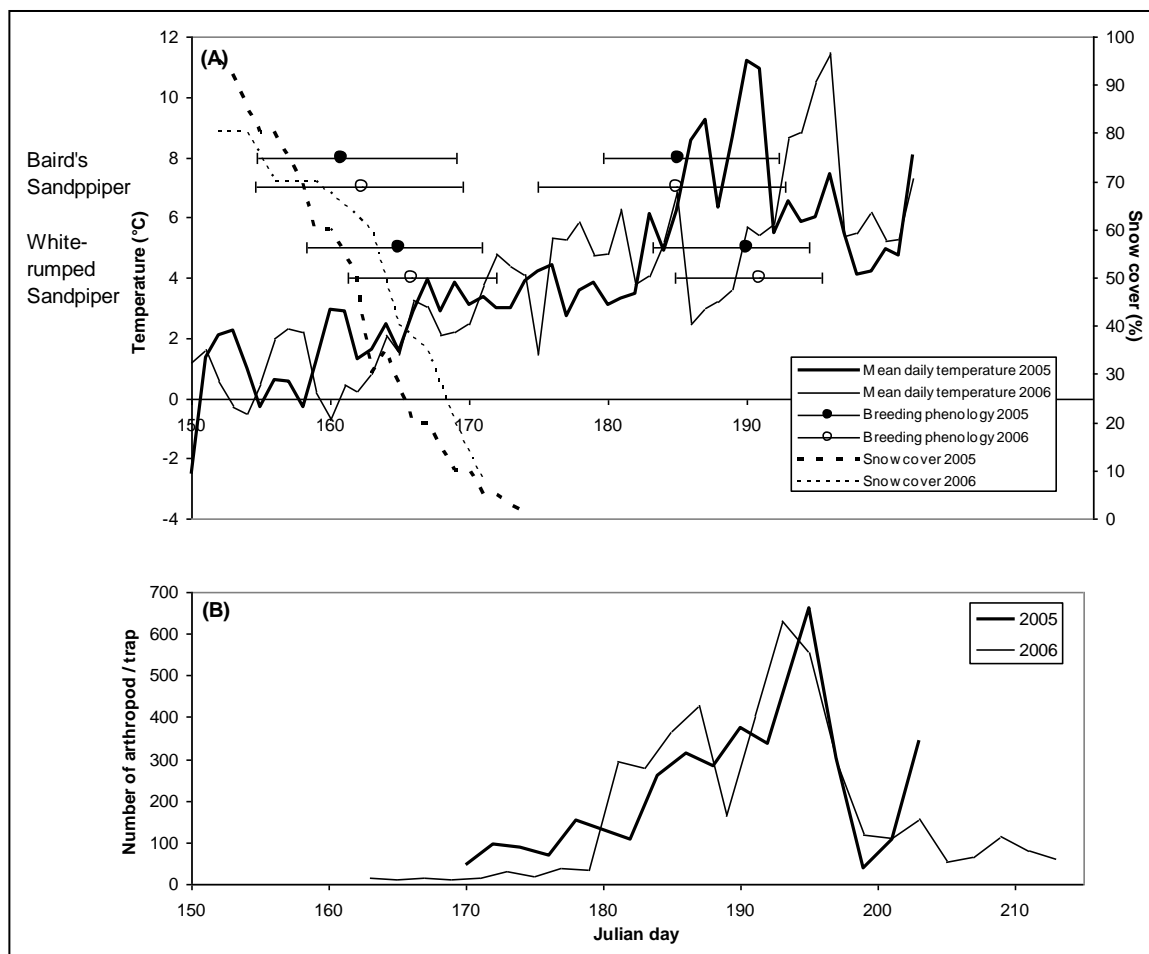
Figure 5. Breeding phenology of the White-rumped and the Baird's Sandpiper (median

laying and hatching dates ± range) in relation to snow cover and mean daily temperature

(A) and seasonal changes in arthropod (B) in summer 2005 and 2006

Climate changes and shorebird phenology

We found no climatic trend over the past 57 years, but when the period 1950 to 1972, and 1973 to 2006 were considered separately, we found significant a decline during the first 23 years, and a significant increase during the last 34 years (in all periods of the shorebirds breeding cycles; Figure 6). The temperature increase has been more pronounced during the pre-breeding and brood-rearing periods than during the two other periods.
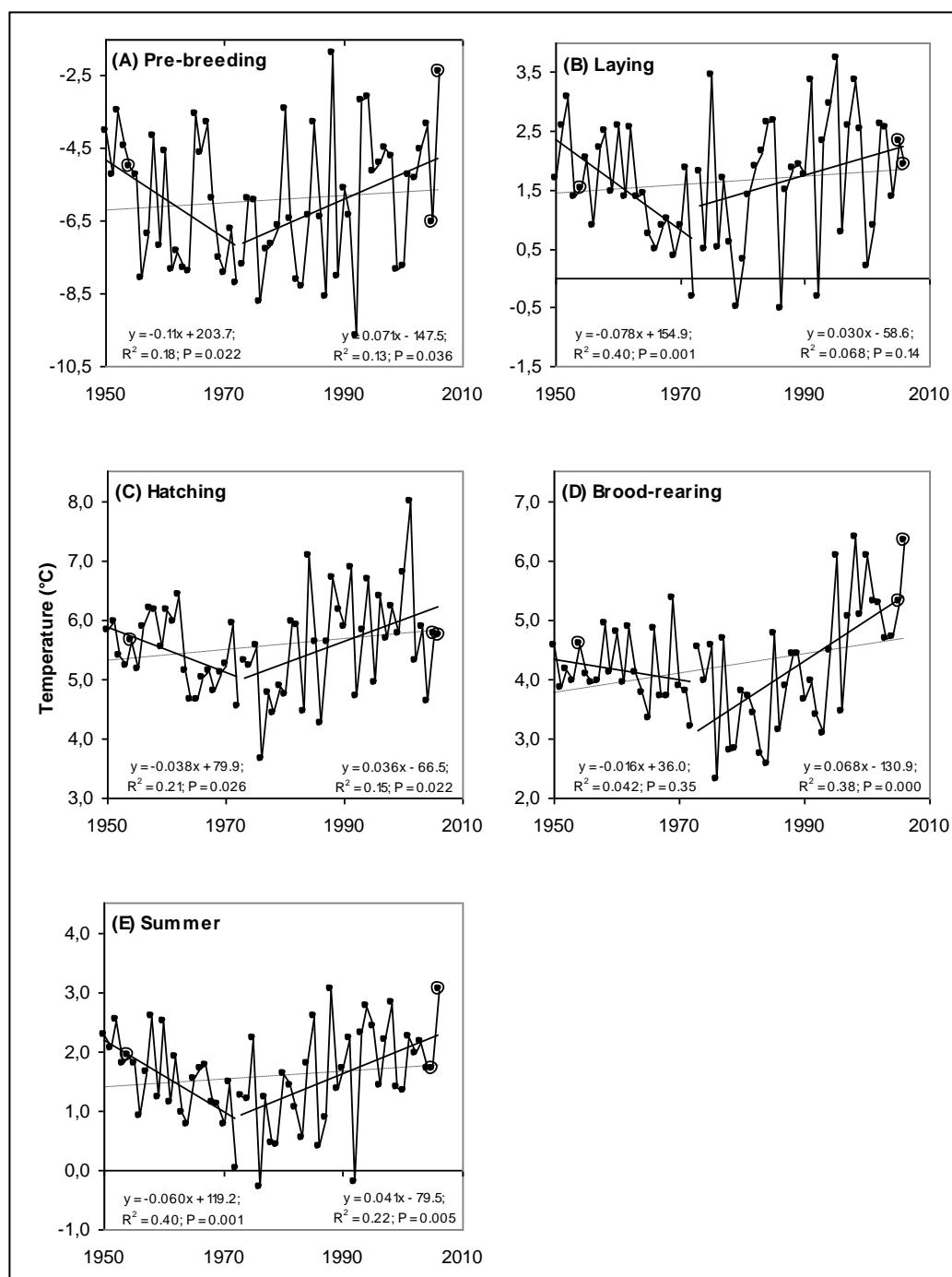
Figure 6. Mean daily air temperature on Bylot Island during the shorebird (A) pre-breeding, (B) laying, (C) hatching, (D) brood-rearing and (E) entire summer from 1950 to

