Institute for Seabird Research and Conservation

Middleton Island Seabird Research and Monitoring

2020 Field Report

INTRODUCTION

The Middleton Island Marine Biological Station is a facility owned and managed by the Institute for Seabird Research and Conservation (ISRC) in support of long-term seabird research and monitoring in the Gulf of Alaska. The 2020 season marked the fourth year the project has contributed to Gulf Watch Alaska, a 20-year effort (2012-2031) funded by the Exxon-Valdez Oil Spill Trustee Council. The program is intended to uncover and monitor natural and anthropogenic factors affecting ecosystem functioning in the Gulf of Alaska and Prince William Sound. The particular contribution of the Middleton project includes quantifying dietary shifts in predator species, especially black-legged kittiwakes and rhinoceros auklets, as indicators of forage fish dynamics in the region.

Although the Covid-19 pandemic imposed some constraints on field operations at Middleton this year—namely, a smaller than usual crew and later start—the effort was largely successful in maintaining the continuity of long-term data sets. Supplemental feeding of tower kittiwakes continued, albeit with a smaller than usual sample of fed pairs, and diet sampling of kittiwakes (April-August) and rhinoceros auklets (July-August) was unaffected.

Special lines of research in 2020 included tagging black-legged kittiwakes with GPS trackers to identify the principal foraging areas used during incubation and chick-rearing. Cooperators from the Prince William Sound Science Center (PWSSC) recovered GLS trackers from tufted puffins to ascertain the winter movements of that species. Investigators from Oregon State University (OSU) deployed GPS and other logging devices on pelagic cormorants as part of a development project that uses bird-borne sensors to monitor physical oceanographic parameters in remote regions. With the partial exception of GPS tracking results for kittiwakes, the outcomes of those special investigations are not included in this report.

In 2020, the Middleton research station was occupied by members of the field crew from 20 April to 15 May and from 10 June through 15 August.

Acknowledgements—Special thanks to Gulf Watch Alaska principal investigators John Piatt and Yumi Arimitsu for administering an ongoing Cooperative Agreement between the U.S. Geological Survey and ISRC and securing vital financial support through the EVOS Trustee Council and USGS. Members of the core field crew in 2020 were Jenna Schlener (Camp Leader), Spencer England, Melissa Morado, Ronan McWilliams, and Harris Kopp. Scott Hatch and Martha Hatch did facilities maintenance tasks and collected kittiwake diet samples during April-May. Kristen Gorman and Anne Schaefer (PWSSC) joined the effort for 2 weeks in July for telemetry studies of tufted puffins, with financial support from the North Pacific Research Board (NPRB). Adam Peck-Richardson, Brendan Higgins, and Jillian Soller (OSU) conducted telemetry studies of tower-nesting pelagic cormorants from 29 June through 10 August. As always, the project benefitted from favors coming from many quarters and we are especially grateful to our friends and island neighbors from the Federal Aviation Administration.

RESULTS AND DISCUSSION

PRODUCTIVITY

Rhinoceros Auklet—In general, rhinoceros auklets have consistently high breeding success on Middleton (Coefficient of variation, CV = 20.3) (Fig. 1), and their population is increasing (currently ~20,000 individuals). At 0.76 chicks/egg laid (Table 1), production in 2020 was higher than the long-term average of 0.67 (n = 23 years, 1997-2020). The installation of nest boxes for rhinoceros auklets on the property is an ongoing effort intended to facilitate productivity measures and other research on this species.

Tufted Puffin—For 5 years prior to 2015, the virtual absence of fish-carrying adults seen around the island was a clear indication of scant chick production by tufted puffins on Middleton. During the six seasons subsequent to that period, puffins have achieved at least a partial return to normal production— between 0.17 and 0.43 late-stage chicks produced per egg-laying pair—despite ocean conditions unfavorable to surface-feeders such as black-legged kittiwakes (see below). Production of 0.38 chicks per egg in 2020 continued that trend (Table 1), and despite their comparatively poor breeding performance (vis-à-vis rhinoceros auklets), puffin numbers have increased substantially on Middleton—i.e., roughly 20,000 individuals today versus 5,000 in the 1970s.

Pelagic Cormorant—Since 2002, pelagic cormorants have been monitored in the tower colony. Numbers (31-145 nest-building pairs) have varied greatly (less so in recent years), whereas breeding success (from ~0.45 to 2.0 fledglings per nest built) is relatively constant (Fig. 1, CV = 56.0; Table 2). Production in 2020 (2.0 fledglings/nest) was the highest (by a slight margin) since 2002, and nearly double the long-term average of 1.05 fledglings/nest. On average, about 90 nests are constructed annually by cormorants on the tower, versus 76 nests in 2020. Thorough banding of adults and chicks done annually on the tower will support a future analysis and report of cormorant survivorship spanning the years since 2002.

Black-legged Kittiwake—Owing to a smaller than normal crew size (Covid-19), the number of kittiwake pairs supplementally fed on the tower was reduced in 2020. Among fed pairs (n = 24), production was 1.04 fledglings/nest, whereas 404 unfed pairs produced 0.83 chicks/nest (Table 3). The moderate difference between food-treatment and control groups in 2020 indicated good foraging conditions for surface-feeding kittiwakes, as was true also for rhinoceros auklets and pelagic cormorants. This season seemed decisively to end a period of poor breeding performance of kittiwakes that began with the emergence in 2014 of an unusual warm-water event in the northeast Pacific. Interannual variation in kittiwake production is high on Middleton (CV = 56.4), especially in comparison to rhinoceros auklets (Fig. 1).

About two-thirds of the pairs normally included in the supplemental feeding group were cut off from that food source in 2020, and it is interesting to examine the effect of that change on the behavior and breeding performance of the affected pairs. It turns out that pairs that were previously fed capelin ad libitum, but which were deprived of supplemental food in 2020, had substantially poorer breeding performance than unfed pairs that had not been fed in prior years. Set-backs were seen in all major performance indices measured—breeding propensity, laying dates, clutch sizes, and production of fledged chicks (Table 4). It would seem that the experience of a relatively poor food supply in such pairs had the effect of reducing their ability and/or motivation to commit fully to a successful breeding effort. Presumably, the strength of the untoward response would diminish over time, though we have no plans to verify that possibility—affected pairs will regain their fed status in 2021.

PHENOLOGY

Breeding phenology of pelagic cormorants varies by at least 3 weeks on Middleton, with the mean date of clutch initiation ranging from 18 May to 10 June in yearly samples averaging ~80 pairs on the tower (Fig. 2, upper panel). For reasons unclear in their particulars—but pertaining presumably to food supply—cormorant breeding was progressively delayed in the decade from 2002 through 2011. The reverse occurred more recently, with the timing of breeding having advanced steadily, or nearly so, after 2011.

The grand average of clutch initiation dates (mean of annual means) among naturally foraging kittiwakes on Middleton is 5 June. Thus, timing in 2020 (3 June) was about average, and that was true for both food-supplemented pairs and controls (Fig. 2, lower panel). As a rule, clutch initiation occurs about 4 days earlier in fed pairs (range 0-9 days) as compared with unfed pairs, and the treatment effect on laying date covaries (r = 0.56) with the treatment effect on chick production (i.e., fed pairs lay earlier and, in most years, fledge more chicks). Not surprisingly, because both parameters reflect foraging conditions in spring, the covariation of food-treatment effect on laying dates and clutch sizes (not shown) is stronger (r = 0.72). Supplemental feeding usually commences about 4-6 weeks after kittiwakes recolonize the island (which occurs in late March or early April), and a month or so prior to the mean date of clutch initiation.

DIETS

Black-legged Kittiwake—In most years since 1996, regurgitated food samples have been collected from adult and/or nestling kittiwakes on the tower from April or May through August (Table 5). From an evaluation of alternate methods of analyzing and reporting diet results (Hatch 2013, Appendix 2), the preferred metric for kittiwakes is prey relative occurrence, for which the relevant sample units are numbers of identified prey types in a given sample (Table 6).

On average, Middleton kittiwakes take about equal amounts of Pacific sand lance, capelin, and invertebrates, and lesser amounts of herring, sablefish, salmon, and myctophids, depending on stage of the season (Fig. 3). A salient finding during the previously mentioned warm-water event was the virtual disappearance of capelin from the kittiwake diet on Middleton, following 6 prior years when capelin were abundant (Fig. 4).

