Exposure to PFAS is associated with telomere length dynamics and demographic responses of an arctic top predator

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Abstract

Environmental factors that can influence telomeres are diverse, but the association between telomeres and exposure to environmental contaminants is far to be elucidated. To date, prior studies focused on legacy persistent chlorinated pollutants POPs, while the effects of poly- and per-fluoroalkyl substances (PFAS) have poorly been documented. Here, we investigated the associations among PFAS congeners, absolute telomere length (cross-sectional approach), and telomere dynamics (rate of telomere length change over time, longitudinal approach), in one of the most contaminated arctic top predators, the glaucous gull *Larus hyperboreus* from Svalbard. We further estimated the effect of PFAS on apparent survival rates and re-sighting probabilities using a 10-year capture/recapture dataset (2010-2019). We found that birds exposed to higher concentration of perfluorononadecanoate PFNA (median of 1565 pg/mL of ww in males and 1370 pg/mL of ww in females) and perfluorotetradecanoate PFTeDA (median of 370 pg/mL of ww in males and 210 pg/mL of ww in females) showed the slowest rate of telomere shortening. We also found that high blood concentration of perfluorooctanoate PFOA (median of 120 pg/mL of ww in males and 150 pg/mL of ww in females) and perfluorohexanesulfonate PFHxS (median of 495 pg/mL of ww in males and 395 pg/mL of ww in females) were positively associated with higher re-sighting probabilities and apparent survival in males but not in females. Our work is the first to report an association between single PFAS compounds and telomeres, and the first to link PFAS exposure with survival probabilities, suggesting that the effect of PFAS exposure might be more tied to the type of compound rather than the total concentration of PFAS.

Introduction

Over the past decades, ecotoxicological studies have extensively investigated the trends and effects of environmental contaminants in both humans and wildlife. Because of their known detrimental effects on endocrine and immune functions [1-3], legacy persistent organic pollutants (POPs), including organochlorine pesticides (OCs) and polychlorinated biphenyls (PCBs), represent global threats for both humans and wildlife and have been widely investigated. In contrast, the effects of per- and polyfluoroalkyl substances (PFAS) on the health of free-living animals remain largely overlooked. PFAS consist of a fluorinated alkyl carbon chain with a terminal functional group [4]. Because the chemical bond between carbon and fluorine atoms is strong, PFAS are chemically and thermally stable, and have therefore been used as surface-active agents in a multitude of manufactured products (e.g. non-stick cookware, fire-fighting foam, food packaging, water proof clothing and stain-resistant carpets, [4]). Among them, PFOS (perfluorooctanesulfonate) and PFOA (perfluorooctanoate) are listed as legacy POPs by the Stockholm Convention since 2009 and 2019, respectively, while others (i.e. PFHxS perfluorohexanesulfonate) are under review. Although PFAS have been produced over the past 50 years, it is only recently that they have come under scientific scrutiny because of their extreme persistence in the environment [5]. Several PFAS have bioaccumulation and biomagnification potential [6] and have been globally detected [7, 8].

Because of their high volatility and long-range oceanic (congeners) and atmospheric (precursors) transport, PFAS may reach remote areas including Arctic regions [9]. While OCs and PCBs have shown decreasing levels over the past decades [10], some PFAS compounds, even if regulated by the Stockholm Convention, have increased or are still found at high concentrations in living organisms and the atmosphere [9, 11, 12]. Once deposited in the marine environment, some PFAS bioaccumulate into living organisms and undergo biomagnification processes, showing increasing concentrations along the food webs [13]. Specifically related to their capacity to bioaccumulate into living organisms, recent studies have shown that i) the biomagnification potential is enhanced for longer and odd carbon-chain-length PFAS [4]; ii) detrimental effects of PFAS exposure may be enhanced as the carbon-chain-length increases [14]; iii) PFAS show high affinity for proteins thus accumulate and persist in protein-rich tissues [15].

Diverse Arctic seabirds are long-lived top predators which are exposed to relatively high levels of environmental contaminants and generally show high site fidelity. Therefore, they are considered extremely valuable to monitor the trends of environmental contaminants. Furthermore, amongst animal taxa, birds lack efficient excretion mechanisms for organic pollutants and are thus potentially vulnerable to PFAS exposure [16, 17]. Recent studies on wild birds demonstrated that PFAS exposure could negatively impact on breeding success, as shown in tree swallows *Tachycineta bicolor* and black-legged kittiwakes *Rissa tridactyla* [18, 19]. Although PFAS may also affect the physiological status [20, 21] and disrupt hormones production in birds (i.e. corticosterone, [18,] thyroid hormones, [22,] prolactine, [23]), other studies have found no physiological and demographic effects following PFAS exposure[24] (but see also [1]) or even a positive association between specific PFAS congener and body condition of birds [18]. To date, our knowledge on PFAS exposure and their effects on physiological traits and demographic parameters of wildlife remains extremely limited, and further ecotoxicological studies are requested to fill in these important research gaps.

Telomeres represent a potential physiological marker that may prove useful to estimate the toxicological consequences of PFAS exposure on wildlife. Previous studies have shown that telomere length and the change in telomere length over time (i.e. telomere dynamics) are associated with longevity and survival in vertebrates including birds[25-28] (also reviewed in [29]), and are thought to reflect individual quality in long-lived birds [30, 31]. Telomere dynamics may however be disrupted by several stressors including exposure to environmental contaminants (reviewed in [32, 33]). One way through which environmental contaminants may impact on telomeres is the increased molecular oxidative damage and disruption of antioxidant defenses [34, 35], with longer-carbon-chain PFAS showing a greater negative effect [14]. The general trend is that telomere length decreases when organisms or cells are exposed to environmental contaminants (rewieved in [36]). In birds, only a few studies have investigated environmental contaminants and absolute telomere length and found no (with heavy metals in the European pied flycatcher *Ficedula hypoleuca* [37]; with organochlorine pesticides OCs and PFAS in White-tailed eagle *Haliaeetus albicilla* chicks [38]) or negative associations (with heavy metals in Great tit *Parus major* chicks [37]; with oxychlordane in Black-legged kittiwakes [39]). The longitudinal study recently carried out in black-legged kittiwakes [40] found that the most PFAS contaminated birds showed the slowest rate of telomere shortening over time [40]. Although results in Blévin et al. [40] deviates from the general expected trend, this result has been very recently corroborated by the positive association between PFAS concentrations and leucocyte absolute telomere length found in humans [41].

The glaucous gull *Larus hyperboreus* is a long-lived Arctic breeding seabird. It is a top predator with a generalist diet which includes fish and crustaceans but also eggs and chicks of other birds [42]. It is one of the most contaminated birds for both organic contaminants and trace elements [43-45], thus constituting an unprecedented opportunity to investigate the association between PFAS exposure and telomere length in free-living birds. Previous work has extensively investigated the effect of OCs on a series of fitness related traits (reviewed in Verreault et al. [44]) and survival in glaucous gull [46], yet the effects of PFAS exposure have been overlooked. The aims of this study were to investigate the relationships between PFAS exposure and absolute telomere length, and the association between PFAS and telomere dynamics. Furthermore, taking advantage of the long-term monitoring of this species, we further investigated whether apparent survival and re-sighting (i.e. used as a proxy of breeding probability; see details in Methods) are associated with PFAS exposure, using long-term individual PFAS blood concentration combined with capture-mark-recapture (CMR) models. If PFAS exert an effect on telomeres as previously suggested [40, 41], we predict that PFAS may show a similar and positive association with telomere length. Furthermore, if exposure to PFAS can be generalized to population-level processes, we expect an association between PFAS and demographic parameters.

Materials and methods

Sampling

Capture and ringing of glaucous gull in Kongsfjorden, Svalbard (78° 55’ N; 11° 56’ E) started in 2009 as part of research programs on contaminants and wintering ecology. Adult birds were captured during the incubation stage on their nests using a nest trap as previously described [47]. Birds were individually marked using a color ring (with a unique code for identification at a distance) and a numbered steel band. Right after capture, 8mL of blood were collected from the brachial vein using a heparinized syringe and a 22 gauge needle. Blood was centrifuged in the field; plasma and red blood cells were kept frozen at -20 °C until laboratory analyses for PFAS and telomeres, respectively. Skull (head and bill) and bill length were then measured with an accuracy of 0.5 mm using a caliper and birds were weighted to the nearest 5 g using a Pesola spring balance. Because males are larger than females, we assumed that birds with a bill >61.5 mm long and skull >152 mm long were males as described previously [47]. When birds could not be sexed according to their size, sex was determined by molecular sexing as previously done [48].