2006. Temporal trends are represented for the 1950 to 1972 and 1973 to 2006 (solid line) and 1950 to 2006 (dashed line) periods. Data from 1950 to 1994 were estimated using regression analyses based on temperatures recorded at other arctic weather stations (see methods and Table 1). Data from 1954, 2005 and 2006 are circled (i.e., shorebird nests monitoring on Bylot Island)

Comparison between the 1954, 2005 and 2006 data

Drury (1961) studied the breeding phenology of the White-rumped and the Baird's Sandpiper at the mouth of the Aktineq River, located in southern Bylot Island (about 35 km from camp-2 and 55 km from camp-1). Field work was carried on from 12 June to 19 July 1954. Although the breeding phenology of the two species overlapped, Baird's median laying and hatching dates were 8 days earlier than those of the White-rumped in 1954, which is consistent with our results. Median laying and hatching dates were 2 to 9 days later in 1954 compared to 2005 and 2006 for the Baird's and the White-rumped (Figure 7).
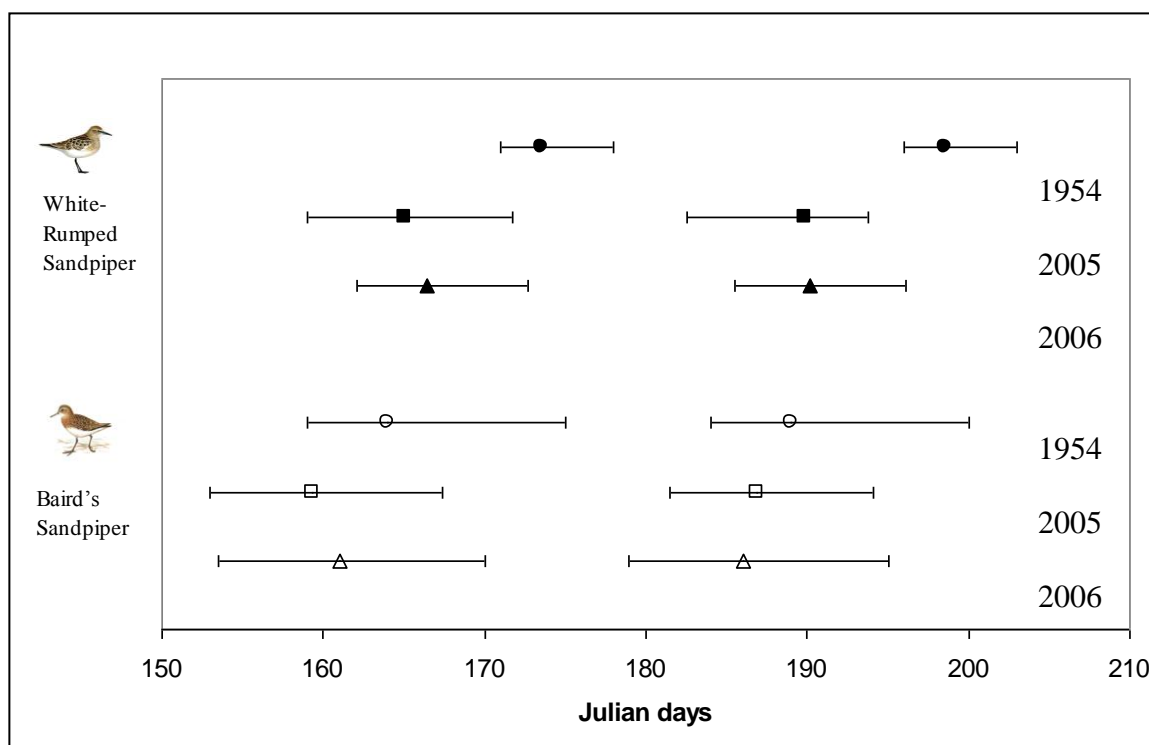
Figure 7. Comparison between the breeding phenology (median laying and hatching dates ± range) of the White-rumped Sandpiper (filled symbols) and the Baird's Sandpiper (open symbols). The 1954 data are from Drury 1961

Differences were statistically significant (or nearly) for the White-rumped (right-sided Fisher's exact test: 1954 vs. 2005: $P = 0.06$; 1954 vs. 2006: $P = 0.04$; 1954 vs. 2005-2006 combined: $P = 0.05$) and Baird's (right-sided Fisher's exact test: 1954 vs. 2005: $P = 0.04$; 1954 vs. 2006: $P = 0.06$; 1954 vs. 2005-2006 combined: $P = 0.07$). Results were similar using standardised or un-standardised data (code 1, code 2; see above). The large overlap in breeding phenology over the 3 years for the Baird's nonetheless suggests that the observed differences may be biologically less significant than for the White-rumped.