Middleton Island is close to the continental shelf break, and for a few weeks after they arrive in spring kittiwakes typically forage over deep ocean waters at night, taking vertically migrating prey such as lanternfish (myctophids), squids, polychaetes, and crustaceans (Fig. 3). This was clearly the case in 2012, a year in which kittiwakes switched to capelin as the primary prey during incubation and chick-rearing (Fig. 4). Notably, because it had never been seen previously, capelin dominated throughout the following year, including even the spring arrival stage (a sizable sample having been obtained in late March 2013). In 2014, the spring diet reverted to a mix of myctophids and invertebrates, and for the first and only time observed, kittiwakes continued to rely on pelagic prey throughout the summer, apparently because prey usually obtained in the neritic (shelf) zone during June-August failed to materialize. In 2015, yet another previously unknown sequence occurred, as neither myctophids nor capelin were available early in the season, and large herring supplemented a predominantly invertebrate diet. During later stages of breeding in 2015, large herring and first-year sablefish comprised the bulk of the diet (Fig. 4).

The 2016 season was another extreme year within an ongoing, exceptional warming event. Increased use of invertebrates seen over the course of the heatwave crested that year with a virtual absence of fish in the diet during both April (Fig. 5) and May (Fig. 6). Typically, the two main contributors to the invertebrate fraction of the diet are squids and polychaetes (the latter being a pelagic species apparently obtained only at night). In 2016, it seemed the kittiwake diet in the first week or two after the birds' spring arrival at the colony (which normally occurs in late March) consisted almost exclusively of polychaetes. By May, squids were the dominant invertebrates and main prey overall (Figs. 5 & 6). As in other years, small numbers of the amphipod *Paracallisoma alberti* appeared regularly in the spring diet. The occurrence of the hydrozoan *Velella velella* was a first in 2016, and was unexpected because the species is normally associated with warmer water than what usually occurs in the northern Gulf of Alaska.

In 2017, squids and polychaetes were less prominent in the early-season diet than in several of the immediately preceding, warm-water years. Instead, the dominant fraction of the invertebrate diet that year consisted of crustaceans such as shrimp, amphipods, and copepods (Figs. 5 & 6). The prevalence of copepods, especially during May, was notable because historically those prey have occurred but rarely in the kittiwake diet at Middleton. Copepods arguably would be a food source of last resort for a bird predator accustomed to having ready access to forage fish like myctophids or herring or energy-rich polychaetes. Also notable in 2017 was the regular occurrence of threespine sticklebacks during April (Fig. 5). Being abundant inhabitants of the intertidal zone and brackish ponds around the island, sticklebacks are an ever-present food source on Middleton, albeit one that is largely ignored by kittiwakes except perhaps when the birds struggle to find much else in the way of oceanic prey. The paucity and generally small mass of regurgitated food samples found around the grounds of the research station was further evidence of poor foraging conditions in spring 2017.

The spring diet of kittiwakes in 2018 showed a continuing rebound of myctophids (Fig. 5), perhaps reflecting those species' resumption of near-surface migration at night. Such behavior would have been encouraged that year by cool-water conditions, at least in comparison to extreme years of the heatwave, spanning 2014 through 2016. The invertebrate fraction of the diet consisted mainly of squid and amphipods during April, but switched substantially to polychaetes, krill and copepods by May 2018. Temporally, an even finer-grained depiction of kittiwake prey during prebreeding would portray the fact that kittiwakes seem to forage opportunistically on whatever invertebrate prey happen to be swarming abundantly at the surface over periods of a few nights or up to a week or two. In May 2018, kittiwakes began taking substantial amounts of fish (herring, eulachon, sand lance, and lingcod), and the number and size of samples obtained from the grounds around the Middleton station indicated a relative abundance of food as compared with several preceding years.

During incubation and chick-rearing in 2018, the kittiwake diet favored herring, sablefish, and sand lance (Fig. 4). Consistent with results since 2014, a notable scarcity of capelin continued that year, and juvenile pink and chum salmon had a poor showing in the chick diet (July and August).

Invertebrates comprised a more typical fraction of the kittiwake diet in spring 2019, declining somewhat between April and May as the fish component increased in the samples (Figs. 5 & 6). However, myctophids seemed to be largely unavailable during that time, when the main constituents of the fish diet were herring and sand lance. In fact, kittiwakes made little effort to forage in the pelagic zone during the prelaying period in 2019 (see below). Herring continued to be important fish prey throughout the summer (Fig. 4). Capelin and sand lance were about equally prevalent in the summer diet, with 18% and 15% relative occurrence, respectively. As such, capelin made a stronger showing in 2019 than in any year since the onset of the heatwave in 2014.

In 2020, invertebrates (especially squids) and myctophids were important in the kittiwake diet during the prelaying period (Apr-May), indicating that extensive foraging off the continential shelf occurred at that time (Fig. 7). To the extent the birds foraged over the shelf in spring, age-1 and older herring were the main fish prey in 2020, as was true also the previous year. Despite an amelioration of warm-water conditions in 2020 (see below), capelin were scarce throughout the season—absent in spring and present only in trace amounts from egg-laying through chick-rearing (Fig. 4). Rather, cooling conditions were associated with the emergence of hexagrammid species, especially age-0 greenlings, as an important part of the kittiwake diet at Middleton (Fig. 7).

A species new to the list of seabird prey at Middleton—chub mackerel (*Scomber japonicus*)—was first encountered in 2019 (4 occurrences), increasing to 15 occurrences in 2020. To date the species appears only in late-season samples obtained from black-legged kittiwakes (earliest occurrences 6 August 2019 and 6 August 2020). Co-occurrence in samples with myctophids, squid, and pelagic crustaceans suggests chub mackerel are coming from the pelagic zone south of Middleton, where only kittiwakes are known to forage with some regularity.

Rhinoceros Auklets—Auklet diets are monitored by collecting bill-loads from chick-provisioning adults, usually once or twice a week from early July through early or mid-August. Sampling in 2020 yielded 322 bill loads and ground samples, comprising about 10 kg of auklet prey in total (Table 7). Overall, the auklet diet at Middleton is composed largely of a few species of forage fish, especially Pacific sand lance, capelin, salmon (including both pink and chum), and sablefish, in that order of importance (Fig. 8). The years 2014 through 2017 saw significant breaks from the past, with historically dominant species—sand lance and capelin—being largely supplanted by sablefish, salmon, and herring (Fig. 9).

Since 1978, about 144 kg of auklet prey samples have been collected on Middleton (Table 7), and auklet diet monitoring provides our single best indicator of forage fish dynamics in the region. By all appearances, sand lance were the overwhelmingly dominant forage species in the late 1970s through the early 1980s. Following a period of reduced availability in the mid 1990s, sand lance made a strong comeback by the end of that decade. Sand lance steadily declined in importance after 2000, however, and contributed little to seabird diets during a cold-water phase that materialized in 2008 (Fig. 9). The appearance of about 30% sand lance in the auklet diet in 2016-2017, and more than 50% by weight in 2018 was consistent with a known association of sand lance with warm-water conditions (Hatch 2013). While herring appeared superficially to have benefitted during a period of warming of surface waters (Fig. 10), the absence of such a signal in herring data generally (PWSSC 2018) suggests that shifts in foraging locations have occurred that may account for the increased capture of herring by auklets and kittiwakes from Middleton (see below). Noteworthy in 2019 was an unusual spike in the occurrence of juvenile gadids—as yet unidentified to species, but definitely not walleye pollock—in the diet of rhinoceros auklets (Fig. 10).

As in two prior years (2018 and 2019), but to an even greater degree in 2020, greenlings were a substantial part of the diet in both kittiwakes (above) and rhinoceros auklets (Figs. 9 & 10). While this analysis focuses on hexagrammid species (greenlings, lingcod, and Atka mackerel) as a group, it is noteworthy that in addition to kelp and rock greenlings (similar fish not identified to species in the field or lab), Atka mackerel (large-bodied relative to other hexagrammids collected) have seen a marked increase, especially in 2020. For reference, the breakdown of Hexagrammidae in 2020 was as follows: 1% lingcod, 4% Atka mackerel, 95% greenlings (biomass) in rhinoceros auklets, and 10% lingcod, 21% Atka mackerel, 69% greenlings (relative occurrence) in kittiwakes. Collectively, hexagrammids constituted in 2020 about 50% of the auklet diet (biomass) and 25% of kittiwake prey (relative occurrence), numbers not seen in any prior year on Middleton (Figs. 9 & 10).