Laboratory analyses

PFAS concentrations in plasma were determined at the Norwegian Institute for Air Research (NILU) in Tromsø, Norway. PFAS with concentrations below the limit of detection (LOD) in less than 30% of samples were replaced with a value equal to ½ x LOD to enable statistical analyses. Therefore, 9 PFAS (perfluorooctanoate (PFOA), perfluorononanoate (PFNA), perfluorodecanoate (PFDA), perfluoroundecanoate (PFUnA), perfluorododecanoate (PFDoDA), perfluorotridecanoate (PFTrDA), perfluorotetradecanoate (PFTeDA), perfluorohexanesulfonate (PFHxS), and linear perfluoroctanesulfonate (L-PFOS)) could be further investigated. A detailed protocol for the methodology used for PFAS, quality assurance/quality control (QA/QC) results, detection frequencies, and LOD of all PFAS analyzed in the study can be found in the Supporting information and in Supporting Table S1.

Telomere analyses were carried out in red blood cell samples collected from 2012 to 2018, at the Centre d'Etudes Biologiques de Chizé (CEBC), France, using a real-time quantitative PCR (qPCR) technique already validated for birds [49]. Further clarifications on the methodology used for telomere length estimation can be found in the Supporting information.

Statistical analyses

The potential association between PFAS and either survival or re-sighting rates was evaluated by using a capture-mark-recapture (CMR) dataset from 2010 to 2019. A total of 89 birds were included in this model (birds for which both CMR and PFAS data were available). A CMR model was built taking into account all encounter occasions following PFAS analyses. This model was parameterized in terms of the probability of survival ϕ (i.e. apparent survival, probability that an individual at time *t* survives to time *t+1* and does not permanently emigrate from the study area) and re-sighting *p* (probability that an individual is encountered at time *t+1*). Because sex-related differences in PFAS concentrations have been previously found in glaucous gulls [48], and since females and males may show dissimilar responses to contaminant exposure in this species [48], we were interested in sex-dependent associations of PFAS and demographic parameters. We have thus included the effect of *sex* on each parameter. Thus, our initial model was ϕ_{sex} p_{sex}. Each parameter (θ) was then modeled as a function of PFAS using a logit link function: $\text{logit}(\theta)=a + b*\text{PFAS}_i$, where *a* is the intercept, *b* is the slope, and PFAS_i is the concentration of a given PFAS for individual *i*. Due to large values of PFAS concentrations, values were log-transformed to facilitate numerical convergence. To additionally test the potential association between telomere length, survival, and re-sighting rates, a similar CMR model was also built taking into account all encounter occasions following telomere length estimation. A total of 78 birds were included in this model (birds for which both CMR and telomere length data were available). To test for an effect of PFAS or telomere length on survival or re-sighting probability we used likelihood ratio tests between the model where the parameter θ (i.e. ϕ or p) was a function of PFAS or telomere length and the model where the parameter θ was only sex-dependent. We inferred an effect of PFAS or telomere length on θ when the P-value of the LRT test was < 0.05 and the 95% confidence interval of the slope parameter b did not include zero. Goodness of fit (GOF) test was performed to test how well our initial model fitted the data using the median c-hat approach [50].

All other statistical analyses were performed using R 3.6.1 [51]. PFAS compounds were analysed separately because: i) longer carbon-chain-length PFAS can have a stronger effect than shorter PFAS [14]; ii) per- and poly-fluorinated compounds, odd and even numbered carbon-chain-length perfluoroalkyl carboxilates (PFCA), and perfluoroalkane sulfonates (PFSA) share different chemical and/or physical proprieties [4, 52]; and iii) correlations among log or square-root transformed PFAS were very variable, being lowest between PFHxS and PFDA (Pearson correlation: r=0.01, P=0.94) and highest between PFUnA and PFDA (Pearson correlation: r=0.84, P<0.001). A correlation matrix including all correlation coefficients among PFAS is reported in the Supporting Information (Figure S1). Individual body mass and morphometric measures were used to calculate a scaled body mass index (BMI) following a previous protocol [53], which was then included in the statistical analyses to control for the body condition of the birds. To test whether the contaminant levels were associated with *absolute telomere length*, we used linear mixed models including telomere length as response variable, while *PFAS*, *sex*, *BMI*, and the interaction between sex and PFAS were treated as predictors. A total of 75 birds (24 males and 51 females) of which 18 were captured two times while 8 were captured three times (i.e. for a total of 109 observations) were available from 2012 to 2017, period for which both PFAS and telomere length were estimated. In this model, the *year* of capture and the individual *ID* were considered as random factors to control for variations in PFAS over time and for pseudoreplications (data from re-captured individuals), respectively. Linear mixed models were also used to test the effect of PFAS exposure on the change in telomere length over time (i.e. *telomere dynamics*) calculated from re-captured individuals, which was considered as response variable. A total of 22 observations from 19 birds re-captured one or two years apart were included in this model. Thus, the model also included an additional covariate named *N. years differenc*e to control for telomere length variation between one or two years. Because it has been previously shown that the rate of telomere shortening is often higher for birds with initial long telomeres, this model also included telomere length at year one as a covariate, named *Telomere Y1.* The average of a given PFAS between the two years was considered as the explanatory variable. Biologically relevant models were built using *averagePFAS*, *sex*, *N. years difference*, *Telomere Y1*, and the interaction between average PFAS levels and the sex as predictors. Also for this model, the *year* and the individual *ID* were considered as random factors to control for variations in PFAS over time and for pseudoreplications (data collected from the same individual), respectively. For each model, we tested the normality of residuals and we visually inspected diagnostic plots to check whether the data met linear model assumptions [54]. Two outliers were found for absolute telomere length (i.e. they exceeded the mean ± 3 SD and were likely due to a methodological issue) and were thus excluded from statistical analyses. Data were transformed to meet these assumptions (i.e. normality and homoscedasticity of residual distribution) when testing for correlations among PFAS and when testing for sex differences for each PFAS congener. When testing for sex differences in PFAS concentration, the first data (first time measurement of PFAS for each bird) of the 75 birds captured from 2012 to 2017 were used. Finally, to visualize effect sizes of PFAS on telomere dynamics, all predictor variables (i.e. PFAS) were scaled to mean of 0 and standard deviation of 1 to be included in the same graph. Bonferroni corrections were not applied when comparing associations among PFAS and telomeres because of the increased probability of producing false negatives [55]. All data transformation and any violation of model assumptions are reported within the manuscript.

Results and discussion

Compounds and levels of PFAS. Mean (± SD), median, and the range of plasma concentrations of each PFAS are reported in Table 1. Except for PFNA, PFHxS and L-PFOS, all PFAS showed a statistically significant difference between males and females, with males usually showing higher levels (Table 1). L-PFOS was the most abundant compound (median of 11050 pg/mL of ww in males and 6600 pg/mL of ww in females) while PFOA was the least abundant (median of 120 pg/mL of ww in males and 150 pg/mL of ww in females) of all PFAS reported in Table 1. Odd carbon-chain-length PFAS (i.e. PFNA, PFUnA, and PFTrDA) were generally more abundant than even carbon-chain-length PFAS (Table 1), a common pattern in Arctic wildlife likely related to the long-range atmospheric transport of odd-chained PFAS [56]. Similar sex-related differences in PFAS concentrations have been previously found in glaucous gulls [48]. Sex-related differences in contaminant exposure may be related to different foraging strategies adopted by males and females during the reproductive season. Males feeding at a higher trophic level than females or in more contaminated areas may explain variation in contaminant levels, although previous work showed that glaucous gull males and females feed on a similar trophic level [57]. Nonetheless, i*n ovo* transfer of organic contaminants represents a significant elimination route in this species [58]. Being opportunistic feeders, dietary preference (e.g. glaucous gulls feeding on eggs vs. fish intake [46, 59]) vary considerably among individual birds and may play a role in the accumulation of high concentrations of contaminants.