DISCUSSION

Recently recorded summer temperatures on Bylot Island appeared very similar to those observed about 6 decades ago. It is not surprising then, that we observed very minor changes in shorebird breeding phenology between 1954 and 2005/2006 (slightly earlier nesting in recent years). Although summer temperatures have significantly increased over the last three decades on Bylot Island (0.4°C per decade), we haven not found evidence supporting the mismatch hypothesis. Indeed, the shorebird's breeding phenology appeared synchronised with seasonal changes in arthropod availability, with hatching occurring slightly prior the peak in food abundance. Our results suggest that arctic-nesting White-rumped and Baird's Sandpiper, two long distance migrants, were able to track environmental changes generated by recent global warming.

Most White-rumped and Baird's Sandpipers hatched slightly before the peak in arthropod abundance, and this peak in arthropod abundance occurred slightly after or before the highest recorded summer temperatures. Hatching before the peak in food availability may be a better strategy than being directly synchronized with it, as it allows chicks to have access to food resources for a longer time period (Lepage *et al.* 1998a). Furthermore, it may allow chicks to have access to greater food abundance at the time of their greatest food requirements. For example, the maximal food requirements of Blue tits (*Parus caeruleus*) nestlings occurs at the age of 9-10 days, and food supply during that critical period can have strong influence on reproductive success and body size of

fledglings (Dias and Blondel 1996). Similar results have been found for Great tits (*Parus major*), where optimally, nestlings need to be 11-12 days old when their food abundance peaks (Visser et al. 2006). White-rumped eggs generally hatched 2 to 5 days before the peak in arthropod abundance (median hatch date) and Baird's eggs hatched 8 to 10 days before food peak (median hatch date). The fact that sandpiper's eggs hatched before the peak in food abundance does not indicate a lack of synchrony, but may rather be an adaptation allowing nestlings to benefit from a higher energy intake during the brood-rearing period. Further research on optimal timing of hatching in arctic-nesting shorebirds would nonetheless be needed to better interpret our results.

Two main periods of warming have occurred over the last 100 years, one from 1910 to 1945, and one from 1976 up to today (Walther *et al.* 2002). Our results are consistent with these findings and indicate that there was a significant decline in summer temperatures in the High Arctic from 1950 to 1972 followed by a significant increase from 1973 to 2006. The temperature increase on Bylot Island over the last 34 years has been more pronounced during the sandpiper's pre-breeding and brood-rearing periods (about 0.7°C per decade) than during the other two periods of the breeding cycle ($\leq$0.36°C per decade). Such seasonal variation in warming intensity can cause asynchrony between the breeding phenology of migrant shorebirds and the emergence of arthropods, especially if migration is not adjusted to warmer spring conditions on the breeding grounds. Consequently, it will be important and interesting to monitor arctic-nesting shorebirds in future years as the rate of warming is predicted to increase.

There are normal year-to-year temperature fluctuations (Houghton 2004), which bring variations to the timing of optimal conditions for chick rearing. Birds can adapt to a certain amount of variation through plasticity, but are still constrained to a window within which reproduction takes place (Visser *et al.* 2004). They usually breed earlier in warm springs (Dunn 2004), and global warming has led to an advancement of the breeding phenology in many bird species (Crick and Sparks 1999; Both and Visser 2001; Parmesan and Yohe 2003; Both *et al.* 2005). We found that most sandpipers laid and hatched slightly earlier in 2005 and 2006 compared to data recorded in 1954. Mean air temperatures extrapolated for each period of the shorebird breeding cycle in 1954 falls within 0.08°C to 2.6°C of those from 2005 and 2006, the greatest difference being during the pre-breeding period, and the smallest during the hatching period. The observed differences in breeding phenology are consistent with inter-annual temperature variations and suggest that recent weather conditions remained within the sandpiper reproductive temperature window (i.e., those observed in the past decades).

Climate during the pre-breeding period may be critical for migrating insectivorous birds. Individuals have to predict the conditions on their breeding grounds while still on their wintering or staging areas and they may not be able to detect earlier spring conditions occurring in their nesting areas, which would trigger the advancement in arthropod emergence. After their arrival on the breeding grounds, birds face constraints, such as incubation duration which limits the potential adjustment in the timing of hatch relative to the peak emergence of arthropods. Climate during brood rearing is also very important, as

it influences the emergence and abundance of their temperature-dependant food resource and thus chick growth and survival. The fact that the shorebird pre-breeding and brood-rearing periods were associated with faster temperature change over the past 34 years on Bylot Island indicate that they may be vulnerable to global warming if the pace increases.

We found strong associations between cumulative degree-days above zero and arthropod biomass and abundance. This is consistent with the fact that arthropod emergence is temperature-dependant (Strathdee and Bale 1998). The dominant arthropod taxon caught on Bylot Island was the Dipterans and the dominant family was the Chironomidae (highest numbers of species and individuals). These results are consistent with previous studies carried out in the arctic tundra (e.g. Ellesmere Island, Brodo 2000). For birds that feed on protein-rich foods such as arthropods, the seasonal changes in food availability can strongly affect nestling growth rates. Arctic invertebrates tend to be smaller than related temperate species (Strathdee and Bale 1998). Thus, a high abundance of arthropods is necessary to reach the bird's energetic needs. Although strongly correlated, we observed some differences between the seasonal variations in arthropod abundance and arthropod biomass. Indeed, specimens caught at the beginning and the end of the summer tended to have higher individual body mass compared to those collected in mid-summer. Such a pattern may be advantageous for birds (i.e., higher prey quality) during breeding phases associated with lower arthropod abundance (egg laying and incubation, and during the brood-rearing period).

