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Long-term within-season changes in the diet of Common Guillemot *Uria aalge* chicks at a North Sea colony: implications for dietary monitoring

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Over four decades there were pronounced within-season changes in the proportion of a key prey species (Lesser Sandeel *Ammodytes marinus*) in Common Guillemot *Uria aalge* chick diet. As Sandeels became scarcer their occurrence was largely confined to the early part of the chick period. Consequently, the mean annual proportion of Sandeels was poorly estimated if sampling occurred within a short time window, particularly if this was early or late in the season. Within-season variation is rarely considered in diet monitoring, but our results highlight the need for further analyses across other species and sites to develop a deeper understanding of how best to optimise sampling protocols.

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Many studies have concluded that climate change influences seabird breeding success indirectly through changes in prey availability (e.g. Frederiksen *et al*. 2013, Sydeman *et al*. 2021). Despite this, monitoring of seabird diet generally receives much less attention than monitoring of productivity. For example, from 1986-2019 the UK Seabird Monitoring Programme archived productivity data for 23 species but diet data for only five species, and diet data were available for many fewer years (JNCC 2021). In part, this disparity arises because collecting data on diet can be logistically challenging since most species provision their young by regurgitation. However, this limitation does not apply to the larger auks Alcidae and terns Sternidae where the parents bring back food items in the bill, making it possible to identify prey species visually and hence document diet without the need to handle adults or chicks (Barrett *et al*. 2007). Typically, the main aim of dietary monitoring is to obtain annual estimates of the proportions of different prey contributing to chick diet. Several studies have, however, shown that there can be marked within-year changes in chick diet that could potentially bias annual estimates if sampling effort was restricted to a short time window (Berruti *et al*. 1993, Kirkwood & Robertson 1997, Centrica Energy 2009, Gaglio *et al*. 2018). Nevertheless, long-term changes in patterns of within-year dietary variability are rarely documented, nor have their implications for how chick diet is monitored been considered.

We assembled a multi-decadal dataset on chick diet of the Common Guillemot *Uria aalge* (hereafter Guillemot) collected using morphological prey identification (Hoenig *et al*. 2021). Guillemots are a major avian predator of small, shoaling, lipid-rich fish in the Northeast Atlantic (Grandgeorge *et al*. 2008) and their breeding performance is widely monitored as an indicator of the state of the marine environment (e.g. Cook *et al.* 2014, Anker-Nilssen *et al.* 2018, JNCC 2021). Previous analyses of some of the data included in our dataset highlighted a reduction in the overall importance of Lesser Sandeel *Ammodytes marinus* and corresponding increase in Clupeidae, predominantly Sprat *Sprattus sprattus*, over the last four decades (Anderson *et al.* 2014, Wanless *et al.* 2018). Here, we document within-season changes in diet over a 38-year period at a major North Sea colony and evaluate the importance of timing of sampling effort for obtaining robust annual estimates of diet. We discuss how within-season dietary changes of predators may provide additional biological information on prey species, using Sandeels, a key mid-trophic forage fish in the North Sea (Engelhard *et al*. 2014) as an example.