Relationship between absolute telomere length and PFAS. The models describing the association between absolute telomere length and each PFAS are reported in Supporting Table S2. The models including PFOA, PFNA, PFUnA, PFDoDA, PFTeDA, L-PFOS, and sumPFAS as explanatory variables reported a significant association between absolute telomere length and the sex, with males showing longer telomeres than females (Supporting Table S2). The model including PFTrDA as explanatory variable showed no significant effects, while the model on PFHxS showed a significant association between absolute telomere length and the sex and the body mass index, with birds owning a higher body mass index having longer telomeres. The model on PFDA levels as explanatory variable showed a significant interaction between PFDA and the sex (P=0.047; Supporting Table S2). This result is due to the opposite trend of the slope calculated for males and females, but both slopes are not significant (Estimate ± SE for females: $-4.39*10^{-5} \pm 3.23*10^{-5}$, P=0.16; Estimates ± SE for males: $4.86*10^{-5} \pm 3.68*10^{-5}$, P=0.18; overall $r^2 = 0.091$).

As stated above, L-PFOS was the PFAS showing the highest concentrations found in the present study, with four females showing concentrations above 100000 pg/mL of ww. Yet, PFDA was the only PFAS associated with absolute telomere length. Importantly, this association was dependent on the sex of the birds. One possible explanation for this PFDA-telomere association may lie in the absolute concentration of PFDA, which showed significantly higher levels in males than females. We cannot, for example, rule out the possibility that the association between PFDA and telomeres would only emerge when PFDA exceeds certain concentrations. Indeed, the positive trend in males was highly influenced by two birds that showed relatively high levels of PFDA (>2400 pg/mL of ww) and also long telomeres. By removing these two data points from the analyses, the interaction term is not significant anymore (*P*=0.73), and the sex is the only remaining significant term (*P*=0.046), which is in agreement with the other models on absolute telomere length. However, these two birds were kept in the model because they are not outliers since no issues with telomere and/or contaminant analyses occurred, thus represent real data. But their removal from the model lead to a non-significant association between PFDA and absolute telomere length. In addition, these two highly PFDA contaminated birds with long telomeres were not re-sampled within two years after capture, thus were not included in the statistical analyses on telomere dynamics, which may explain the lack of association between telomere dynamics and PFDA. However, it is of great importance to consider that: i) the association between PFDA and absolute telomere length was purely related to the difference in the slopes calculated from males and females, thus neither males nor females showed a significant association with PFDA, and ii) the large inter-individual variation in absolute telomere length may be driven by other factors that have not been included in our study. For instance, because telomere length is suspected to be associated with survival and longevity [25, 60], age is one important factor that can contribute to variation in telomere length within bird populations [61]. Telomere loss mainly occurs early in life and it is associated with developmental conditions [62]. Telomere length also declines between the chick stage and the adulthood, but during adulthood, the rate at which telomere shorten can be highly reduced especially for long-lived species [62]. Age-dependent mechanisms of environmental contaminants accumulation may also occur, therefore knowing the age of the studied individuals is of great importance when dealing with both telomeres and persistent organic pollutants. In the glaucous gull, however, previous work pointed out that PCBs and OCs are unrelated to age and that steady-state levels of contaminant accumulation are reached relatively early in life [63], thus the present results ought to be unaffected by the age of the studied birds. Regarding PFAS, there is no published study on the effect of adult age. Only one study on white-tailed sea eagle suggests that in nestlings, PFAS burden increase with increasing age during the nestling phase[64]. Other factors rather than age may still mask the effects of environmental contaminants when using a cross-sectional approach, thus some caution is needed to interpret these findings, and further work in advised to support the suspected sex-related association between PFDA and absolute telomere length.

Relationship between telomere dynamics and PFAS. The models describing the association between telomere dynamics and each PFAS are reported in Supporting Table S2. None of the models showed a significant interaction between average PFAS levels and the sex (all *P*>0.49) and thus were not reported in Supporting Table S2, while all models reported a highly significant association between telomere dynamics and telomere length at year 1 (all *P*<0.055, Supporting Table S2). Briefly, a shortening in telomere length was more likely to occur in birds with longer telomeres at year 1. Finally, we found that PFNA (Estimate ± SE: $9.68*10^{-5} \pm 3.24*10^{-5}$, *P*=0.0088, Figure 1a, Figure 2, Supporting Table S2) and PFTeDA (Estimate ± SE: $5.06*10^{-4} \pm 1.87*10^{-4}$, *P*=0.02, Figure 1b, Figure 2, Supporting Table S2) were strongly and positively associated with telomere dynamics independently from the sex of the birds, although only five males were included in the analyses. Birds with higher PFNA or PFTeDA levels were the ones showing the slowest rate of telomere shortening. Except PFOA, all other carboxylic PFAS showed a similar positive association with telomere dynamics (Figure 2), and a trend was found for both PFDA and PFDoDA (*P*=0.11 and

P=0.14, respectively; Figure 2, Supporting Table S2). Using a longitudinal approach (i.e. therefore considering the dynamic of telomeres over time) limits the number of confounding factors that might influence telomere length. Our results show that several carboxylic PFAS (and more specifically, PFNA and PFTeDA) were positively associated with a change in telomere length over time. This result was not related to the sex of the birds. But given the small sample size for males, further studies should try to additionally assess whether a sex-dependent effect exists. To the best of our knowledge, only two studies have investigated the association between PFAS exposure and telomere dynamics [38, 40], and no study has previously reported an association between a specific PFAS and telomere dynamics of wild birds. Our research provides an essential contribution for our understanding on the link between PFAS and telomeres of wild animals. Our results are in agreement with the work of Blévin et al., [40], which found that PFAS predicted telomere dynamics in black-legged kittiwakes, with most contaminated birds showing the slowest rate of telomere shortening over time. A previous study found that although the concentration of shorter-carbon-chain PFAS was higher, PFTeDA exposure showed the strongest association with protein oxidative damage [14]. Not only we found that PFNA and PFTeDA, and in a lesser extent, some other PFAS were positively associated with telomere dynamics, but some of the studied birds displayed telomere elongation. Telomere maintenance and elongation is carried out by the activity of the telomerase [65], the enzyme responsible for adding new nucleotides at the telomeric site of the DNA after each DNA replication event. Telomere elongation has been previously described in adult Leach's storm petrels *Oceanodroma leucorhoa*, suggesting that long-lived species such as seabirds can "escape" from telomere shortening and possibly possess mechanisms to upregulate telomerase activity later in life [66], but the underlying mechanisms remain unknown. Here we provide three explanations for the positive association between PFAS and telomere dynamics. First of all, some PFAS, and especially long-chain carboxylates can bind to plasma proteins which are essential for hormone displacement and are thus suspected to disrupt the endocrine system [67]. Although only a few studies have investigated the effects of PFAS on the endocrine system in birds, recent work found that higher levels of PFTrDA and PFTeDA are associated with lower baseline corticosterone CORT in black-legged kittiwakes [18]. Glucocorticoids have been widely used to describe the effect of environmental conditions on telomere dynamics of vertebrates because they alter telomerase activity [32]. An up-regulation of telomerase activity mediated by PFAS-induced reduction in circulating CORT as previously shown in birds [18] may explain why birds with higher levels of certain PFAS showed the slowest rate of telomere shortening, but this hypothesis will need to be specifically tested. Second, glaucous gulls in Svalbard are exposed to a complex cocktail of persistent organic pollutants and trace elements [43, 48]. These contaminants, which were not analyzed in the present study, can occur at high concentrations and may potentially impact on telomeres in synergy with PFAS. Third, we cannot exclude the possibility that exposure to PFAS during the breeding season leads to invest less in reproduction (e.g. through a reduced clutch size), which in turn may positively reflect on certain physiological traits.