Pearce-Higgins and Yalden (2004) studied the diet of the Golden Plover (*Pluvialis apricaria*) chicks in South Pennines, UK. They found that tipulid larvae are the most important prey, followed by adult tipulids, beetles (particularly carabids and curculionids), spiders and caterpillars. They also found that the diet is influenced by temporal (age, date), weather and habitat variables. Drury (1961) found that Tipulidae, Carabidae, spiders, Anthomyiidae and Mycetophilidae are part of the diet of the White-rumped and Baird's. The fact that these families were the only one confirmed in the summer diet of the Baird's and White-rumped (Drury 1961) does not exclude the possibility that other families can be regularly consumed during the breeding season. Indeed, their diet is known to include a wide variety of arthropods (Montalti *et al.* 2003). For instance, Muscidae and Chironomidae have been reported to be part of the diet of two other wader species from the *calidris* gender breeding in the High Arctic. Those insect families were also found in the foraging habitat of the sandpipers breeding on Bylot and were among the most dominant families. Finally, the laying periods of both White-rumped and Baird's occurred during the peak abundance of spiders, suggesting that the presence of these arthropods may be crucial during their pre-laying and laying periods. Further investigations would be required to better identify the main food item consumed during these critical phases since the entire breeding cycle depends on the timing of nest initiation.

CONCLUSION

Changes in climate are expected to affect all ecosystems. A better knowledge of the interactions between different trophic levels and their environments will help to predict or at least anticipate consequences of climate change. We showed that the hatching date of the White-rumped and Baird's Sandpipers occurs a few days before the peak in abundance of their food resource. This synchronization may allow chicks to have access to the resource for a longer period time or allow them to have access to greater food abundance at the period of their maximal food requirements (2 to 9 days after hatching, in our study).

Many studies have outlined the importance of food availability during hatching and early brood-rearing periods. Our results showed similar trends, with eggs hatching shortly before the peak in arthropod abundance. Thus, a mismatch is an unlikely factor negatively affecting this population of White-rumped and Baird's. Yet, the importance of food abundance prior to egg laying has also been outlined. The phenology of arthropods is temperature-dependant; the fact that the pre-breeding and brood rearing periods have known the most pronounced temperature increases over the past 34 years may eventually have consequences on the synchrony of the breeding phenology of sandpipers and their food resource. If the birds do not adequately track climate changes, a mismatch may become a factor of population declines.

REFERENCES

Anisimov, O. A.; D. G. Vaughan; T. V. Callaghan; C. Furgal; H. Marchant; T. D. Prowse; H. Vilhjálmsson; J. E. Walsh. 2007. « Polar regions (Arctic and Antarctic) ». Dans M. L. Parry; O. F. Canziani; J. P. Palutikof; P. J. van der Linden; C. E. Hanson. 2007. **Climate Change 2007: Impacts, Adaptation and Vulnerability. Contribution of Working Group II to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change**. Cambridge: Cambridge University Press, pp. 653-685.

Berteaux, D.; D. Réale; A.G. McAdam; S. Boutin. 2004. « Keeping pace with fast climate change: can Arctic life count on evolution? ». **Integrative and Comparative Biology**, volume 44, pp. 140-151.

Both, C.; R. G. Bijlsma; M. E. Visser. 2005. « Climatic effects on timing of spring migration and breeding in a long-distance migrant, the pied flycatcher, *Ficedula hipoleuca* ». **Journal of Avian Biology**, volume 36, pp. 368-373.

Both, C.; M. E. Visser. 2001. « Adjustment to climate change is constrained by arrival date in a long-distance migrant bird ». **Nature**, volume 411, pp. 296-298.

Both, C.; M. E. Visser. 2005. « The effect of climate change on the correlation between avian life-history traits ». **Global Change Biology**, volume 11, pp. 1606-1613.

Brodo, F. 2000. « The insects, mites and spiders of Hot Weather Creek, Ellesmere Island, Nunavut ». **Geological Survey of Canada**, Bulletin 529, pp. 145-173.

Crick, H. Q. P.; T. H. Sparks. 1999. « Climate change related to egg-laying trends ». **Nature**, volume 399, pp. 423-424.

Dias, P. C.; J. Blondel. 1996. « Breeding time, food supply and fitness components of Blue Tits *Parus caeruleus* in Mediterranean habitats ». **Ibis**, volume 138, pp. 644-649.

Drury, W. H. 1961. « The breeding biology of shorebirds on Bylot Island, Northwest Territories, Canada ». **Auk**, volume 78, pp. 176-219.

Dunn, P. 2004. « Breeding dates and reproductive performance ». **Advances in Ecological Research**, volume 35, pp. 69-87.

Ellis, C. J.; L. Rochefort. 2004. « Century-scale development of polygon-patterned tundra wetland, Bylot Island (73º N, 80º W) ». **Ecology**, volume 85, numéro 4, pp. 963-978.

Environnement Canada. Service météorologique du Canada. (Page consultée le 16 octobre 2006). Adresse URL : http://www.climate.weatheroffice.ec.gc.ca/climateData/menu_f.html.

Environnement Canada. Service météorologique du Canada. (Page consultée le 16 décembre 2007). Bulletin des tendances et des variations climatiques, [En ligne]. Adresse URL : http://www.msc.ec.gc.ca/ccrm/bulletin/summer07/national_f.cfm.

Gauthier, G.; J. Tardif. 1991. « Female feeding and male vigilance during nesting in Greater Snow Geese ». **Condor**, volume 93, numéro 3, pp. 701-711.

Geological Survey of Canada. 2000. « Environmental response to climate change in the Canadian High Arctic ». **Geological Survey of Canada**, Bulletin 529, 401 p.

Gwinner, E. 1996. « Circannual clocks in avian reproduction and migration ». **Ibis**, volume 138, pp. 47-63.

Hodkinson, I. D.; S. J. Coulson; N. R. Webb; W. Block; A. T. Strathdee; J. S. Bale; M. R. Worland. 1996. « Temperature and the biomass of flying midges (Diptera: Chironomidae) in the high Arctic ». **Oikos**, volume 75, pp. 241-248.