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METHODS

The study was carried out on the Isle of May National Nature Reserve (56° 11'N, 02° 33'W), southeast Scotland in 1982-2019, where large numbers of breeding Guillemots can be observed using binoculars or a telescope at distances of less than 30 m. During chick rearing, parents return to the colony holding a single fish longitudinally in the bill making the prey easy to identify. Sampling methods followed guidelines in Walsh *et al.* (1995) and remained constant throughout the study. Observer consistency was high with MPH and SW contributing data in 38 and 36 years, respectively, and MAN and CG data in 15 and 8 years, respectively. Data from other observers were fewer in number and covered shorter time periods, usually just a couple of years. Most observations were made opportunistically during daylight hours (mainly 05:30-21:30 h BST although the times of observations were not recorded), on most days during the chick-rearing period. In addition, for all years except 1982, 1- 8 (median 3) systematic all-day (03.30-22.30 h; Supporting Information Appendix S1) watches were made of study plots containing up to 124 young (median = 42). Together, these observations provided good coverage of all hours of daylight and thus estimates should be robust to any bias associated with diurnal variation in chick diet. The opportunistic and systematic data were combined to provide annual diet information across the chick-rearing period (mean ± SD: 38.0 ± 5.6 days, range 25−50 days, *n* = 38 years), and a mean ± SD annual total of 971 ± 476 fish (range 453–2882). In most cases individual birds were not identifiable and since observations covered an area where there were > 4 000 Guillemots breeding, each fish is considered to be an independent observation. Fish were identified to family level – Ammodytidae (37.3% of 36 909 fish recorded throughout the season over the 38 years), Clupeidae (60.5%) or Gadidae and others (2.2%). All 457 Ammodytidae collected from breeding ledges were Lesser Sandeel (hereafter Sandeel) that were at least one years old (1+ group). Of the 151 Clupeidae identified 139 (92%) were Sprat, the rest were Herring *Clupea harengus*, so for convenience hereafter we refer to all Clupeidae as Sprat. Very few Gadidae were available for specific identification but included Whiting *Merlangius merlangus* and Saithe *Pollachius virens.*

Each year 500-1000 pairs of Guillemots (mean ± SD: 832 ± 114 pairs) were followed to determine mean dates of hatching and fledging, and age at fledging (Harris & Wanless 1988). The areas

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where these birds bred coincided with those where the majority of observations on chick diet were made. Since mean annual hatching date varied by 20 days (30 May–19 June), year-specific chick-rearing periods were estimated to commence on the mean hatching date – 1 standard deviation, and to end on the mean hatching date + 1 standard deviation + the mean fledging age of chicks in that year. This period (mean ± SD: 35.6 ± 2.2 days, range 32−43 days) excluded 13% of all days when diet data were recorded (mainly those at the end of the season), but only 1.7% of all fish. Data for this standardised period were used for all analyses (see Supporting Information Table 1).

The number of fish recorded per day varied between 1 and 497 (median = 11; details in Supporting Information Fig. S1) across the years. Given this variability we fitted a Generalized Linear Model (GLM) to the binomial responses to estimate the proportion of Sandeel in the total number of fish for each day (Anderson *et al.* 2014), using the Genstat statistical package (VSN International 2020). This approach effectively weights the days by the sample size. The full model fitted was Julian day + year + the interaction Julian day-by-year (Supporting Information Appendix S2). The interaction allowed a test of whether the within-season change in the proportion of Sandeel varied between years (the slope on the logit scale), as well as different intercepts for each year. To assess the consequences of varying the timing of sampling effort within the chick-rearing period we modelled the effect of using 10-day periods on the estimated proportion of Sandeel each year, defining early, mid and late sampling periods as Julian day 156-165, 166-175 and 176-185, respectively. Again, we used a GLM to model the binomial proportions across years but without considering Julian day or its interaction with year, specifically testing to see if the slopes and displacements differed between the three sampling periods. For displaying and reporting, estimates on the logit scale were back transformed to proportions. The approach is well illustrated by comparison of the four years 1991-94 where we show the proportions of Sandeels (filled circles) for each day that fish were sampled and the fitted logistic regression for each year (Supporting Information Fig. S2).

RESULTS

The overall model, including date, year and their interaction, explained 88% of the total deviance in chick diet (see Table 1 and Supporting Information Appendix S2). Most of this variation was

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associated with differences in the proportions of the main prey between years (mean deviance = 405.8, *df* = 37, $P < 0.0001$), with Sandeel dominant in the early years and Sprat dominant in the last two decades (Fig. 1a). In addition, Sandeel tended to become scarcer as the chick-rearing season progressed (Julian day slope on the logit scale = -0.0634 ± 0.0014, $P < 0.001$). However, there were highly significant between-year differences in the slopes of within-season trends in chick diet over the decades (Julian day-by-year interaction: Deviance $\text{ratio}_{37,\,1127} = 11.7$, $P < 0.001$). The proportion of Sandeel increased over the standardised chick-rearing period in five (56%) of the nine years between 1982-1990, but subsequently trends were increasingly likely to be negative. Hence, in 1991-2000 only three out 10 were positive, in 2001–10 only one was positive, and in 2011–19 none was positive (Fig. 2). Thus, as Sandeels became scarcer in the chick diet they were largely confined to the early part of the season with very few fed to chicks after Julian Day 160.