Relationship between CMR data and PFAS. Results of the models testing for an effect of PFAS on survival and re-sighting probabilities are reported in Table 2. Our initial model fitted the data (median c-hat = 1.008). Male birds exposed to higher blood PFOA concentration at time of sampling had higher re-sighting rates (slope ± SE: 0.91 ± 0.26; P_{LRT}<0.001, Table 2, Figure 3a) and apparent survival probabilities (slope ± SE: 1.13 ± 0.47; P_{LRT}=0.003, Table 2, Figure 3b) over the following years. CMR models also showed that male birds exposed to higher blood concentrations of PFHxS at time of sampling had higher re-sighting rates (slope ± SE: 1.74 ± 0.43; P_{LRT}<0.001, Table 2, Figure 3c) over the following years, but there was no clear association with apparent survival (P_{LRT}=0.056 although the 95% CI of the slope in males did not contain zero; slope ± SE: 1.10 ± 0.48; 95% CI 0.17, 2.04, Table 2), likely due to the wide confidence intervals (Figure 3d). All other PFAS and telomere length were not associated neither with re-sighting rate (although for telomere P_{LRT}=0.09 and the CI of the slope in males did not contain zero; slope ± SE: -0.56 ± 0.28; 95% CI -1.12, -0.01) nor apparent survival. Because glaucous gulls are highly philopatric and most birds occupy the same nest for several years [68], and because most nests are monitored annually, we may assume that breeding birds are more re-sighted than non-breeding birds. Previous work in humans found that PFOA and PFHxS are positively associated with prolactin and follicle-stimulating hormone (FSH), respectively [69]. In birds, recent findings further suggest that PFAS can stimulate the production of prolactin [23]. When not incubating, glaucous gull males spend more time at the nest site than females [70]. If exposure to PFAS lead to an increased secretion of the hormones implicated in parental commitment, males exposed to higher levels of PFOA and PFHxS may allocate more time in nest defense, incubating or in providing parental care, a condition that will increase their re-sighting probabilities. Furthermore, other factors that could not be accounted for in this study (e.g. overwintering in different locations; feeding strategies) may also be responsible for the variation in PFAS exposure, survival, or both. For instance, some males may specialize in food items containing lower PFOA and PFHxS (e.g. eggs from other breeding glaucous gull, which contain low to undetectable levels of PFOA and PFHxS [15], or on lower trophic level preys), strategies that may negatively associate with survival and re-sighting probability. Because food intake is the main route through which birds gets exposed, feeding on the highly nutritional fish-based diet may positively reflect on both physiological and demographic parameters, while at the same time increase exposure to PFAS. Further studies measuring PFAS in birds should therefore additionally measure stable isotopes as a proxy of their feeding ecology, that would strongly benefit with the interpretation of the results.

To date, our study represents one of the most comprehensive work to provide evidence in wild vertebrates that PFAS exposure is associated with telomere length dynamics. We found a significant association between PFAS and telomere dynamics, with the most PFNA and PFTeDA contaminated birds showing the slowest rate of telomere shortening. We also found that PFOA and PFHxS were positively associated with apparent survival and re-sighting probabilities in our species. These results corroborate the hypothesis that PFAS positively associate with telomere length as previously suggested [40, 41]. Our study also provides new evidences that compared to legacy chlorinated pesticides and polychlorinated biphenyls, PFAS may associate with physiological biomarkers in a different way [21, 48]. To the extent of our knowledge, this is the first study to report that the association between PFAS exposure and telomere length is tied to specific PFAS congeners, and that the effect does not rely on total PFAS concentrations. The latter statement is further supported by the significant and positive association between exposure to specific PFAS congeners and demographic responses in this long-lived bird. Previous work suggested that PFAS are unlikely to cause detrimental effects given the low environmental concentrations [67]. But our results corroborate the positive association between PFAS and physiological traits of wildlife previously found in seabirds [23, 24, 48] and dolphins *Tursiops truncatus* [71]. Yet, further experimental work on telomere length dynamics (e.g. using laboratory animals) to assess the mechanisms through which PFAS would impact on telomeres is strongly advised. Most importantly, our results call for further studies to elucidate how exposure to PFAS would positively associate with apparent survival and re-sighting probabilities in this species.

Supporting Information

Detailed protocols for PFAS and telomere analyses, and a Quality Assurance/Quality Control (QA/QC) statement is provided. The Supporting Table S1 summarizes the detection frequency (Df) and the limit of quantification of all PFAS analysed in the study. The Supporting Table S2 further summarizes the statistical results of the best fit linear mixed models on the association between either absolute telomere length or telomere dynamics and each PFAS congener. The Supporting information also includes a correlation matrix describing the association among PFAS (Figure S1).

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Table 1: Plasma PFAS concentrations expressed as mean ± standard deviation (pg/mL of ww) and median value of male (n=24) and female (n=51) glaucous gulls *Larus hyperboreus* from Kongsfjorden, Svalbard. PFAS data refer to the period 2012-2017, for which both telomere length and PFAS were estimated, and only include one PFAS measurement for each bird (PFAS data related to the first capture event of each bird). Significant P-values are showed in bold. Asterisks indicate that data were square-root (a) or log10-transformed (b) to meet linear model assumptions.

	Males		**Females**			
	Mean ± SD	**Median (range)**	**Mean ± SD**	**Median (range)**	**$F_{1,73}$**	**P-value**
Carboxilates						
PFOA[a]	115 ± 110	120 (<10-390)	210 ± 210	150 (<10-790)	4.02	**<0.05**
PFNA[b]	1930 ± 1100	1565 (950-5485)	1610 ± 970	1370 (300-4420)	3.03	0.09
PFDA[b]	1105 ± 640	870 (440-2790)	750 ± 470	620 (155-2095)	9.38	**<0.01**
PFUnA[b]	4220 ± 1985	3775 (1555-9640)	3260 ± 2120	2730 (680-10605)	6.05	**<0.05**
PFDoDA	1080 ± 450	1060 (105-1810)	700 ± 475	605 (<40-2495)	11.06	**<0.01**
PFTrDA[a]	5215 ± 4580	3525 (940-16300)	2390 ± 1675	2120 (<100-9770)	17.03	**<0.001**
PFTeDA	350 ± 245	370 (<120-790)	235 ± 180	210 (<120-710)	5.05	**<0.05**
Sulfonates						
PFHxS[b]	585 ± 370	495 (30-1600)	1465 ± 3355	395(<30-18725)	<0.01	0.99
L-PFOS[b!]	13305 ± 6595	11050 (5020-33340)	29845 ± 79850	6600 (1390-507665)	0.71	0.40

! For L-PFOS, normality of residuals could not be achieved.

Table 2: Effect of PFAS and sex on re-sighting and survival rates of adult glaucous gulls (n=89), Svalbard, Norway. Models are ranked from lowest to highest ΔAIC_c. P_{LRT} refers to the significance of the likelihood ratio test between the model with the effect and the model with no effect on either ϕ (survival) or *p* (re-sighting). Only models for which this difference was significant are presented. PFOA and PFHxS concentrations were log10-transformed to facilitate convergence of CMR models. Asterisks indicate an interaction between sex and the individual covariates (i.e. PFOA or PFHxS).

Hypothesis	**AICc**	**ΔAICc**	**Deviance**	**Slope ± SE (95% CI)**	P_{LRT}
logPFOA					
Effect of PFOA*sex on *p*	549.2	0	536.9	Males: 0.91 ± 0.26 (0.40, 1.42) Females: -0.28 ± 0.19 (-0.65, 0.09)	**<0.001**
Effect of PFOA*sex on ϕ	552.6	3.4	540.3	Males: 1.13 ± 0.47 (0.21, 2.05) Females: -0.07 ± 0.20 (-0.47, 0.32)	**0.003**
No effect on ϕ or p	559.9	10.7	661.8		
logPFHxS					
Effect of PFHxS*sex on *p*	542.6	0	530.3	Males: 1.74 ± 0.43 (0.89, 2.59) Females: 0.29 ± 0.17 (-0.05, 0.63)	**<0.001**
Effect of PFHxS*sex on θ	558.3	15.7	546.0	Males: 1.10 ± 0.48 (0.17, 2.04) Females: 0.03 ± 0.19 (-0.35, 0.40)	0.056
No effect on ϕ or *p*	559.9	17.3	551.8		