Houghton, J. 2004. **Global Warming: The Complete Briefing, 3rd ed**. New York (NY, USA): Cambridge University Press. 351 p.

Hughes, L. 2000. « Biological consequences of global warming: is the signal already apparent? ». **Trends in Ecology and Evolution**, volume 15, numéro 2, pp. 56-61.

International wader Study Group. 2003. **Waders are declining worldwide. Conclusions from the 2003 International Wader Study Group Conference**. Cádiz, Spain. Wader Study Group, Bulletin 101/102, pp. 8-12.

Lepage, D.; G. Gauthier; A. Reed. 1998a. « Seasonal variation in growth of greater snow goose goslings: the role of food supply ». **Oecologia**, volume 114, pp. 226-235.

Lepage, D.; D. N. Nettleship; A. Reed. 1998b. « Birds of Bylot Island and adjacent Baffin Island, Northwest Territories, Canada, 1979 to 1997 ». **Arctic**, volume 51, numéro 2, pp. 125-141.

Liebezeit J. R.; P. A. Smith; R. B. Lanctot; H. Schekkerman; I. Tulp; S. J. Kendall; D. M. Tracy; R. J. Rodrigues; H. Meltofte; J. A. Robinson; C. Gratto-Trevor; B. J. McCaffery; J. Morse; S. W. Zack. 2007. « Assessing the development of shorebird eggs using the flotation method: species-specific and generalized regression models ». **The Condor**, volume 109, pp. 32-47.

McCarty, J. P. 2001. « Ecological consequences of recent climate change ». **Conservation biology**, volume 15, numéro 2, pp. 320-331.

Meltofte, H.; T. T. Høye; N. M. Schmidt; M. C. Forchhammer. 2007. « Differences in food abundance cause inter-annual variation in the breeding phenology of High Arctic waders ». **Polar Biology**, volume 30, pp. 601-606.

Molau, U.; U. Nordenhäll; B. Eriksen. 2005. « Onset of flowering and climate variability in an alpine landscape: A 10-year study from Swedish Lapland ». **American Journal of Botany**, volume 92, numéro 3, pp. 422-431.

Montalti, D.; A. M. Arambarri; G. E. Soave; C. A. Darrieu; A. R. Camperi. 2003. « Seeds in the diet of the White-Rumped Sandpiper in Argentina ». **Waterbirds**, volume 26, numéro 2, pp. 166-168.

Morrison, R. I. G.; C. Downes; B. Collins. 1994. « Population trends of shorebirds on fall migration in Eastern Canada 1974-1991 ». **Wilson Bulletin**, volume 106, numéro 3, pp. 431-447.

Parmesan, C.; G. Yohe. 2003. « A globally coherent fingerprint of climate change impacts across natural systems ». **Nature**, volume 421, pp. 37-42.

Pearce-Higgins, J. W.; D. W. Yalden. 2004. « Habitat selection, diet, arthropod availability and growth of a moorland wader: the ecology of European Golden Plover *Pluvialis apricaria* chicks ». **Ibis**, volume 146, pp. 335-346.

Pearce-Higgins, J. W.; D. W. Yalden; M. J. Whittingham. 2005. « Warmer springs advance the breeding phenology of golden plovers *Pluvialis apricaria* and their prey (Tipulidae) ». **Oecologia**, volume 143, pp. 470-476.

Peñuelas, J.; I. Filella. 2001. « Responses to a warming world ». **Science**, volume 294, pp. 794-795.

Piersma, T.; J. van Gils; P. Wiersma. 1996. « Family Scolopacidae (Sandpipers, snipes and phalaropes) ». Dans del Hojo, J.; A. Elliott; J. Sargatal. 1996. **Handbook of the Birds of the World. Vol. 3, Hoatzin to Auks**. Barcelona: Lynx Edicions, pp. 444-533.

Sanz, J. J.; J. Potti; J. Moreno; S. Merino; O. Frías. 2003. « Climate change and fitness components of a migratory bird breeding in the Mediterranean region ». **Global Change Biology**, volume 9, pp. 461-472.

Schekkerman, H.; I. Tulp; K. M. Calf; J. J. de Leeuw. 2004. « Studies on breeding shorebirds at Medusa Bay, Taimyr, in summer 2002 ». Wageningen, Alterra, Alterra-rapport 922.

Strathdee, A. T., J. S. Bale. 1998. « Life on the edge: insect ecology in Arctic environments ». **Annual Reviews of Entomology**, volume 43, pp. 85-106.

Strode, P. K. 2003. « Implications of climate change for North American wood warblers (Parulidae) ». **Global Change Biology**, volume 9, pp. 1137-1144.

Thomas, D. W.; J. Blondel; P. Perret; M. M. Lambrechts; J. R. Speakman. 2001. « Energetic and fitness costs of mismatching resource supply and demand in seasonally breeding birds ». **Science**, volume 291, pp. 2598-2600.

Thomas, G. H.; R. B. Lanctot; T. Székely. 2006. « Can intrinsic factors explain population declines in North American breeding shorebirds? A comparative analysis ». **Animal Conservation**, volume 9, pp. 252-258.

Thórhallsdóttir, T. E. 1998. « Flowering phenology in the central highland of Iceland and implications for climatic warming in the Arctic ». **Oecologia**, volume 114, numéro 1, pp. 43-49.

Visser, M. E.; C. Both; M. M. Lambrechts. 2004. « Global climate change leads to mistimed avian reproduction ». **Advances in Ecological Research**, volume 35, pp. 89-110.

Visser, M. E.; L. J. M. Holleman; P. Gienapp. 2006. « Shifts in caterpillar biomass phenology due to climate change and its impact on the breeding biology of an insectivorous bird ». **Oecologia**, volume 147, pp. 164-172.

Visser, M. E.; A. J. van Noordwijk; J. M. Tinbergen; C. M. Lessells. 1998. « Warmer springs lead to mistimed reproduction in great tits (*Parus major*) ». **Proceedings of the Royal Society B: Biological Sciences**, volume 265, numéro 1408, pp. 1867-1870.