As a result of these contrasting within-season trends, different proportions of Sandeel would have been estimated if diet had been sampled for only limited periods of the Julian calendar. This is well illustrated by the variability in estimates for 10-day sampling windows: early (P1: Julian Day 156-165), mid (P2: Julian Day 166-175) and late (P3: Julian Day 176-185), compared with those estimated for the full chick-rearing period. In particular, annual means were poorly estimated from 10-day windows in the 1990s when within-season variation in chick diet was marked (Fig. 1b). In general, sampling early in the season (Fig. 3a) increased the estimates of the proportion of Sandeels in the chick diet by a mean ± SD of 0.041 ± 0.107 (range -0.17 to 0.26) while sampling late in the season (Fig. 3c) consistently under-recorded the importance of Sandeel (mean ± SD: -0.068 ± 0.121, range -0.16 to 0.16). However, sampling for 10 days in mid-chick rearing (Fig. 3b) resulted in less bias (mean ± SD: 0.018 ± 0.066, range -0.44 to 0.21). Although the slopes for the three periods were parallel, they were significantly displaced (Fig. 3d: displacement along the x-axis of relative proportions e.g.: 0.50: $F_{2,107} = 4.42$, $P = 0.014$). This was largely due to the difference between P2 and P3 ($F_{1,67} = 4.52$, $P = 0.037$), since there was no significant difference between P1 and P2 ($F_{1,68} = 0.33$, $P > 0.5$). By contrast, there was no difference in estimates of the long-term rate of decline in the proportion of Sandeel in chick diet over years (differences in slopes: $F_{2,107} = 0.8$, $P > 0.5$). In addition, the mean confidence intervals of the estimates in these 10-day sampling periods (Fig. 3a, b, c) were approximately twice as large in the early and late periods, as in mid-season (mean ± SD: P1 = 0.204 ± 0.167; P2 = 0.114 ± 0.05; P3 = 0.253 ± 0.269).

DISCUSSION

Observation-based morphological prey identification of provisioning events revealed pronounced within-season changes in chick diet in the Guillemot population on the Isle of May, as well as extending previous findings of an extreme dietary shift across years from predominantly Sandeel to predominantly Sprat (Anderson *et al*. 2014, Wanless *et al.* 2018). Thus, in the 1980s, when Sandeel was the predominant prey, the proportion of Sandeel in chick diet increased in just over half the years, whereas from 2001 onwards when Sprat was the predominant prey, the proportion of Sandeel increased within the season only once and Sandeels were largely confined to the early part of the chick-rearing period. Trends in diet composition during the dietary shift phase in the 1990s were particularly variable with highly contrasting within-season species trajectories in consecutive years.

Within-season dietary changes can also provide additional biological information on prey species. In the case of Guillemot chick diet, the Sandeel eaten are almost exclusively 1+ group fish. This age group moves from the water column into sandy seabed sediments in May–July (Winslade 1974) becoming largely unavailable to Guillemots and many other seabirds (Wanless *et al*. 2018). If dietary changes reflect changes in local prey availability, the disappearance of 1+ group Sandeels from Guillemot chick diet could provide a proxy for the onset of burying behaviour. Marked within-season declines in the proportion of 1+ group Sandeels have previously been recorded in the diet of breeding Black-legged Kittiwakes *Rissa tridactyla*, European Shags *Gulosus aristotelis* and Guillemots on the Isle of May (Lewis *et al*. 2001, Wilson *et al*. 2004, Howells *et al.* 2017), and other species such as Sandwich Tern *Sterna sandvicensis* elsewhere in the North Sea (Cramp 1985, Centrica Energy 2009). However, in these studies data were reported for only a few years so long-term changes in the timing of 1+ disappearance could not be assessed. A study using Sandeel fishery catch per unit effort (CPUE) data suggested that the ratio between May and June CPUE could be used to indicate the timing of the availability of 1+ group Sandeels to seabirds with high ratios indicative of availability peaking early (Rindorf *et al*. 2000). However,