The juxtaposition of time series for kittiwakes and rhinoceros auklets since 1978 (Fig. 9) shows general agreement vis-à-vis the decline of sand lance and, after 2008, the emergence of capelin as a dominant forage species. However, in several recent years, when neither sand lance nor capelin were prevalent, the diets of surface-feeding kittiwakes and diving auklets diverged substantially (Fig. 9). In 2019, the trade-off appeared to occur primarily between herring (more prevalent in kittiwake diet) and juvenile greenlings (taken mainly by auklets). As noted, both predators took many greenlings in 2020.

FORAGING AMBITS OF KITTIWAKES AND AUKLETS

Spring foraging by kittiwakes in 2019 was more widespread than previously recorded or anticipated, with some individuals traveling far to the east and west of Middleton or visiting interior waters of Prince William Sound (Fig. 11). Foraging tracks gave the impression of birds sampling intermittently the pelagic zone off the continental shelf, but not staying or foraging extensively, as though food-searching there was generally unproductive. Kittiwake movements during incubation and chick-rearing (Jun-Aug) were similar to patterns observed in 2018, except for the near absence this year of deep-ocean foraging (Figs. 11 & 12). A comparison with 2008—a year with cold water and abundant capelin—shows how markedly the foraging patterns of Middleton kittiwakes can change depending on prevailing ocean conditions. In the earlier year, spring foraging occurred almost exclusively in the pelagic zone, then shifted to the continental shelf prior to egg-laying (Fig. 12, lower panel). Also striking is the contrast in foraging ranges at mid season. Whereas chick-rearing kittiwakes in 2008 foraged within about 50 km of the island, and herring were all but absent from the diet, food-gathering parents have in recent years made regular trips to coastal waters from Montague and Hinchinbrook islands to Cape St. Elias (Fig. 12), where presumably they obtained the Age 1+ herring that figure prominently in the diet (Fig. 4).

GPS tracking of kittiwakes in 2020 was limited to deployments on 11 individuals during late incubation and chick-rearing (Fig. 13). The pattern of foraging observed was similar to other years since 2015, with most trips accessing nearshore waters from Montague Island to Kayak Island and little use of the pelagic zone (Fig. 13).

It is noteworthy that visits by kittiwakes to barrier islands and beaches at the Copper River mouth probably occur every year during a narrow period in spring when pre-spawning eulachon aggregate at that location (Willson et al. 2006).

No tracking of rhinoceros auklets was undertaken in 2020. In 2019, however, the foraging area of chick-rearing rhinoceros auklets overlapped that of kittiwakes and was concentrated in nearshore waters of southeast Montague Island from Patton Bay to Cape Cleare (Fig. 14). That would seem to be the location where age-0 greenlings and gadids were unusually abundant in 2019. We were surprised to find auklets delivering fish from as far as 100 km from their nest sites on Middleton. Additional telemetry will likely find considerable flexibility in that regard, but the early lesson is that rhinoceros auklets, consistent with their reliable success at breeding, are well adapted for coping whenever local food shortages occur. Similar to kittiwakes, the information they furnish as prey samplers is relevant to a sizable portion of the northern Gulf.

OCEAN REGIME INDICATORS

Using data from Middleton Island seabird monitoring through 2011, Hatch (2013) described an apparent regime shift in the Gulf of Alaska ecosystem that occurred around 2008. This transition entailed: (1) a switch from mostly positive PDO indices (since 1977) to negative values after 2008, (2) the emergence of capelin as a dominant prey species at Middleton, and (3) markedly improved breeding performance by black-legged kittiwakes. These patterns persisted for at least 6 years (i.e., through 2013) and, with occasional interludes of opposing conditions, can be expected to continue for another 2 decades or longer (Hatch 2013). One such interlude is now evident for the period 2014-2017, a widespread anomaly nicknamed “The Blob.” Examples of dramatic species range shifts associated with this warm-water event are listed in Bond et al. (2015), to which we can add the first-ever appearance of male California sea lions (*Zalophus californianus*) among ~100 Steller sea lions hauling out on Middleton in April, May and June of 2016. A similar complement of California sea lions was observed among the males hauling out on Middleton in April 2017.

Anomalous conditions are also reflected in monthly PDO indices and in seabird indicators from Middleton Island—namely, dietary capelin and kittiwake productivity—both of which dropped precipitously beginning in 2014 (Table 8, Fig. 15). The prevalence of invertebrates (mainly polychaetes and squids, but also including copepods and the normally warm-water hydrozoan *Velella velella*) in the spring diet during 2016-2017 is especially noteworthy. As nocturnal vertical migrants from mesopelagic depths, myctophids are available to foraging kittiwakes only at night, and then only if the fish rise to within a meter or so of the ocean surface. Evidently, anomalous surface conditions in 2015 and 2016 prevented myctophids from doing so in April, and mesopelagic fish remained a relatively minor component of the spring diet through 2019, April 2018 being a partial exception. While seabirds and forage fish gave early signs of returning to normal in 2018, a constellation of physical conditions in fall 2019 prompted references in the popular media to “Son of Blob” (e.g., Yulsman 2019). That event did not materialize, however, as cool conditions returned in early 2020, and Middleton seabirds had an exceptionally good year. If the incipient change to cool conditions seen in 2020 persists and strengthens, we predict a re-emergence of capelin as a dominant part of the food base in the Gulf of Alaska and correspondingly high breeding performance in seabirds.

The comparison of breeding performance in fed and unfed kittiwake pairs on Middleton furnishes a powerful indicator of ocean conditions, for the simple reason that kittiwakes prefer to feed themselves. In poor years, characterized by positive PDO, low capelin availability, and poor kittiwake breeding performance, the difference between fed and unfed treatment groups is accentuated, and vice versa (Table 8, Fig. 16). The events of 2014-2020 have only increased the strength and predictive power of relations among the PDO, prey dynamics, and kittiwake breeding performance (Table 10). As of spring 2020, the PDO showed signs of a possible return to ocean conditions expected if a predominantly negative phase of the PDO would prevail in spite of temporary disruptions such as the warm-water anomaly so notorious of late. Thus, we look forward to the next iteration, if it comes, of this natural experiment, when a return to cold water conditions, capelin, and high kittiwake performance would more or less clinch these simple, yet portentous, relationships. As noted, a predominantly cold phase of the PDO is expected to last through the 2030s, all else being equal. Global warming and climate change could have countervailing effects, however, with far-reaching consequences for seabirds, marine mammals, and fisheries. It remains to be seen whether the recent and exceptional warm-water event in the Gulf of Alaska, was really an "anomaly" or, rather, a window on the future.

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Table 1. Productivity of rhinoceros auklets and tufted puffins breeding on Middleton Island in 2015-2020.

	Rhinoceros auklet						Tufted puffin					
Parameter	2015	2016	2017	2018	2019	2020	2015	2016	2017	2018	2019	2020
Burrows with eggs	60	61	62	61	72	62	52	82	71	71	60	32
Eggs hatched	42	38	40	35	51	54	21	27	17	17	19	16
Late-stage chicks	38	33	32	33	44	47	18	20	12	12	19	12
Chicks/egg laid	0.63	0.54	0.52	0.54	0.61	0.76	0.35	0.24	0.17	0.43	0.32	0.38

Table 2. Breeding performance of pelagic cormorants on the Middleton tower, 2002-2020.[a]