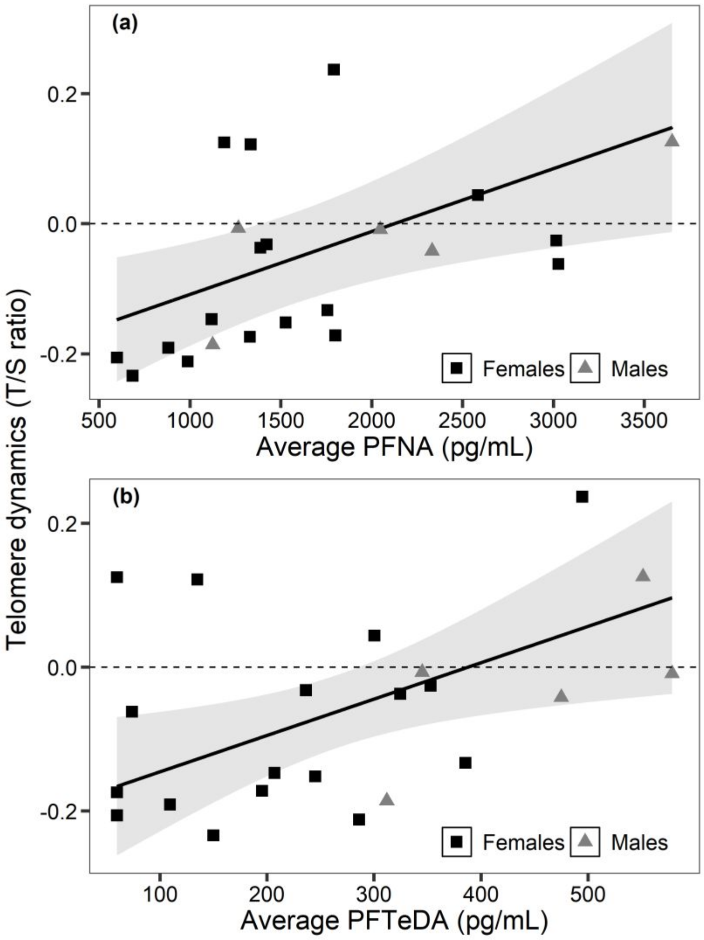


Figure 1: Relationship between telomere dynamics (expressed as the difference in T/S ratio between two years) and a) PFNA expressed as pg/mL; and b) PFTeDA expressed as pg/mL, in adult Glaucous gulls from Svalbard. Individuals above the dashed line showed an elongation in telomere length, whereas the ones below showed a shortening in telomere length. Analyses are based on 19 individuals with repeated measures of telomere length. The solid line represents the trend while the grey area represents 95% confidence intervals.

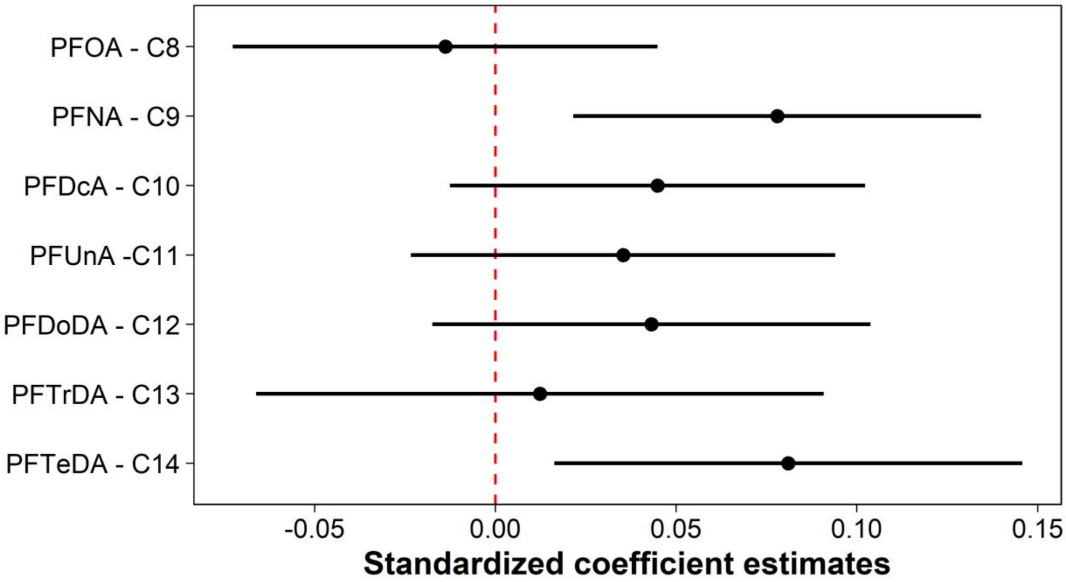


Figure 2: Effect size of all carboxylic PFAS on telomere dynamics in adult Glaucous gulls from Svalbard. All PFAS except PFOA were positively associated with telomere dynamics. The figure illustrates model averaging outputs (conditional averaged estimates and 95% confidence interval) from the selected models. PFAS were ordered based on their carbon-chain-length (C8 to C14).

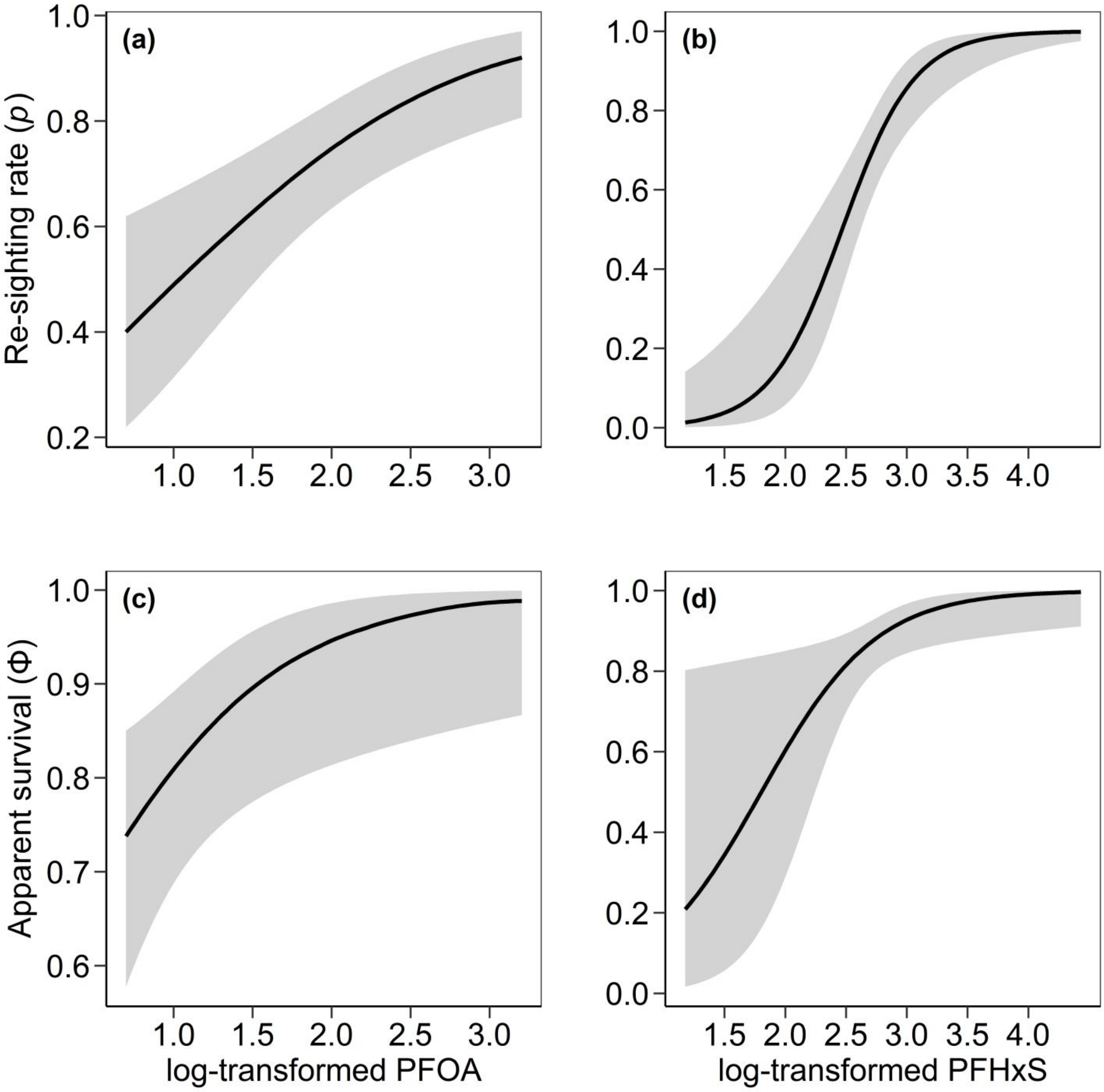


Figure 3: Relationships between log-transformed PFOA and a) re-sighting and c) survival, and between log-transformed PFHxS and b) re-sighting and d) survival in male glaucous gulls from Svalbard, Norway. The solid line represents the modeled relationship while the grey area represents 95% confidence intervals (CIs). CIs are meant not to fall below zero or to exceed one since re-sighting and survival are probabilities.