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again data were only available for a short period (five years), precluding any evaluation of long-term changes.

Using the slope of the within-season Sandeel trend in Guillemot chick diet as a proxy for temporal changes in Sandeel availability (assuming that positive slopes indicate that availability peaked late and negative slopes indicate early peaks), suggests that the timing of burying behaviour in 1+ group Sandeels around the Isle of May became earlier over the four decades (Supporting Information Fig. S3). Although the timing of breeding of Guillemots varied between years it showed no trend over time during our study period (Keogan *et al*. 2018, Supporting Information Table S1)). Nonetheless, because of changes in Sandeel phenology it is possible that the Guillemot chick-rearing period has become progressively mismatched from when 1+ group Sandeels are in the water column. Evidence from European Shags that feed on Sandeels when they are buried in the sediment, indicated that 1+ group Sandeels were still present in the area when Guillemots were feeding their chicks mainly on other prey (Watanuki *et al.* 2008, Howells *et al*. 2017). However, whilst within-season changes in Guillemot chick diet are consistent with an earlier onset of 1+ group Sandeel burying behaviour, Sprat stocks in the North Sea, including those close to the Isle of May, increased in the 2000s (Lenoir *et al*., 2011; Jennings *et al*., 2012) and both Sandeel and Sprat have become smaller (Wanless *et al.* 2018, unpubl. data). These changes in prey availability and profitability could also contribute to Guillemots shifting to feed their chicks on Sprat earlier in the season.

In the context of dietary monitoring, our study highlights that contrasting within-season trends in prey composition can potentially produce important bias in annual estimates of diet if monitoring occurs during restricted periods of the season. Although the long-term decline in Sandeel in Guillemot chick diet on the Isle of May would have been detected irrespective of when sampling was carried out, annual means were poorly estimated from 10-day windows during the period when the diet shift occurred. More generally, sampling either early or late would have over- or under-estimated the importance of Sandeel. In part, these biases arise because there are not always 10 days of sampling in these windows due to between-year differences in the timing of breeding, hence the larger confidence intervals compared to mid-season sampling. Despite this effect and the

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large day-to-day variation in fish sample sizes across adjacent sampling days, the mean estimate for that interval in any year appears robust, but typically is too short to estimate the within-season trend, since it represents less than a third of the mean chick-rearing period. Overall, our findings highlight how variable sampling periods between years in relation to breeding phenology of the predator, may introduce noise that might mask weaker temporal or spatial patterns in seabird diets. Furthermore, the ability of short sampling windows to detect patterns of change over time might be reduced in cases where within-season trends are weak.

Other studies of seabirds, including Guillemots, have reported long-term changes in chick diet (Ainley *et al*. 1996, Österblom *et al*. 2006, Howells *et al*. 2017, Riordan & Birkhead 2018, Montevecchi *et al.* 2019, Mills *et al.* 2020), but fine-scale details of within-season changes are rarely reported, and hence probably not accounted for. This lack of information currently limits our ability to assess whether sampling bias is likely to be a widespread problem. Moreover, within-season diet variation is likely to be species- and site-specific so we caution against simply generalising from our results to other situations. Rather we hope that our findings will stimulate similar analyses of other datasets thereby helping to develop a deeper understanding of how best to optimise diet sampling under changing environmental conditions. At the very least, our study reinforces the importance of having a rigorous, explicitly described sampling design for diet monitoring programmes. There is also a need for transparent reporting of meta-data, for example sampling dates relative to the breeding season, and breeding success in comparison to the long-term mean, that would be informative for multi-site, multi-species analyses. Furthermore, given the increased likelihood of breeding failure as a consequence of increased environmental variability when most, or all, chicks die before reaching fledging age (Ashbrook *et al*. 2010, Sydeman *et al.* 2021), guidelines for dietary monitoring should advocate the collection of data from as soon as feasible in extreme years.