	A-egg date (Julian day)				Clutch size				Chicks fledged/nest built			
Year	n	Mean	SE	SD	n	Mean	SE	SD	n	Mean	SE	SD
2002	77	139.7	0.95	8.325	86	3.7	0.18	1.707	86	1.6	0.15	1.371
2003	78	138.2	0.97	8.540	80	4.0	0.16	1.441	80	1.9	0.16	1.400
2004	62	144.0	0.88	6.941	76	2.8	0.18	1.607	76	0.4	0.07	0.650
2005	31	142.5	1.32	7.352	31	3.5	0.18	1.028	31	1.2	0.23	1.283
2006	92	148.3	0.90	8.635	101	3.0	0.12	1.228	101	1.1	0.12	1.156
2007	142	147.8	0.93	11.130	144	3.8	0.11	1.275	144	1.6	0.12	1.425
2008	145	146.4	0.94	11.370	145	3.8	0.10	1.165	145	1.6	0.11	1.319
2009	113	155.0	0.68	7.223	128	2.9	0.11	1.232	128	1.4	0.10	1.175
2010	71	154.7	0.72	6.037	71	2.6	0.10	0.851	71	0.1	0.05	0.445
2011	95	161.3	0.96	9.314	109	2.5	0.12	1.281	109	0.5	0.07	0.741
2012	85	159.4	0.86	7.884	85	3.0	0.12	1.107	85	0.5	0.08	0.765
2013	89	150.3	0.73	6.842	90	3.4	0.09	0.880	90	1.9	0.12	1.167
2014	--	--	--	--	--	--	--	--	~87	~1.2	0.13	1.170
2015	58	155.0	0.91	6.910	85	2.1	0.16	1.470	85	0.6	0.09	0.823
2016	53	152.8	1.62	11.78	53	2.9	0.17	1.210	53	0.9	0.14	1.050
2017	69	150.9	1.08	8.951	69	3.3	0.10	0.845	69	1.6	0.16	1.306
2018	84	150.8	1.14	10.492	84	3.4	0.10	0.898	84	0.8	0.09	0.784
2019	75	149.3	1.03	8.918	75	3.6	0.10	0.841	75	0.4	0.10	0.838
2020	64	145.6	0.81	6.478	76	3.4	0.11	0.938	76	2.0	0.2	1.322
Totals	1,483	149.5	0.97	8.51	1,588	3.2	0.13	1.167	1,588	1.1	0.12	1.063

[a] The estimate of fledglings in 2014 is 102 chicks from 87 nests built, a relatively crude figure that should not be taken as strictly comparable to other years. The estimate is based on a final (premature) count of chicks in tower nests on 14 July, >3 weeks before final checks in other years. Additional mortality that would have occurred before fledging was perhaps offset by 10 nests still being incubated on 14 July, which are assumed to have produced no fledged chicks.

Table 3. Breeding performance of supplementally fed and unfed pairs of black-legged kittiwakes on the Middleton tower, 1996-2020.[a]

	Unfed pairs												Fed pairs											
	Julian lay date				Clutch size[a]				Chicks fledged				Julian lay date				Clutch size[a]				Chicks fledged			
Year	n	Mean	s.e.	s.d.	n	Mean	s.e.	s.d.	n	Mean	s.e.	s.d.	n	Mean	s.e.	s.d.	n	Mean	s.e.	s.d.	n	Mean	s.e.	s.d.
1996	59	159	0.75	5.728	63	1.73	0.07	0.574	63	0.60	0.08	0.636	25	157	1.07	5.342	27	1.74	0.11	0.594	27	1.22	0.15	0.801
1997	59	158	0.44	3.386	65	1.48	0.08	0.664	65	0.32	0.06	0.503	25	155	1.09	5.427	25	1.80	0.08	0.408	25	0.96	0.16	0.790
1998	59	160	0.92	7.032	70	1.29	0.09	0.745	70	0.36	0.06	0.539	27	155	1.12	5.797	29	1.69	0.14	0.761	29	0.62	0.12	0.622
1999	65	169	0.59	4.771	156	0.47	0.05	0.606	156	0.21	0.04	0.468	44	161	1.01	6.684	46	1.61	0.09	0.614	46	0.59	0.11	0.717
2000	135	151	0.63	7.322	152	1.68	0.06	0.706	152	0.99	0.07	0.814	67	149	0.66	5.403	71	1.83	0.07	0.609	71	1.18	0.10	0.833
2001	166	153	0.46	5.942	174	1.78	0.04	0.560	174	1.03	0.06	0.853	67	151	0.41	3.342	71	1.93	0.07	0.569	71	1.28	0.10	0.848
2002	168	149	0.66	8.581	179	1.73	0.04	0.586	179	0.97	0.06	0.796	70	149	0.94	7.825	72	1.83	0.06	0.475	72	0.97	0.09	0.769
2003	95	157	0.47	4.600	102	1.67	0.06	0.603	102	0.50	0.06	0.609	66	152	0.74	6.003	69	1.81	0.07	0.550	69	0.91	0.10	0.836
2004	88	154	0.42	3.949	102	1.58	0.07	0.750	102	0.18	0.04	0.432	68	151	0.70	5.742	69	1.99	0.04	0.364	69	0.97	0.10	0.804
2005	214	157	0.30	4.321	221	1.67	0.04	0.553	221	0.37	0.04	0.553	71	151	0.57	4.775	72	1.86	0.05	0.421	72	1.03	0.08	0.712
2006	216	158	0.38	5.537	233	1.56	0.04	0.627	233	0.47	0.04	0.587	71	151	0.43	3.642	73	1.90	0.05	0.446	73	1.14	0.10	0.822
2007	172	163	0.43	5.606	197	1.34	0.05	0.693	197	0.42	0.04	0.606	63	158	0.74	5.900	73	1.58	0.08	0.725	73	0.77	0.10	0.874
2008	125	153	0.58	6.498	130	1.73	0.05	0.554	130	0.78	0.06	0.707	70	150	0.70	5.887	71	1.92	0.06	0.470	71	0.90	0.10	0.813
2009	90	155	0.57	5.439	98	1.69	0.07	0.649	98	0.20	0.04	0.405	75	150	0.81	7.056	76	1.89	0.04	0.386	76	0.75	0.08	0.656
2010	68	148	0.87	7.160	74	1.81	0.07	0.612	74	0.78	0.09	0.815	58	150	1.07	8.174	61	1.82	0.07	0.563	61	0.89	0.10	0.819
2011	41	158	0.64	4.092	42	1.62	0.08	0.539	42	0.50	0.09	0.552	47	152	1.26	8.624	48	1.83	0.07	0.519	48	0.92	0.11	0.794
2012	72	153	0.78	6.582	78	1.82	0.07	0.619	78	0.87	0.09	0.779	72	152	0.86	7.262	75	1.88	0.06	0.544	75	0.93	0.09	0.811
2013	63	148	1.06	8.413	68	1.84	0.06	0.507	68	1.00	0.10	0.792	67	148	0.97	7.965	70	1.97	0.06	0.538	70	1.04	0.10	0.842
2014	--	--	--	--	--	--	--	--	143	0.45	0.04	0.526	--	--	--	--	--	--	--	--	--	--	--	--
2015	296	153	0.29	4.986	352	1.51	0.04	0.762	352	0.21	0.02	0.422	70	152	0.47	3.895	72	1.90	0.05	0.449	72	0.96	0.09	0.740
2016	79	165	0.73	6.444	155	0.74	0.06	0.806	155	0.08	0.02	0.301	73	156	0.99	8.434	74	1.80	0.05	0.437	74	0.81	0.06	0.541
2017	72	161	0.52	4.407	104	0.95	0.07	0.755	104	0.22	0.04	0.417	72	155	0.58	4.948	74	1.82	0.04	0.371	74	0.76	0.08	0.679
2018	113	155	0.56	5.981	134	1.48	0.06	0.752	134	0.31	0.04	0.492	72	151	0.70	5.958	72	1.97	0.03	0.238	72	0.99	0.08	0.687
2019	326	154	0.30	5.471	368	1.61	0.04	0.691	368	0.50	0.03	0.586	73	150	0.46	3.922	73	1.99	0.04	0.311	73	1.07	0.09	0.770
2020	316	154	0.28	4.919	404	1.69	0.03	0.615	404	0.83	0.04	0.724	20	154	1.61	7.210	24	1.71	0.11	0.550	24	1.04	0.15	0.751

[a] Clutch size (and chicks fledged) include zero-egg nests, thus incorporating breeding propensity into clutch size and reflecting (for fledging) the overall productivity of site-holding pairs.

Table 4. Effect of discontinuation of supplemental feeding on the breeding performance of kittiwake pairs on the Middleton tower in 2020.

	Treatment (Prior years/2020)		
Parameter	Fed/Fed	Unfed/Unfed	Fed/Unfed
Breeding propensity			
n (pairs)	24	356	48
% breeding	0.96	0.93	0.85
SE	0.041	0.014	0.051
Clutch initiation			
n (pairs)	20	282	34
Mean date (Julian)	154.4	153.9	156.8
SE	1.61	0.27	1.13
Clutch size			
n (pairs)	24	356	48
Mean (eggs/pair)	1.71	1.71	1.56
SE	0.112	0.032	0.107
Productivity			
n (pairs)	24	356	48
Mean (fledglings/pair)	1.04	0.85	0.65
SE	0.153	0.038	0.105

Table 5 Temporal distribution of diet samples from black-legged kittiwakes on Middleton Island, 1978 – 2020.