Walther, G.-R.; E. Post; P. Convey; A. Menzel; C. Parmesan; T. J. C. Beebee; J.-M. Fromentin; O. Hoegh-Guldberg; F. Bairlein. 2002. « Ecological responses to recent climate change ». **Nature**, volume 416, pp. 389-395.

ANNEXES

APPENDIX 1. Detailed arthropod biomass

Individual arthropod mass for each family and size class was calculated using samples collected in 2005. We also investigated seasonal variation when data were sufficient. Variation in average individual biomass per size class or family is indicated in figures below. Seasonal variations were relatively weak for each given category; we thus used the average calculated over the entire summer (for a family or size class) to convert the abundance measures in total biomass measures for the 2006 season (size class not available in 2005 data set).
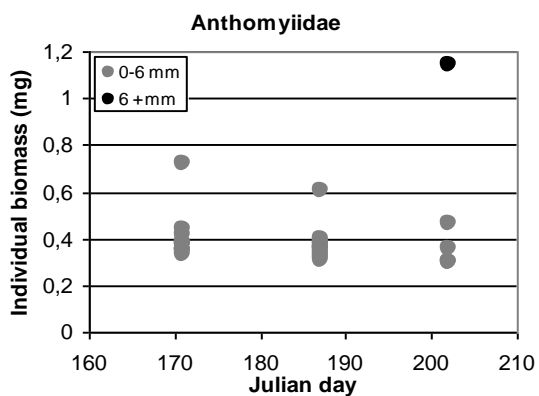
Mean individual biomass: 0-6 mm: 0.38mg
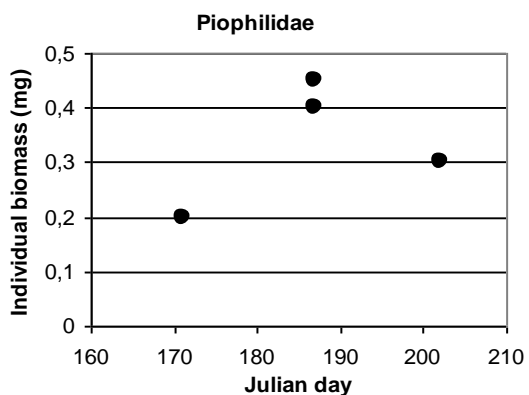6 + mm: 1.14mg
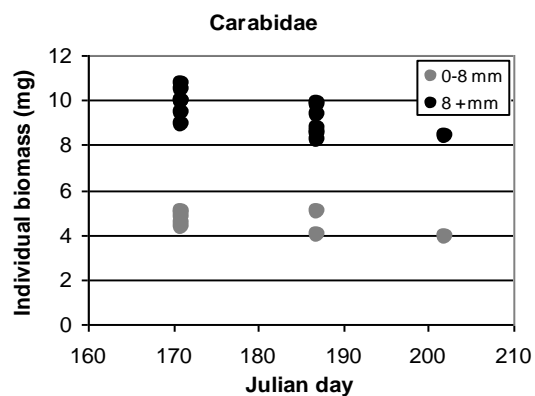
Mean individual biomass: 0-8 mm: 4.54mg
8 + mm: 9.33mg
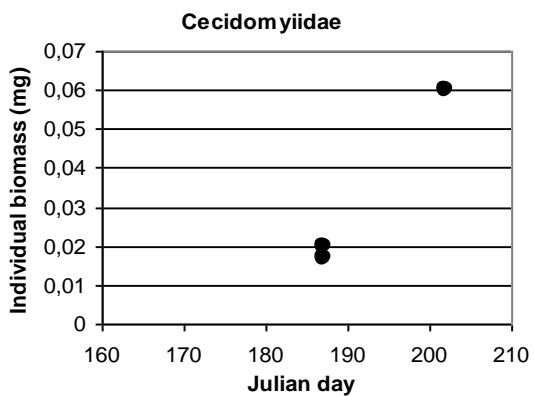
Mean individual biomass: 0.032mg
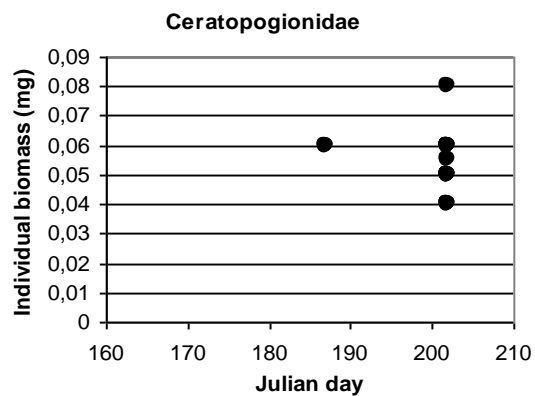
Mean individual biomass: 0.054mg

Chironomidae
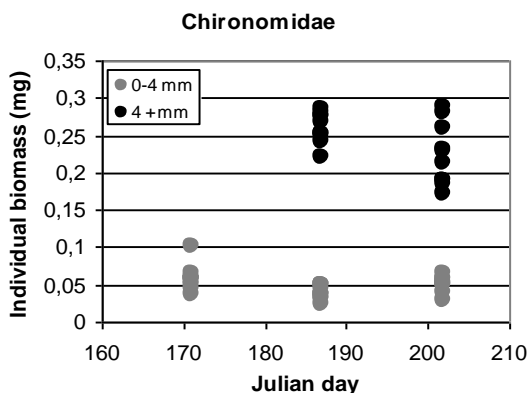
Mean individual biomass: 0-4 mm: 0.049mg
4 + mm: 0.24mg

Culicidae
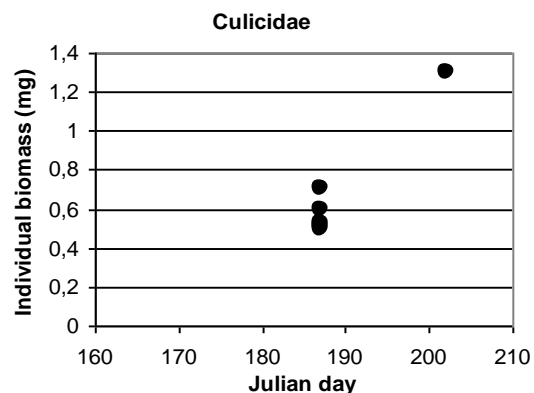
Mean individual biomass: 0.67mg