More generally, given predicted changes in the abundance, distribution and phenology of many prey species, and seabirds' role as sentinels of environmental change (Einoder 2009, Sydeman *et al*. 2021), there is an urgent need for dietary monitoring to be leveraged both to exploit the wealth of existing information through improved analytical methods, and to take full advantage of the advent of laboratory-based techniques such as DNA-based methods, stable isotope analyses and dietary biomolecule tracing (Hoenig *et al*. 2021). As with morphological prey identification,

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indirect methods for estimating prey composition all have strengths and weaknesses associated with them and in many cases require specialised equipment and skilled operators, However, they have the potential to add dietary information outside the breeding season which is largely lacking for seabird species, and across time scales ranging from hours to years depending on the tissue sampled (Bearhop *et al*. 2003, Inger & Bearhop 2008, Hobson & Bond 2012, Owen *et al*. 2013). Traditional morphological prey identification methods also have the potential to be extended through the use of camera traps to record data in remote regions or nocturnal species and artificial intelligence to process large amounts of data. Finally, there is scope to combine dietary, demographic and tracking data to describe 'nutritional seascapes' of seabirds for key periods of the life cycle such as moult (e.g. St. John Glew *et al.* 2019).

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AUTHOR CONTRIBUTIONS

MPH, SW and FD won funding for the long-term study. MPH, SW, MN and CG collected the data. The paper was conceived by SA, MPH and SW and evolved through discussions with FD. SA did the statistical analysis, while MPH and SW led the writing of the paper, with contributions from all the authors.

DATA AVAILABILITY STATEMENT

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DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available on request from the authors.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Table S1. Annual mean Julian hatching dates and numbers of fish recorded during the restricted year-specific chick-rearing periods.

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Appendix S1. Systematic all-day watches of fish deliveries to chicks.

Appendix S2. Modelling the changes in the proportion of Sandeel in the diet.

Figure S1. Frequency distribution of the number of fish recorded per day during chick-rearing periods 1982-2019.

Figure S2. The proportion of Sandeel in daily fish samples collected in the chick-rearing period of Guillemots in 1991-94.

Figure S3. Within-season change in the proportion of Sandeel plotted each year 1982-2019

Figure S4. Modelled hourly variation in the median number of fish and proportion of fish that were Sandeel fed to young Guillemots 1983-2019.

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Table 1. The model of the proportion of Sandeels in the daily diet of chicks over the 38 year study showing the partitioning of Deviance (2 log-likelihood) into that attributed to each of the explanatory terms in the model.

	Deviance	*df*	Mean Deviance	Deviance ratio	*P*
Overall model	18138.1	75	241.8	110.1	< 0.001
Residual	2476.2	1127	2.2		
Explanatory terms					
Julian Day-by-Year	954.5	37	25.8	11.7	< 0.001
Julian Day	204.4	1	204.4	92.9	< 0.001
Year	15013.1	37	405.8	184.5	< 0.001

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Figure 1. Temporal changes in the annual proportion of Sandeel in Guillemot chick diet. (a) The modelled proportion ± 95% confidence interval using all the data. The fitted logistic regression explains 76.7% of the annual variation. (b) The difference between estimates using all data (a) and the three 10-day windows in the Julian calendar (P1-early, P2-middle, P3-late).