	Adults			June			July			August			
Year	Mar	April	May	Adults	Chicks	Total	Adults	Chicks	Total	Adults	Chicks	Total	Total
1978								38	38		2	2	40
1989		2	2				5		5				9
1990		17	7	18		18	21	9	30				72
1992			1							3		3	4
1994		3											3
1996			19					37	37		17	17	73
1997			4	4	3	7	3	107	110	1	35	36	157
1998			32	11	16	27	13	130	143	7	64	71	273
1999			11	11		11	9	51	60	2	45	47	129
2000		41	7	13	1	14	4	87	91		29	29	182
2001		10	19	7	23	30	10	321	331		31	31	421
2002		26	14	2	22	24	1	193	194		22	22	280
2003		4	22	24	3	27	22	15	37	5	2	7	97
2004		9	8		1	1	11	7	18				36
2005		4	12	3		3	5	10	15	1	2	3	37
2006			6	6	8	14		100	100		19	19	139
2007		1	21	4		4	13	3	16	1	3	4	46
2008		44	10	4	2	6	2	40	42	2	13	15	117
2009		36	21	16	2	18	22	27	49	2	7	9	133
2010		39	51	39	34	73	27	128	155	4	36	40	358
2011		32	14	3		3	9	18	27	8	13	21	97
2012		10	75	5	10	15	60	238	298	11	67	78	476
2013	114	7	64	50	17	67	23	110	133	8	26	34	419
2014		179	6	1	1	2	3	100	103	14	14	28	318
2015		63	63	12	4	16	33	32	65	4	12	16	223
2016		135	129	27	5	32	42	123	165	3	26	29	490
2017		87	67	34	0	34	69	77	146	6	31	37	371
2018		197	40	18	5	23	27	92	119	4	53	57	436
2019		58	45	11	11	22	17	187	204	7	54	61	390
2020		58	34	1	18	19	1	351	352	4	142	146	609
Total	114	1062	804	324	186	510	452	2631	3083	97	765	862	6435

Table 6. Numbers of prey types identified in kittiwake food samples—the basis for computations of relative occurrence—by month on Middleton Island from 1978 through 2020.

	Prey type identifications						
Year	March	April	May	June	July	August	Total
1978					56	4	60
1989		4	3		10		17
1990		25	9	34	46		114
1992			1			4	5
1994		7					7
1996			21		38	19	78
1997			4	9	132	47	192
1998			40	34	190	111	375
1999			14	15	75	65	169
2000		64	7	16	108	41	236
2001		12	21	30	409	44	516
2002		41	14	24	222	28	329
2003		6	31	34	47	9	127
2004		11	10	2	22		45
2005		5	13	3	17	4	42
2006			7	17	143	24	191
2007		1	26	4	21	4	56
2008		69	13	6	44	15	147
2009		48	22	23	65	11	169
2010		45	58	78	160	48	389
2011		37	17	3	34	29	120
2012		12	80	20	339	89	540
2013	129	7	64	68	139	44	451
2014		218	6	2	156	39	421
2015		77	71	23	88	20	279
2016		202	158	45	260	46	711
2017		134	74	46	207	48	509
2018		329	51	29	190	70	669
2019		68	48	29	289	83	517
2020		98	46	23	543	200	910
Total	129	1520	929	617	4050	1146	8391

Table 7. Food samples (bill loads, partial bill loads, and ground samples) obtained annually from rhinoceros auklets on Middleton Island from 1978 through 2020.

Year	No. samples	TotalMass (g)
1978	72	3,109
1986	4	98
1990	17	199
1993	70	1,407
1994	190	3,680
1995	146	2,217
1996	78	1,488
1997	138	1,708
1998	315	7,817
1999	100	2,688
2000	106	2,538
2001	126	3,889
2002	95	2,707
2003	121	3,462
2004	107	2,890
2005	95	2,749
2006	113	4,394
2007	100	2,470
2008	130	4,515
2009	111	3,079
2010	175	6,298
2011	115	3,431
2012	260	7,012
2013	248	8,732
2014	180	5,920
2015	334	9,351
2016	306	8,989
2017	328	10,057
2018	210	6,989
2019	319	10,786
2020	322	9,691
All years	5031	144,357

Table 8. Time series of kittiwake productivity, dietary capelin and PDO index during the breeding season on Middleton Island from 1978 through 2020.

Year	Mean PDO index (Jun-Aug)	Productivity	Capelin in diet (Jun-Aug)
1978	-0.55	0.14	0.0000
1979	0.51	--	--
1980	0.17	--	--
1981	0.90	0.47	--
1982	0.06	0.30	--
1983	2.57	0.03	--
1984	-0.01	0.76	--
1985	0.69	0.04	--
1986	0.83	0.05	--
1987	1.86	0.00	--
1988	0.52	0.21	--
1989	0.43	0.00	--
1990	0.27	0.00	0.0500
1991	-0.40	0.22	--
1992	1.53	0.24	--
1993	2.46	0.01	--
1994	-0.09	0.32	--
1995	1.06	0.17	--
1996	0.58	0.60	0.0526
1997	2.63	0.32	0.0000
1998	0.05	0.42	0.1373
1999	-0.97	0.19	0.0452
2000	-0.76	0.99	0.5394
2001	-0.85	1.03	0.1677
2002	-0.02	0.97	0.2956
2003	0.84	0.50	0.2333
2004	0.44	0.20	0.0000
2005	0.69	0.37	0.0000
2006	0.25	0.47	0.0163
2007	0.46	0.42	0.2414
2008	-1.57	0.78	0.6462
2009	-0.25	0.20	0.3535
2010	-0.85	0.78	0.8322
2011	-1.43	0.50	0.6061
2012	-1.44	0.87	0.7634
2013	-1.02	1.00	0.8247
2014	0.73	0.45	0.0152
2015	1.65	0.21	0.0076
2016	1.27	0.08	0.0313
2017	0.33	0.22	0.0332
2018	0.08	0.31	0.0519
2019	0.83	0.50	0.1820
2020	-0.25	0.83	0.0287

Table 9. Effects of supplemental feeding on laying dates, clutch sizes and overall productivity of black-legged kittiwakes on the Middleton tower since 1996.

	Treatment effect (Fed - Unfed pairs)		
Year	Julian lay date	Clutch size	Chicks fledged
1996	-2.30	0.01	0.62
1997	-3.23	0.32	0.64
1998	-5.19	0.40	0.26
1999	-8.78	1.14	0.38
2000	-2.03	0.15	0.19
2001	-2.65	0.15	0.25
2002	0.79	0.10	0.00
2003	-4.58	0.14	0.41
2004	-2.87	0.41	0.79
2005	-6.67	0.19	0.66
2006	-7.09	0.34	0.67
2007	-4.90	0.24	0.35
2008	-3.13	0.19	0.12
2009	-4.40	0.20	0.55
2010	2.24	0.01	0.11
2011	-5.55	0.21	0.42
2012	-1.55	0.06	0.06
2013	0.15	0.13	0.04
2014	--	--	--
2015	-1.62	0.39	0.75
2016	-8.52	1.06	0.73
2017	-6.00	0.87	0.54
2018	-4.00	0.49	0.68
2019	-4.70	0.38	0.57
2020	0.10	0.02	0.21
Mean	-3.60	0.32	0.42

Table 10. Pearson correlations among the Pacific Decadal Oscillation (PDO) index (June to August), relative occurrence of dietary capelin, and kittiwake chick production on Middleton Island over 40 years between 1978 and 2019.