References

1. Letcher, R. J.; Bustnes, J. O.; Dietz, R.; Jenssen, B. M.; Jorgensen, E. H.; Sonne, C.; Verreault, J.; Vijayan, M. M.; Gabrielsen, G. W., Exposure and effects assessment of persistent organohalogen contaminants in arctic wildlife and fish. *Science of the Total Environment* **2010,** *408*, (15), 2995-3043.

2. Gascon, M.; Morales, E.; Sunyer, J.; Vrijheid, M., Effects of persistent organic pollutants on the developing respiratory and immune systems: a systematic review. *Environmental International* **2013,** *52*, 51-65.

3. Giesy, J. P.; Feyk, L. A.; Jones, P. D.; Kannan, K.; Sanderson, T., Review of the effects of endocrine-disrupting chemicals in birds. In *Pure and Applied Chemistry*, 2003; Vol. 75, p 2287.

4. Buck, R. C.; Franklin, J.; Berger, U.; Conder, J. M.; Cousins, I. T.; de Voogt, P.; Jensen, A. A.; Kannan, K.; Mabury, S. A.; van Leeuwen, S. P. J., Perfluoroalkyl and polyfluoroalkyl substances in the environment: terminology, classification, and origins. *Integrated Environmental Assessment and Management* **2011,** *7*, (4), 513-541.

5. Muir, D. C. G.; Bossi, R.; Carlsson, P.; Evans, M.; De Silva, A.; Halsall, C.; Rauert, C.; Herzke, D.; Hung, H.; Letcher, R.; Rigét, F.; Roos, A., Levels and trends of poly- and perfluoroalkyl substances in the Arctic environment – An update. *Emerging Contaminants* **2019,** *5*, 240-271.

6. Conder, J. M.; Hoke, R. A.; De Wolf, W.; Russell, M. H.; Buck, R. C., Are PFCAs bioaccumulative? A critical review and comparison with regulatory criteria and persistent lipophilic compounds. *Environmental Science & Technology* **2008,** *42*, (4), 995-1003.

7. Houde, M.; Martin, J. W.; Letcher, R. J.; Solomon, K. R.; Muir, D. C. G., Biological monitoring of polyfluoroalkyl substances: A review. *Environmental Science & Technology* **2006,** *40*, (11), 3463-73.

8. Giesy, J. P.; Kannan, K., Global distribution of perfluorooctane sulfonate in wildlife. *Environmental Science & Technology* **2001,** *35*, (7), 1339-42.

9. Wong, F.; Shoeib, M.; Katsoyiannis, A.; Eckhardt, S.; Stohl, A.; Bohlin-Nizzetto, P.; Li, H.; Fellin, P.; Su, Y.; Hung, H., Assessing temporal trends and source regions of per- and polyfluoroalkyl substances (PFASs) in air under the Arctic Monitoring and Assessment Programme (AMAP). *Atmospheric Environment* **2018,** *172*, 65-73.

10. Bignert, A.; Olsson, M.; Persson, W.; Jensen, S.; Zakrisson, S.; Litzén, K.; Eriksson, U.; Häggberg, L.; Alsberg, T., Temporal trends of organochlorines in Northern Europe, 1967–1995. Relation to global fractionation, leakage from sediments and international measures. *Environmental Pollution* **1998,** *99*, (2), 177-198.

11. Sun, J.; Bossi, R.; Bustnes, J. O.; Helander, B.; Boertmann, D.; Dietz, R.; Herzke, D.; Jaspers, V. L. B.; Labansen, A. L.; Lepoint, G.; Schulz, R.; Sonne, C.; Thorup, K.; Tøttrup, A. P.; Zubrod, J. P.; Eens, M.; Eulaers, I., White-Tailed Eagle (*Haliaeetus albicilla*) Body Feathers Document Spatiotemporal Trends of Perfluoroalkyl Substances in the Northern Environment. *Environmental Science & Technology* **2019**, 53, (21), 12744–12753.

12. Land, M.; de Wit, C. A.; Bignert, A.; Cousins, I. T.; Herzke, D.; Johansson, J. H.; Martin, J. W., What is the effect of phasing out long-chain per- and polyfluoroalkyl substances on the concentrations of perfluoroalkyl acids and their precursors in the environment? A systematic review. *Environmental Evidence* **2018,** *7*, (1), 4.

13. Kelly, B. C.; Ikonomou, M. G.; Blair, J. D.; Surridge, B.; Hoover, D.; Grace, R.; Gobas, F. A. P. C., Perfluoroalkyl Contaminants in an Arctic Marine Food Web: Trophic Magnification and Wildlife Exposure. *Environmental Science & Technology* **2009,** *43*, (11), 4037-4043.

14. Costantini, D.; Blevin, P.; Herzke, D.; Moe, B.; Gabrielsen, G. W.; Bustnes, J. O.; Chastel, O., Higher plasma oxidative damage and lower plasma antioxidant defences in an Arctic seabird exposed to longer perfluoroalkyl acids. *Environmental Research* **2019,** *168*, 278-285.

15. Verreault, J.; Houde, M.; Gabrielsen, G. W.; Berger, U.; Haukås, M.; Letcher, R. J.; Muir, D. C. G., Perfluorinated Alkyl Substances in Plasma, Liver, Brain, and Eggs of Glaucous Gulls (*Larus hyperboreus*) from the Norwegian Arctic. *Environmental Science & Technology* **2005,** *39*, (19), 7439-7445.

16. Guigueno, M. F.; Fernie, K. J., Birds and flame retardants: A review of the toxic effects on birds of historical and novel flame retardants. *Environmental Research* **2017,** *154*, 398-424.

17. Chen, D.; Hale, R. C., A global review of polybrominated diphenyl ether flame retardant contamination in birds. *Environment International* **2010,** *36*, (7), 800-811.

18. Tartu, S.; Gabrielsen, G. W.; Blévin, P.; Ellis, H.; Bustnes, J. O.; Herzke, D.; Chastel, O., Endocrine and Fitness Correlates of Long-Chain Perfluorinated Carboxylates Exposure in Arctic Breeding Black-Legged Kittiwakes. *Environmental Science & Technology* **2014,** *48*, (22), 13504-13510.

19. Custer, C. M.; Custer, T. W.; Dummer, P. M.; Etterson, M. A.; Thogmartin, W. E.; Wu, Q.; Kannan, K.; Trowbridge, A.; McKann, P. C., Exposure and Effects of Perfluoroalkyl Substances in Tree Swallows Nesting in Minnesota and Wisconsin, USA. *Archives of Environmental Contamination and Toxicology* **2014,** *66*, (1), 120-138.

20. Eckbo, N.; Le Bohec, C.; Planas-Bielsa, V.; Warner, N. A.; Schull, Q.; Herzke, D.; Zahn, S.; Haarr, A.; Gabrielsen, G. W.; Borga, K., Individual variability in contaminants and physiological status in a resident Arctic seabird species. *Environmental Pollution* **2019,** *249*, 191-199.

21. Blévin, P.; Tartu, S.; Ellis, H. I.; Chastel, O.; Bustamante, P.; Parenteau, C.; Herzke, D.; Angelier, F.; Gabrielsen, G. W., Contaminants and energy expenditure in an Arctic seabird: Organochlorine pesticides and perfluoroalkyl substances are associated with metabolic rate in a contrasted manner. *Environmental Research* **2017,** *157*, 118-126.

22. Nøst, T. H.; Helgason, L. B.; Harju, M.; Heimstad, E. S.; Gabrielsen, G. W.; Jenssen, B. M., Halogenated organic contaminants and their correlations with circulating thyroid hormones in developing Arctic seabirds. *Science of The Total Environment* **2012,** *414*, 248-256.