Figure 2. Modelled logistic regression curves of the trends in the proportion of Sandeel in the diet of Guillemot chicks during the chick-rearing period in each of 38 years, grouped into decades. (light blue - 1991, 2001 & 2011; orange – 1982, 1992, 2002, 2012; light grey – 1983, 1993, 2003, 2013; yellow – 1984, 1994, 2004, 2014; mid-blue – 1985, 1995, 2005, 2015; green – 1986, 1996, 2006, 2016; dark blue – 1987, 1997, 2007, 2017; dark red – 1988, 1998, 2008, 2018; dark grey – 1989, 1999, 2009, 2019; brown – 1990, 2000, 2010).

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Figure 3. The annual proportion and 95% confidence intervals of Sandeel in Guillemot chick diet in three 10-day periods each year between 1982 and 2019. (a) Early Julian day 156-165, (b) Middle Julian day 166-175, (c) Late Julian day 176-185. Within each period, the long-term decline in Sandeel is evident from the fitted logistic regression. (d) The fitted logistic regressions for the three periods, together with the fitted curve using all the data within the defined chick rearing season (black dashed curve) each year.

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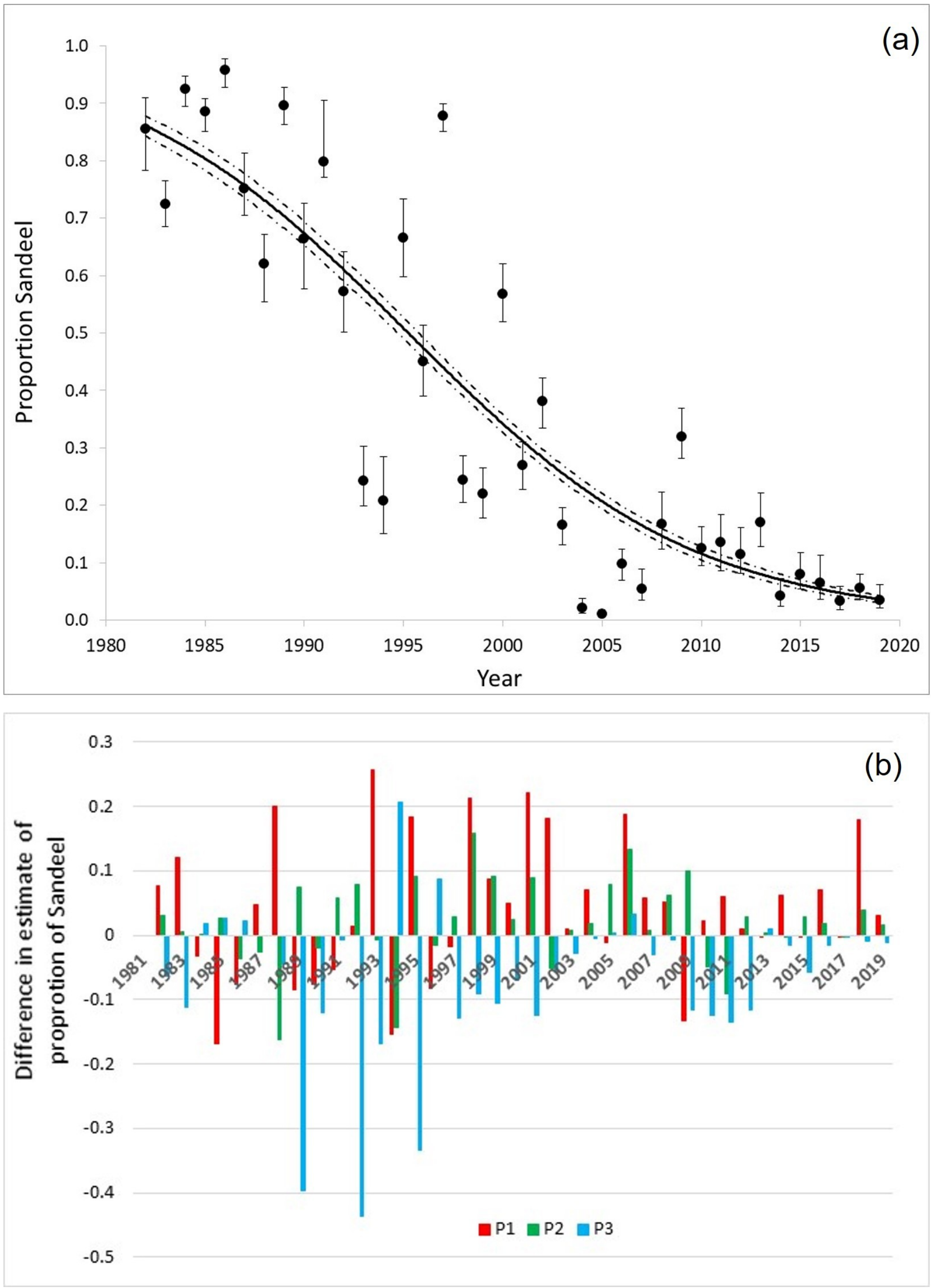