		Variable	
Variable	Statistic	Chick production	Capelin in diet
Capelin in diet			
	Pearson's *r*	0.637	---
	P (2-tailed)	<0.001	---
	n (years)	27	---
PDO (Jun-Aug)			
	Pearson's *r*	-0.596	-0.676
	P (2-tailed)	<0.001	<0.001
	n (years)	41	27

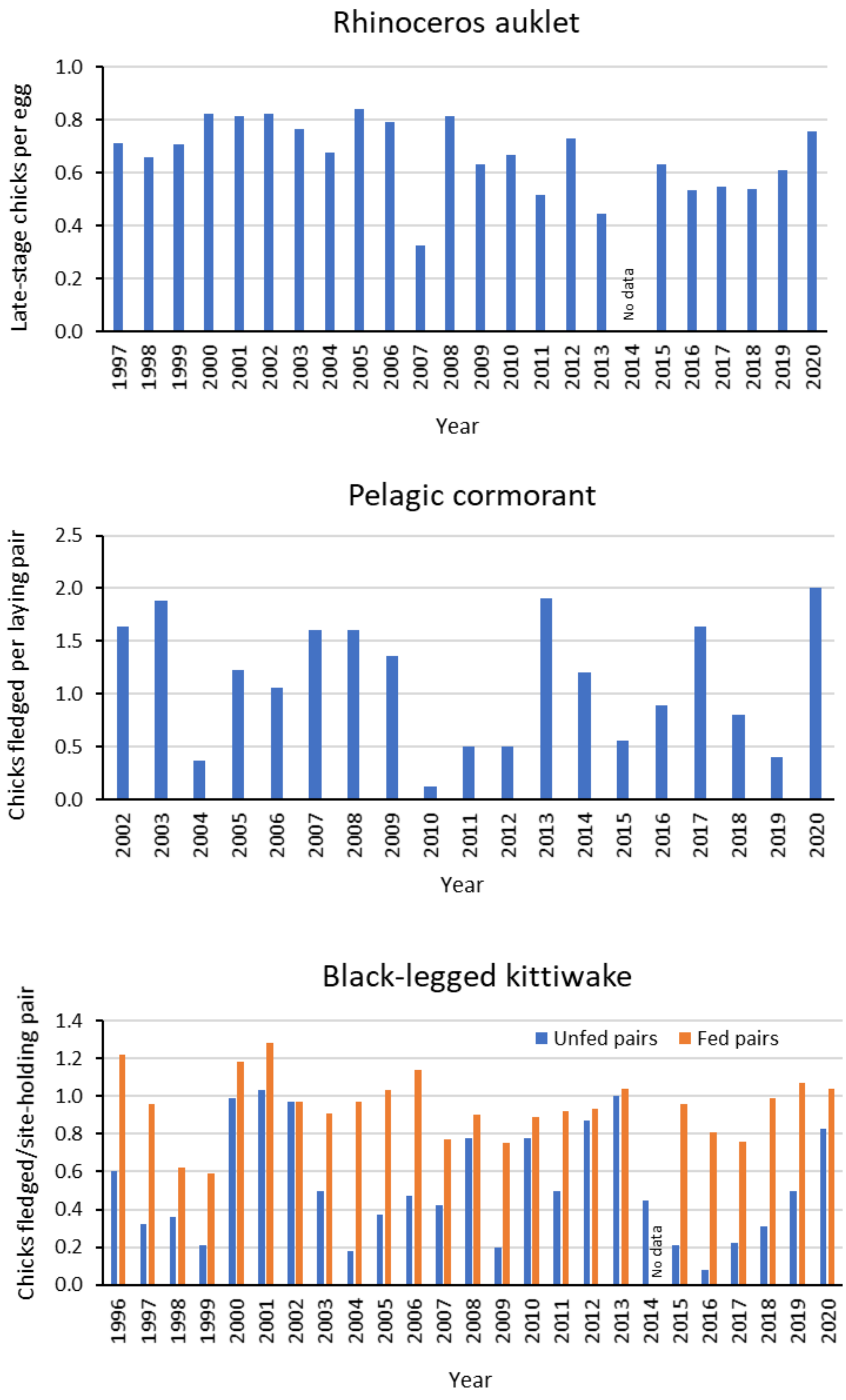
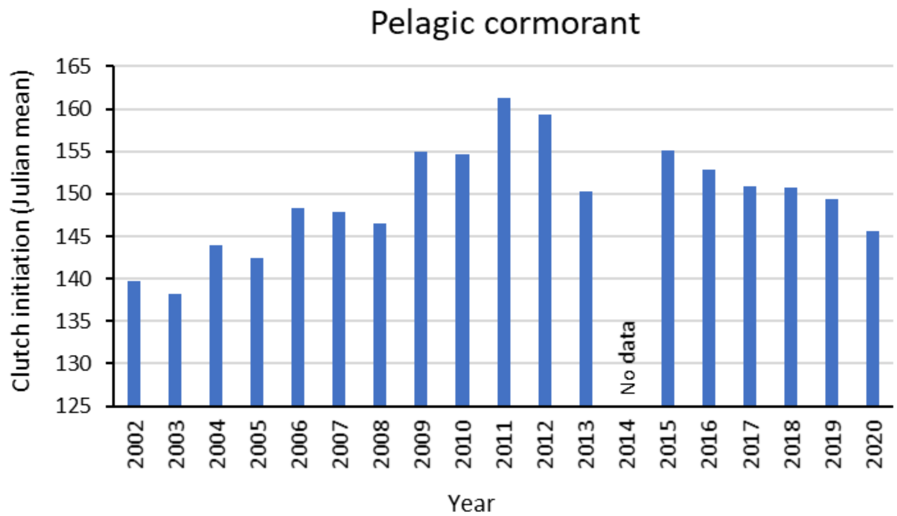


Figure 1. Annual production of offspring in three species of seabirds monitored on Middleton Island in the north-central Gulf of Alaska. Lower panel compares the breeding performance of kittiwakes subjected to supplemental feeding (ad libitum) at the nest site with control samples of naturally foraging pairs.



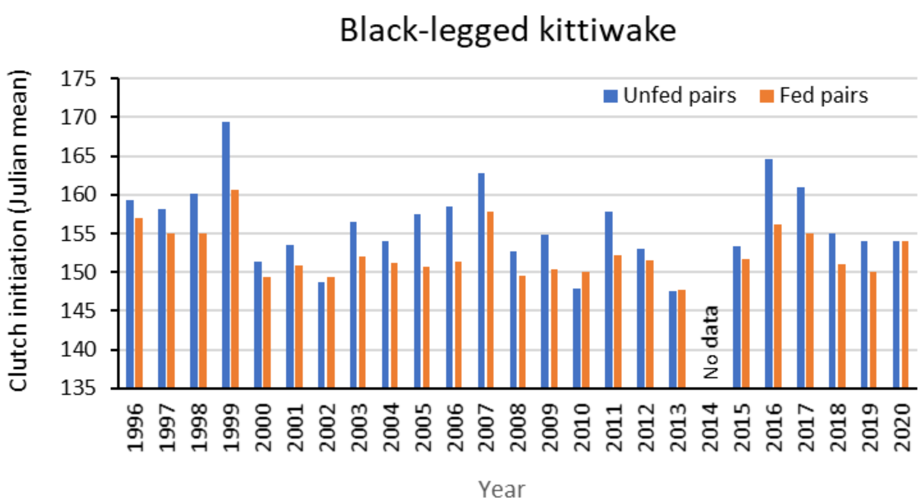


Figure 2. Breeding chronology of pelagic cormorants and black-legged kittiwakes on Middleton Island. On average, food-supplemented kittiwake pairs breed 4 days earlier than controls (lower panel).