Curculionidae
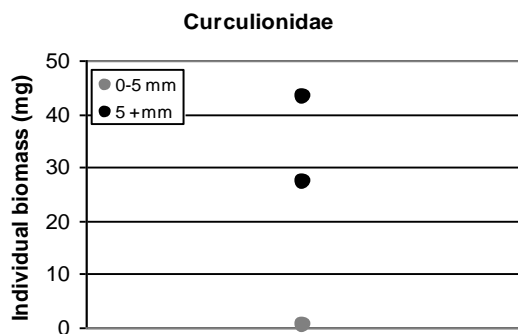
Mean individual biomass: 0-5 mm: 0.38mg
5 + mm: 35.2mg

Dolichopodidae
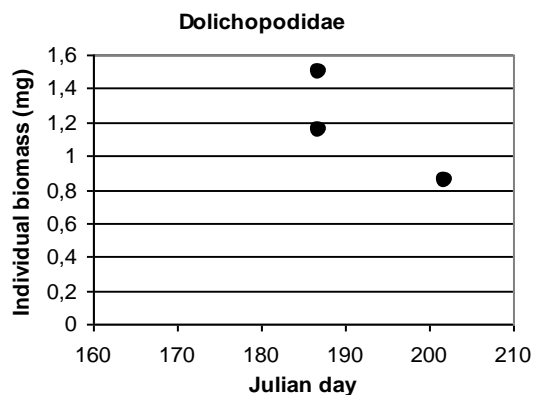
Mean individual biomass: 1.17mg

Empididae
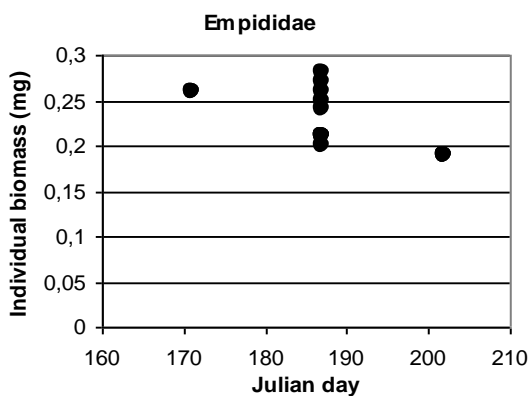
Mean individual biomass: 0.23mg

Muscidae
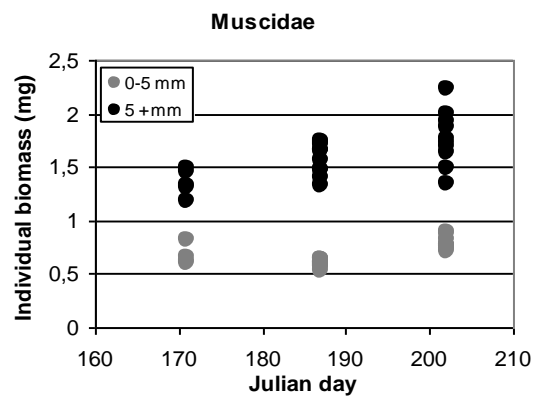
Mean individual biomass: 0-5 mm: 0.68mg
5 + mm: 1.60mg

Mycetophilidae

Mean individual biomass: 0.27mg

Phoridae
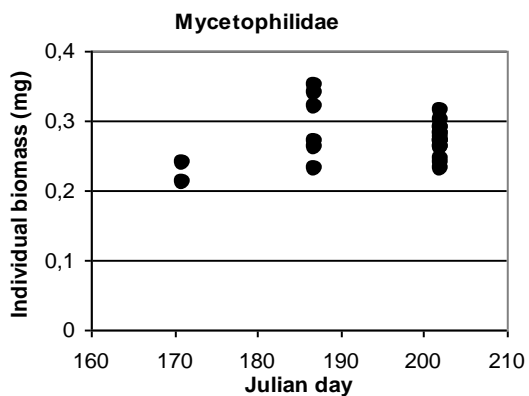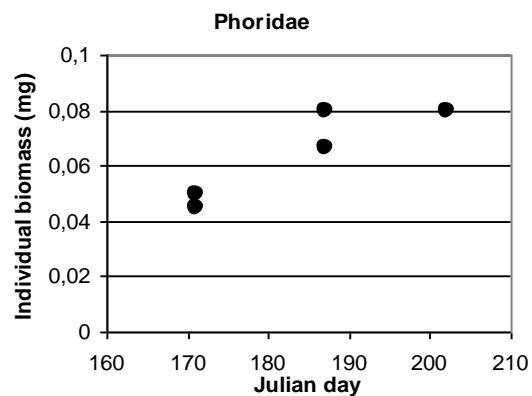
Mean individual biomass: 0.064mg

Piophilidae

Mean individual biomass: 0.34mg

Scathophagidae
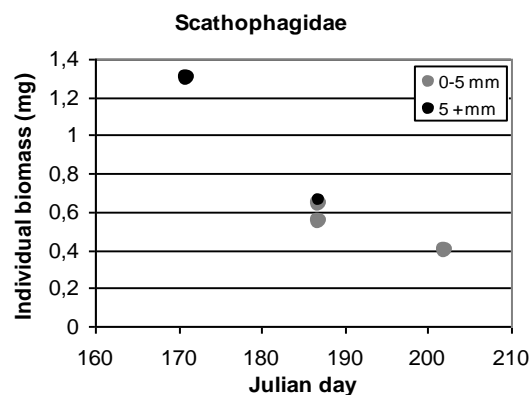
Mean individual biomass: 0-5 mm: 0.53mg
5 + mm: 0.98mg

Sciaridae
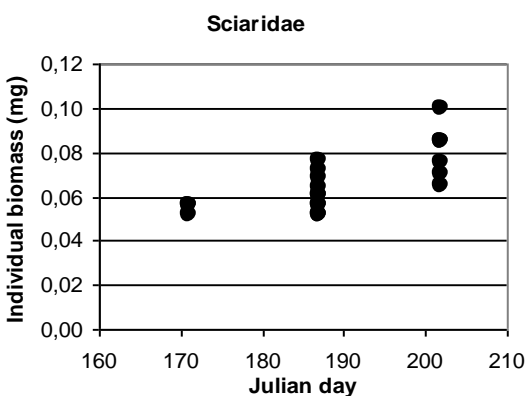
Mean individual biomass: 0.066mg