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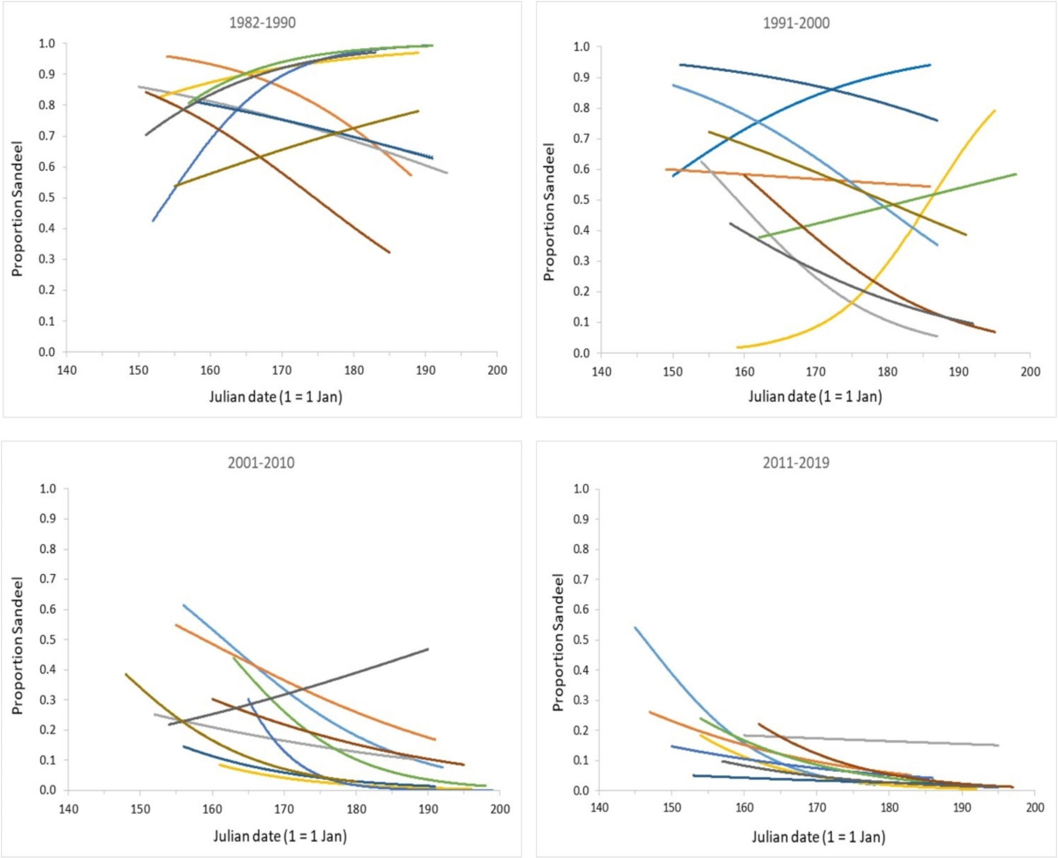