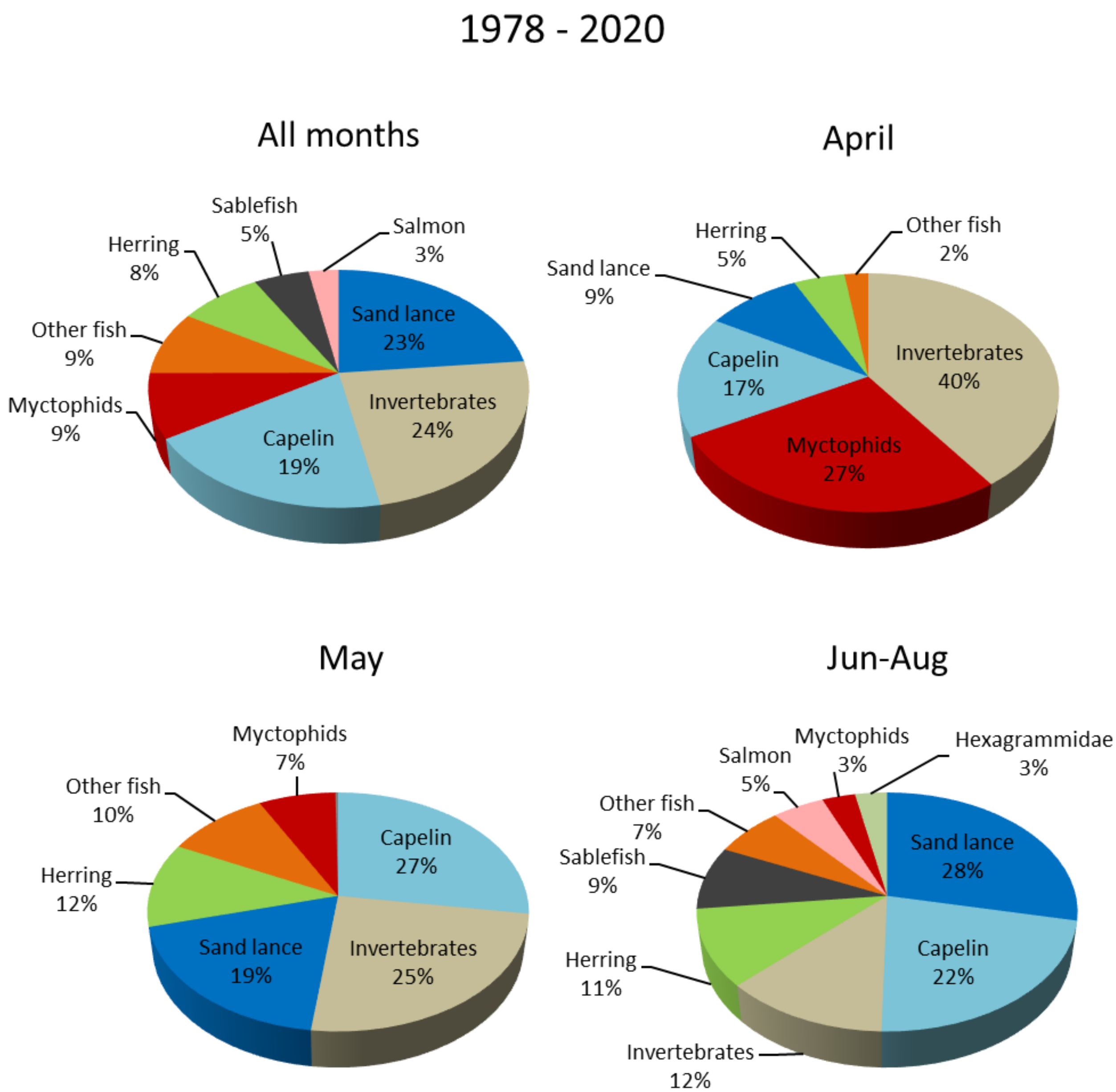


Figure 3. Overall composition of food samples obtained from black-legged kittiwakes (relative occurrence, April – August) on Middleton Island from 1978 to 2020.

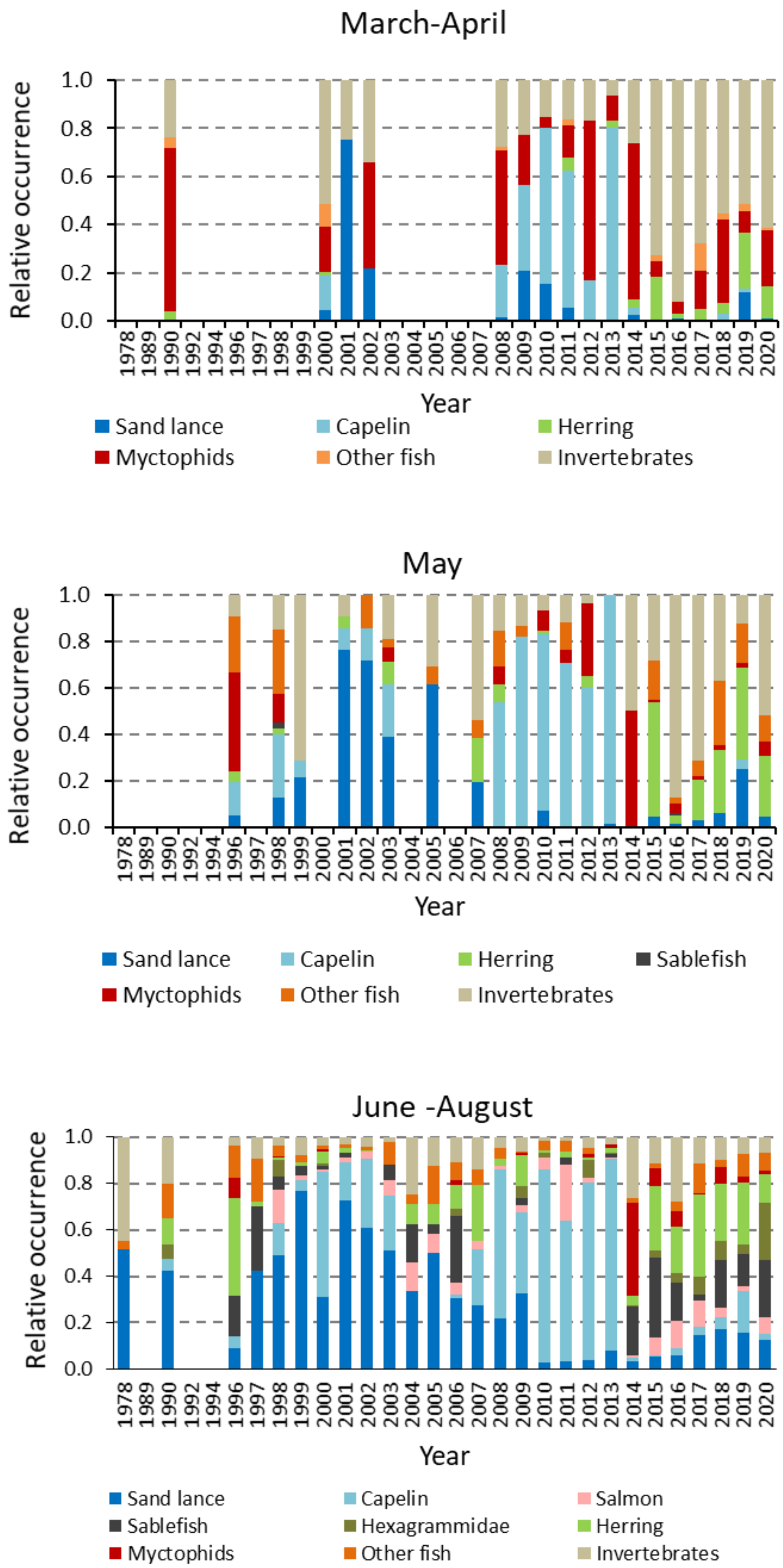


Figure 4. Interannual variation in kittiwake diet composition at three stages of breeding on Middleton Island, 1978 to 2020. Sample sizes as listed in Tables 5 and 6.