23. Blévin, P.; Shaffer, S. A.; Bustamante, P.; Angelier, F.; Picard, B.; Herzke, D.; Moe, B.; Gabrielsen, G. W.; Bustnes, J. O.; Chastel, O., Contaminants, prolactin and parental care in an Arctic seabird: Contrasted associations of perfluoroalkyl substances and organochlorine compounds with egg-turning behavior. *General and Comparative Endocrinology* **2020,** *291*, 113420.

24. Bustnes, J. O.; Erikstad, K. E.; Lorentsen, S.-H.; Herzke, D., Perfluorinated and chlorinated pollutants as predictors of demographic parameters in an endangered seabird. *Environmental Pollution* **2008,** *156*, (2), 417-424.

25. Barrett, E. L. B.; Burke, T. A.; Hammers, M.; Komdeur, J.; Richardson, D. S., Telomere length and dynamics predict mortality in a wild longitudinal study. *Molecular Ecology* **2013,** *22*, (1), 249-259.

26. Bize, P.; Criscuolo, F.; Metcalfe, N.; Nasir, L.; Monaghan, P., Telomere dynamics rather than age predict life expectancy in the wild. *Proceedings of the Royal Society B: Biological Sciences* **2009,** *276*, 1679-83.

27. Haussmann, M. F.; Winkler, D. W.; Vleck, C. M., Longer telomeres associated with higher survival in birds. *Biology Letters* **2005,** *1*, (2), 212-214.

28. Salomons, H. M.; Mulder, G. A.; Zande, L. v. d.; Haussmann, M. F.; Linskens, M. H. K.; Verhulst, S., Telomere shortening and survival in free-living corvids. *Proceedings of the Royal Society B: Biological Sciences* **2009,** *276*, (1670), 3157-3165.

29. Tricola, G. M.; Simons, M. J. P.; Atema, E.; Boughton, R. K.; Brown, J. L.; Dearborn, D. C.; Divoky, G.; Eimes, J. A.; Huntington, C. E.; Kitaysky, A. S.; Juola, F. A.; Lank, D. B.; Litwa, H. P.; Mulder, E. G. A.; Nisbet, I. C. T.; Okanoya, K.; Safran, R. J.; Schoech, S. J.; Schreiber, E. A.; Thompson, P. M.; Verhulst, S.; Wheelwright, N. T.; Winkler, D. W.; Young, R.; Vleck, C. M.; Haussmann, M. F., The rate of telomere loss is related to maximum lifespan in birds. *Philosophical Transactions of the Royal Society B: Biological Sciences* **2018,** *373*, (1741), 20160445.

30. Angelier, F.; Weimerskirch, H.; Barbraud, C.; Chastel, O., Is telomere length a molecular marker of individual quality? Insights from a long-lived bird. *Functional Ecology* **2019,** *33*, (6), 1076-1087.

31. Eastwood, J. R.; Hall, M. L.; Teunissen, N.; Kingma, S. A.; Hidalgo Aranzamendi, N.; Fan, M.; Roast, M.; Verhulst, S.; Peters, A., Early-life telomere length predicts lifespan and lifetime reproductive success in a wild bird. *Molecular Ecology* **2019,** *28*, (5), 1127-1137.

32. Angelier, F.; Costantini, D.; Blevin, P.; Chastel, O., Do glucocorticoids mediate the link between environmental conditions and telomere dynamics in wild vertebrates? A review. *General and Comparative Endocrinology* **2018,** *256*, 99-111.

33. Chatelain, M.; Drobniak, S. M.; Szulkin, M., The association between stressors and telomeres in non-human vertebrates: a meta-analysis. *Ecology Letters* **2020,** *23*, (2), 381-398.

34. Marasco, V.; Costantini, D., Signaling in a Polluted World: Oxidative Stress as an Overlooked Mechanism Linking Contaminants to Animal Communication. *Frontiers in Ecology and Evolution* **2016,** *4*, (95).

35. Reichert, S.; Stier, A., Does oxidative stress shorten telomeres in vivo? A review. *Biology letters* **2017,** *13*, (12).

36. Louzon, M.; Coeurdassier, M.; Gimbert, F.; Pauget, B.; de Vaufleury, A., Telomere dynamic in humans and animals: Review and perspectives in environmental toxicology. *Environment International* **2019,** *131*, 105025.

37. Stauffer, J.; Panda, B.; Eeva, T.; Rainio, M.; Ilmonen, P., Telomere damage and redox status alterations in free-living passerines exposed to metals. *Science of the Total Environment* **2017,** *575*, 841-848.

38. Sletten, S.; Bourgeon, S.; Bardsen, B. J.; Herzke, D.; Criscuolo, F.; Massemin, S.; Zahn, S.; Johnsen, T. V.; Bustnes, J. O., Organohalogenated contaminants in white-tailed eagle (*Haliaeetus albicilla*) nestlings: An assessment of relationships to immunoglobulin levels, telomeres and oxidative stress. *Science of the Total Environment* **2016,** *539*, 337-349.

39. Blévin, P.; Angelier, F.; Tartu, S.; Ruault, S.; Bustamante, P.; Herzke, D.; Moe, B.; Bech, C.; Gabrielsen, G. W.; Bustnes, J. O.; Chastel, O., Exposure to oxychlordane is associated with shorter telomeres in arctic breeding kittiwakes. *Science of the Total Environment* **2016,** *563-564*, 125-30.

40. Blévin, P.; Angelier, F.; Tartu, S.; Bustamante, P.; Herzke, D.; Moe, B.; Bech, C.; Gabrielsen, G. W.; Bustnes, J. O.; Chastel, O., Perfluorinated substances and telomeres in an Arctic seabird: Cross-sectional and longitudinal approaches. *Environmental Pollution* **2017,** *230*, 360-367.

41. Huang, H.; Wang, Q.; He, X.; Wu, Y.; Xu, C., Association between polyfluoroalkyl chemical concentrations and leucocyte telomere length in US adults. *Science of The Total Environment* **2019,** *653*, 547-553.

42. Anker-Nilssen, T.; Bakken, V.; Strøm, H.; Golovkin, A.; Bianki, V.; Tatarinkova, I., *The Status of Marine Birds Breeding in the Barents Sea Region*. Norsk polarinstitutt 2000.

43. Sagerup, K.; Helgason, L. B.; Polder, A.; Strom, H.; Josefsen, T. D.; Skare, J. U.; Gabrielsen, G. W., Persistent organic pollutants and mercury in dead and dying glaucous gulls (*Larus hyperboreus*) at Bjornoya (Svalbard). *Science of the Total Environment* **2009,** *407*, (23), 6009-16.

44. Verreault, J.; Gabrielsen, G. W.; Bustnes, J. O., The Svalbard glaucous gull as bioindicator species in the European arctic: insight from 35 years of contaminants research. *Reviews of Environmental Contamination and Toxicology* **2010,** *205*, 77-116.

45. Malinga, M.; Szefer, P.; Gabrielsen, G. W., Age, sex and spatial dependent variations in heavy metals levels in the Glaucous Gulls (*Larus hyperboreus*) from the Bjørnøya and Jan Mayen, Arctic. *Environmental Monitoring and Assessment* **2010,** *169*, (1), 407-416.

46. Erikstad, K. E.; Sandvik, H.; Reiertsen, T. K.; Bustnes, J. O.; Strøm, H., Persistent organic pollution in a high-Arctic top predator: sex-dependent thresholds in adult survival. *Proceedings of the Royal Society B: Biological Sciences* **2013,** *280*, (1769), 20131483-20131483.

47. Bustnes, J. O.; Bakken, V.; Erikstad, K. E.; Mehlum, F.; Skaare, J. U., Patterns of Incubation and Nest-Site Attentiveness in Relation to Organochlorine (PCB) Contamination in Glaucous Gulls. *Journal of Applied Ecology* **2001,** *38*, (4), 791-801.

48. Melnes, M.; Gabrielsen, G. W.; Herzke, D.; Sagerup, K.; Jenssen, B. M., Dissimilar effects of organohalogenated compounds on thyroid hormones in glaucous gulls. *Environmental Research* **2017,** *158*, 350-357.

49. Criscuolo, F.; Bize, P.; Nasir, L.; Metcalfe, N. B.; Foote, C. G.; Griffiths, K.; Gault, E. A.; Monaghan, P., Real-time quantitative PCR assay for measurement of avian telomeres. *Journal of Avian Biology* **2009,** *40*, (3), 342-347.