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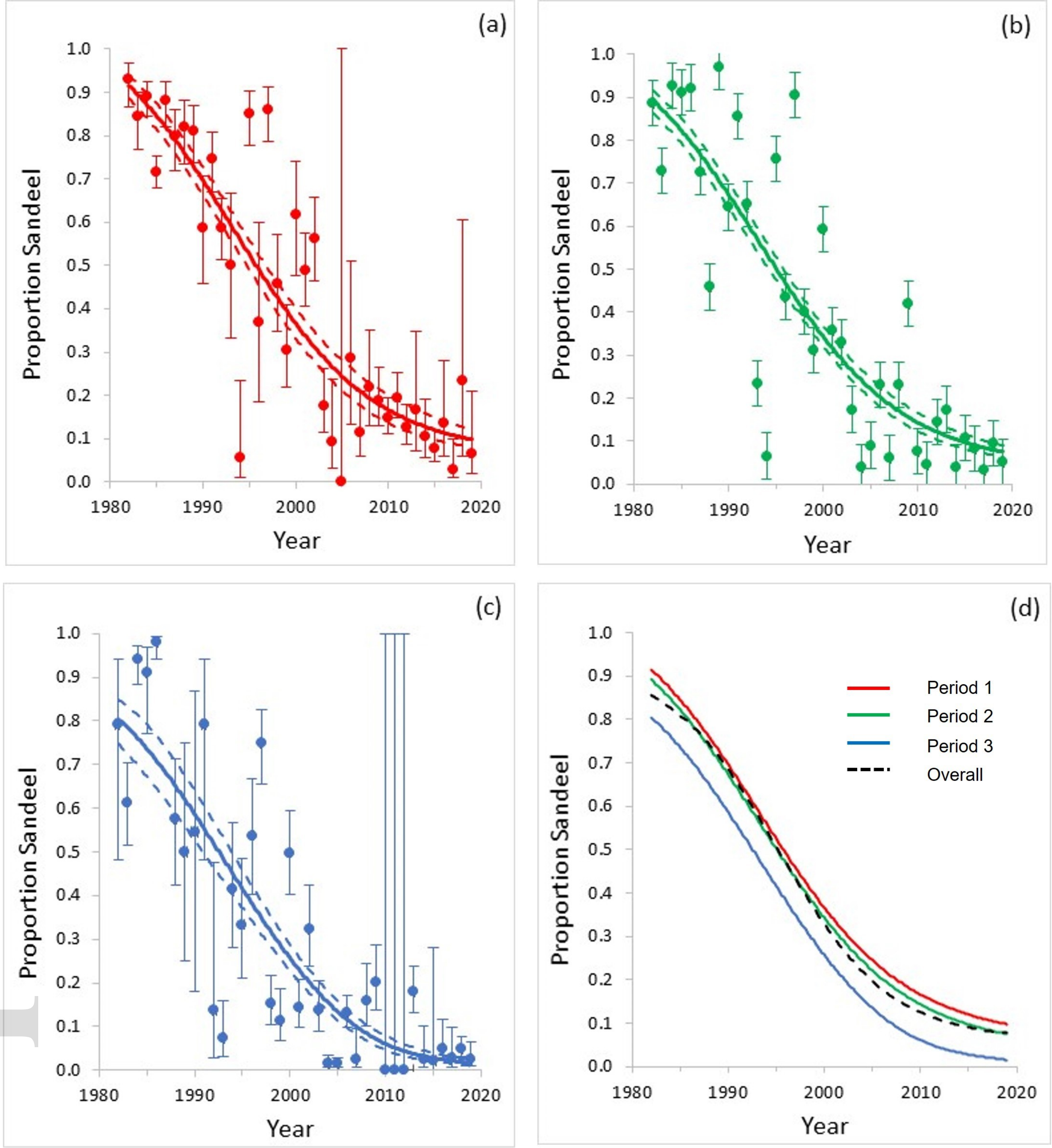

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