Syrphidae
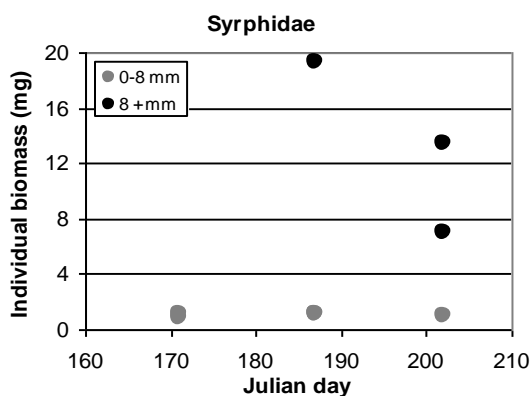
Mean individual biomass: 0-8 mm: 1.04mg
8 + mm: 13.2mg

Tachinidae
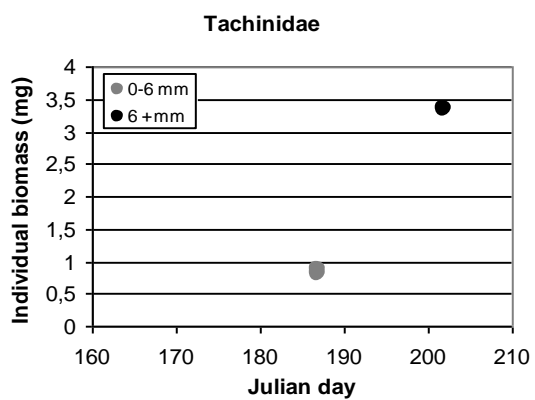
Mean individual biomass: 0-6 mm: 0.84mg
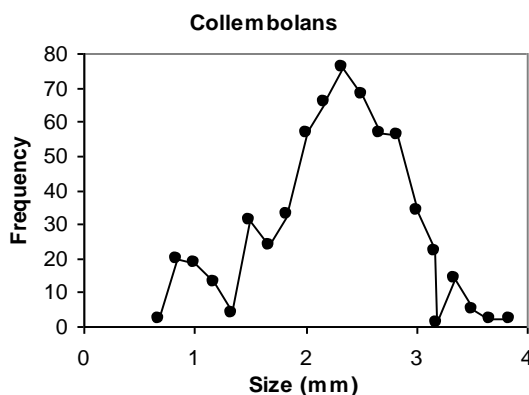6 + mm: 3.35mg

Tipulidae
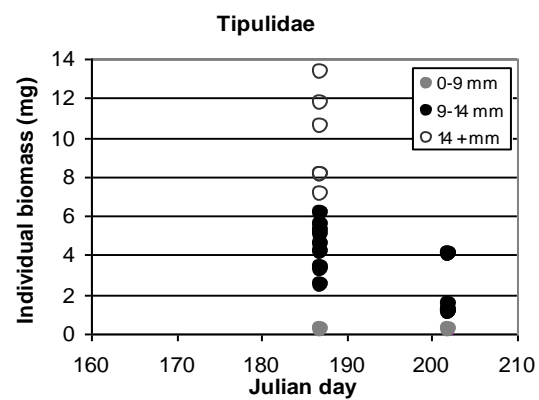
Mean individual biomass: 0-9 mm: 0.20mg
9-14 mm: 3.50mg
14 + mm: 9.78mg

Trichoceridae
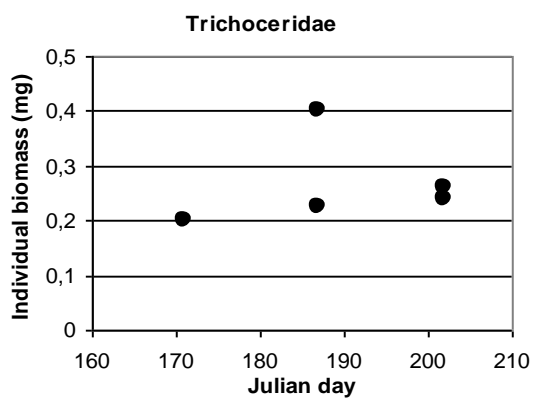
Mean individual biomass: 0.27mg

Since the size of the Collembolans showed a normal distribution, we used the mean individual biomass of median size as the average individual biomass to convert the 2006 abundance in total biomass measures.

Collembolans

Mean individual biomass : 0.04mg

We calculated the biomass of the spiders by log-transforming the individual size of the specimens and entering it into a linear regression.

Spiders
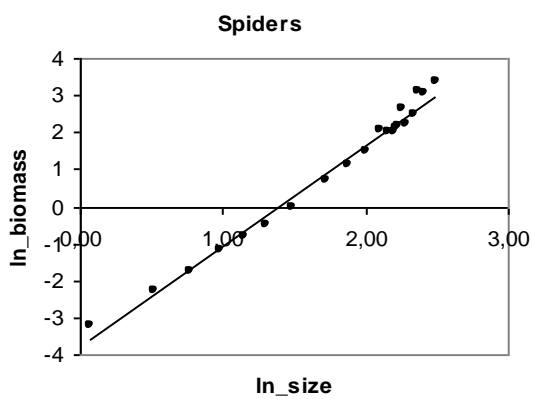
ln (biomass) = -3.8159 + 2.7319 * ln (size); $R^2 = 0.98$; $P < 0.0001$

APPENDIX 2. Seasonal variations of the arthropods caught in 2005 and 2006 in the

modified pitfall traps

Families for which there were less than 10 captures (Ephydridae, Heleomyzidae, Rhagionidae and Staphylinidae) were judged not significant and were not included in the analyses; their seasonal variations are not shown here. Total arthropod abundance was divided by the number of trap (8 and 10 traps in 2005 and 2006, respectively) to account for the different sampling effort.

Ceratopogonidae

Empididae

Culicidae

Mycetophilidae

Curculionidae

Dolichopodidae

Muscidae

Sciaridae

Phoridae

Syrphidae

Piophilidae

Scathophagidae