50. Cooch, E. G.; White, G. C., Program Mark, a gentle introduction. Available at http://www.phidot.org/software/mark/docs/book/. **2019**.

51. R, C. T., R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing. **2019**.

52. ITRC-Report, Naming Conventions and Physical and Chemical Properties of Per- and Polyfluoroalkyl Substances (PFAS). **2017**.

53. Peig, J.; Green, A. J., New perspectives for estimating body condition from mass/length data: the scaled mass index as an alternative method. *Oikos* **2009,** *118*, (12), 1883-1891.

54. Zuur, A.; Ieno, E. N.; Walker, N.; Saveliev, A. A.; Smith, G. M., *Mixed Effects Models and Extensions in Ecology with R*. Springer New York: 2009.

55. Moran, M., Arguments for rejecting the sequential Bonferroni in ecological studies. *Oikos* **2003,** *100*, 403-405.

56. Munoz, G.; Labadie, P.; Geneste, E.; Pardon, P.; Tartu, S.; Chastel, O.; Budzinski, H., Biomonitoring of fluoroalkylated substances in Antarctica seabird plasma: Development and validation of a fast and rugged method using on-line concentration liquid chromatography tandem mass spectrometry. *Journal of Chromatography A* **2017,** *1513*, 107-117.

57. Sagerup, K.; Henriksen, E. O.; Skaare, J. U.; Gabrielsen, G. W., Intraspecific Variation in Trophic Feeding Levels and Organochlorine Concentrations in Glaucous Gulls (*Larus hyperboreus*) from Bjørnøya, the Barents Sea. *Ecotoxicology* **2002,** *11*, (2), 119-125.

58. Verreault, J.; Villa, R. A.; Gabrielsen, G. W.; Skaare, J. U.; Letcher, R. J., Maternal transfer of organohalogen contaminants and metabolites to eggs of Arctic-breeding glaucous gulls. *Environmental Pollution* **2006,** *144*, (3), 1053-1060.

59. Bustnes, J. O.; Erikstad, K. E.; Bakken, V.; Mehlum, F.; Skaare, J. U., Feeding Ecology and the Concentration of Organochlorines in Glaucous Gulls. *Ecotoxicology* **2000,** *9*, 179-186.

60. Heidinger, B. J.; Blount, J. D.; Boner, W.; Griffiths, K.; Metcalfe, N. B.; Monaghan, P., Telomere length in early life predicts lifespan. *Proceedings of the National Academy of Sciences USA* **2012,** *109*, (5), 1743-8.

61. Angelier, F.; Vleck, C. M.; Holberton, R. L.; Marra, P. P., Telomere length, non-breeding habitat and return rate in male American redstarts. *Functional Ecology* **2013,** *27*, (2), 342-350.

62. Hall, M. E.; Nasir, L.; Daunt, F.; Gault, E. A.; Croxall, J. P.; Wanless, S.; Monaghan, P., Telomere loss in relation to age and early environment in long-lived birds. *Proceedings of the Royal Society of London. Series B: Biological Sciences* **2004,** *271*, (1548), 1571-1576.

63. Bustnes, J. O.; Bakken, V.; Skaare, J. U.; Erikstad, K. E., Age and accumulation of persistent organochlorines: A study of arctic-breeding glaucous gulls (*Larus hyperboreus). Environmental Toxicology and Chemistry* **2003,** *22*, (9), 2173-2179.

64. Løseth, M. E.; Briels, N.; Eulaers, I.; Nygård, T.; Malarvannan, G.; Poma, G.; Covaci, A.; Herzke, D.; Bustnes, J. O.; Lepoint, G.; Jenssen, B. M.; Jaspers, V. L. B., Plasma concentrations of organohalogenated contaminants in white-tailed eagle nestlings - The role of age and diet. *Environmental Pollution* **2019,** *246*, 527-534.

65. Zvereva, M. I.; Shcherbakova, D. M.; Dontsova, O. A., Telomerase: structure, functions, and activity regulation. *Biochemistry (Moscow)* **2010,** *75*, (13), 1563-83.

66. Haussmann, M. F.; Winkler, D. W.; O'Reilly, K. M.; Huntington, C. E.; Nisbet, I. C. T.; Vleck, C. M., Telomeres shorten more slowly in long-lived birds and mammals than in short-lived ones. *Proceedings of the Royal Society B: Biological Sciences* **2003,** *270*, (1522), 1387-1392.

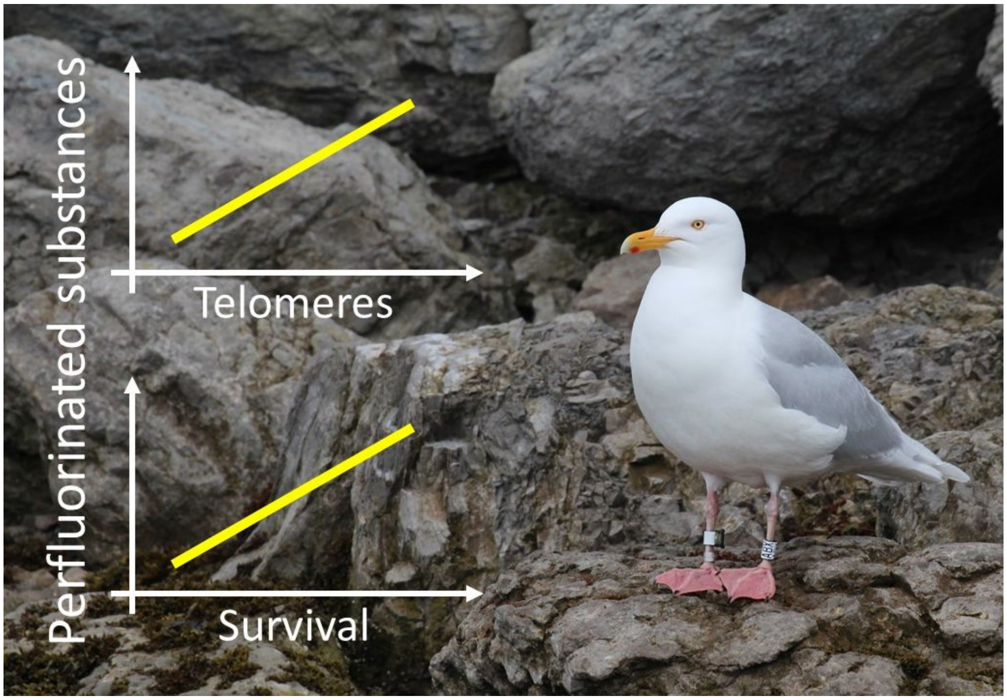
67. Jones, P. D.; Hu, W.; De Coen, W.; Newsted, J. L.; Giesy, J. P., Binding of perfluorinated fatty acids to serum proteins. *Environmental Toxicology and Chemistry* **2003,** *22*, (11), 2639-2649.

68. Bustnes, J. O.; Miland, O.; Fjeld, M.; Erikstad, K. E.; Skaare, J. U., Relationships between ecological variables and four organochlorine pollutants in an artic glaucous gull (*Larus hyperboreus*) population. *Environ Pollut* **2005,** *136*, (1), 175-85.

69. Zhang, S.; Tan, R.; Pan, R.; Xiong, J.; Tian, Y.; Wu, J.; Chen, L., Association of Perfluoroalkyl and Polyfluoroalkyl Substances With Premature Ovarian Insufficiency in Chinese Women. *The Journal of Clinical Endocrinology & Metabolism* **2018,** *103*, (7), 2543-2551.

70. Verboven, N.; Verreault, J.; Letcher, R. J.; Gabrielsen, G. W.; Evans, N. P., Nest temperature and parental behaviour of Arctic-breeding glaucous gulls exposed to persistent organic pollutants. *Animal Behaviour* **2009,** *77*, (2), 411-418.

71. Fair, P. A.; Schaefer, A. M.; Houser, D. S.; Bossart, G. D.; Romano, T. A.; Champagne, C. D.; Stott, J. L.; Rice, C. D.; White, N.; Reif, J. S., The environment as a driver of immune and endocrine responses in dolphins (*Tursiops truncatus*). *PLOS ONE* **2017,** *12*, (5), e0176202.



Exposure to perfluorinated substances is associated with telomere dynamics and demographic parameters in a marine top predator in Svalbard, Norway.