March - April

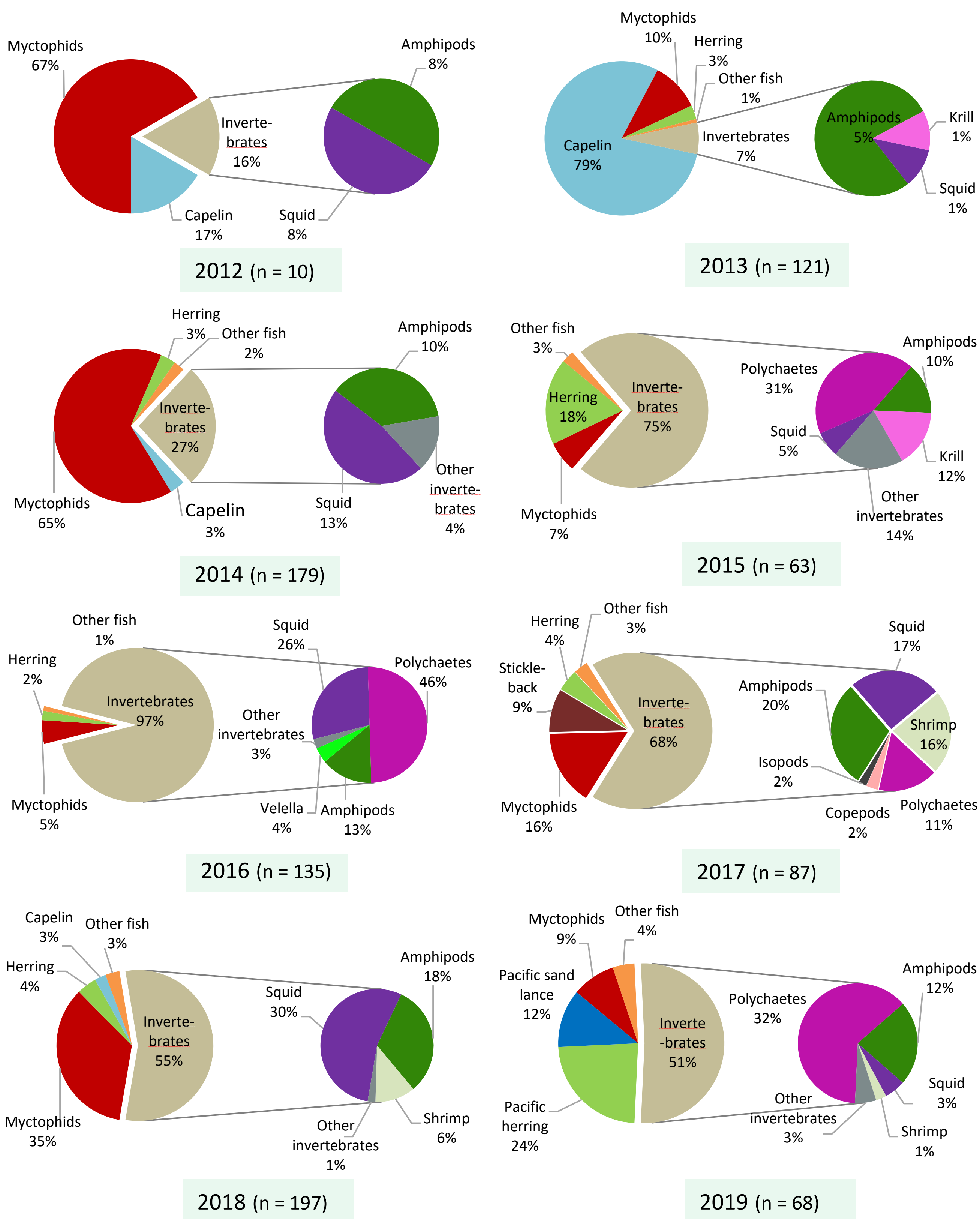


Figure 5. Variation in the relative occurrence and composition of fish and invertebrates in the diet of black-legged kittiwakes on Middleton Island from spring arrival through April in 2012-2019.

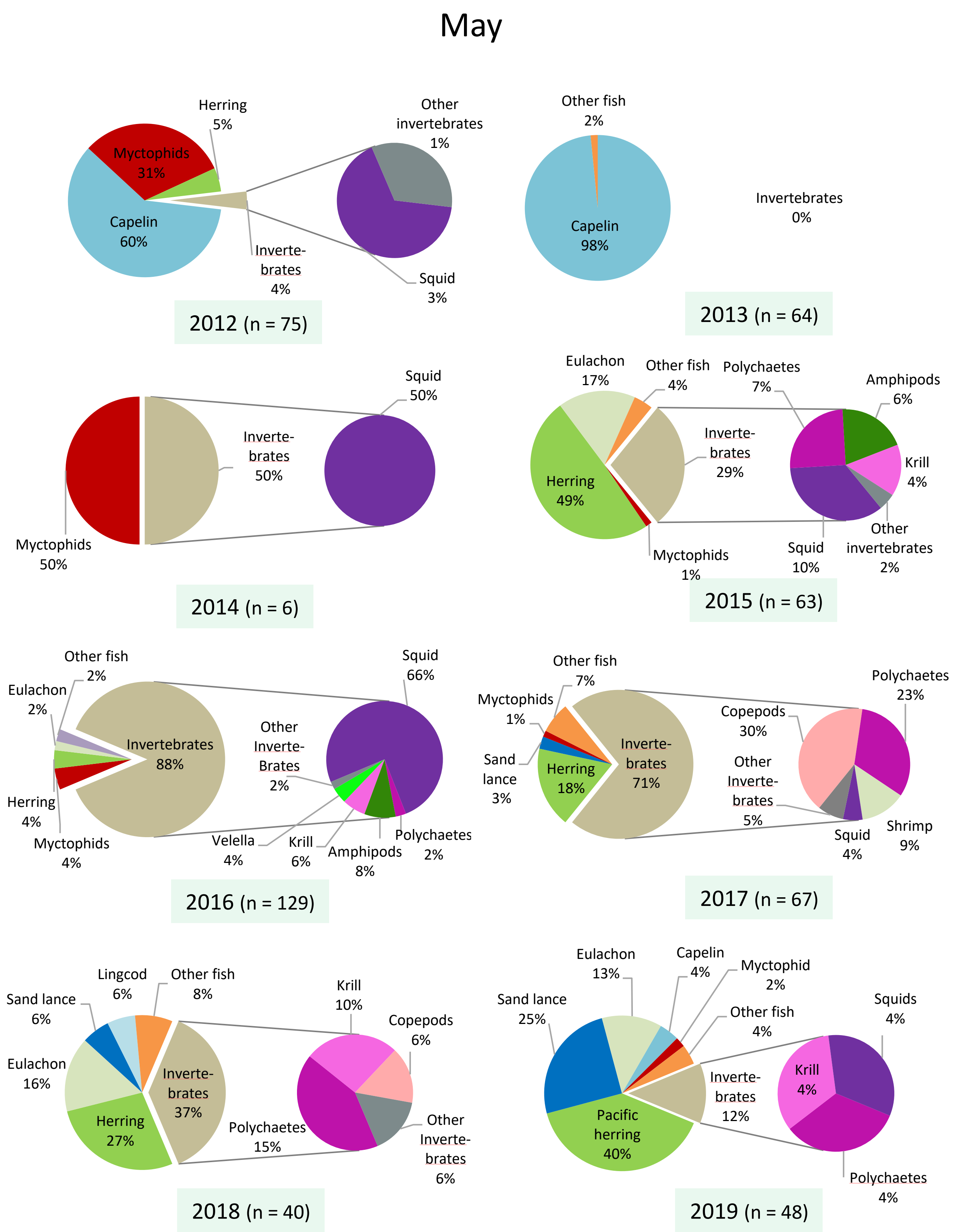


Figure 6. Variation in the relative occurrence and composition of fish and invertebrates in the diet of black-legged kittiwakes on Middleton Island during May in 2012-2019.

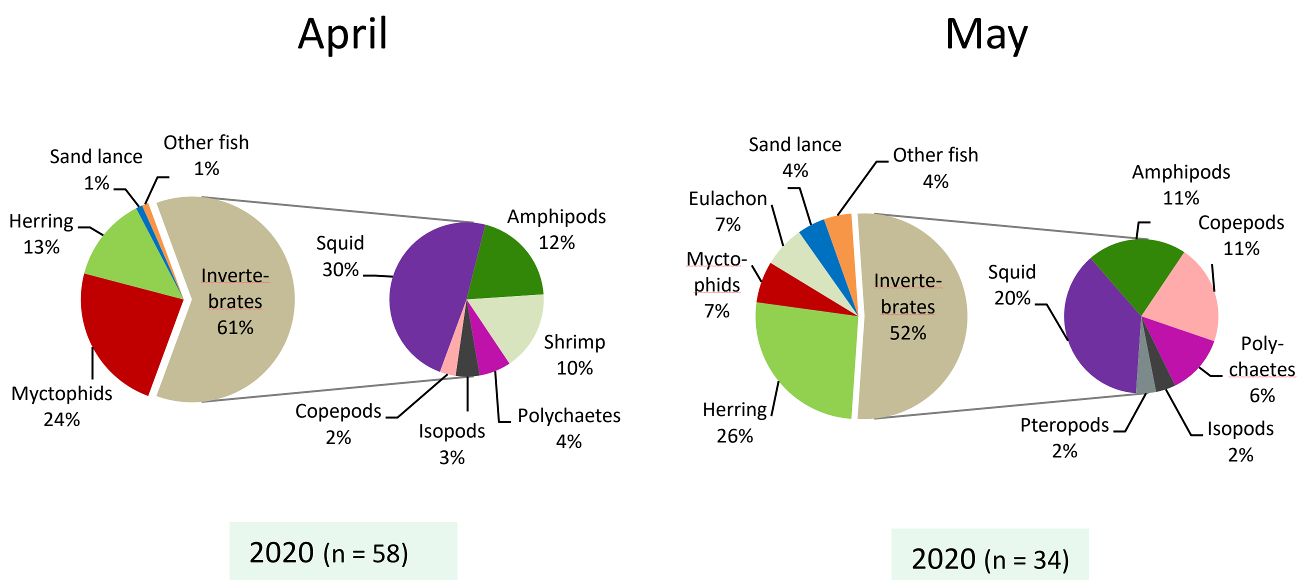


Figure 7. Variation in the relative occurrence and composition of fish and invertebrates in the diet of black-legged kittiwakes on Middleton Island during April and May, 2020.

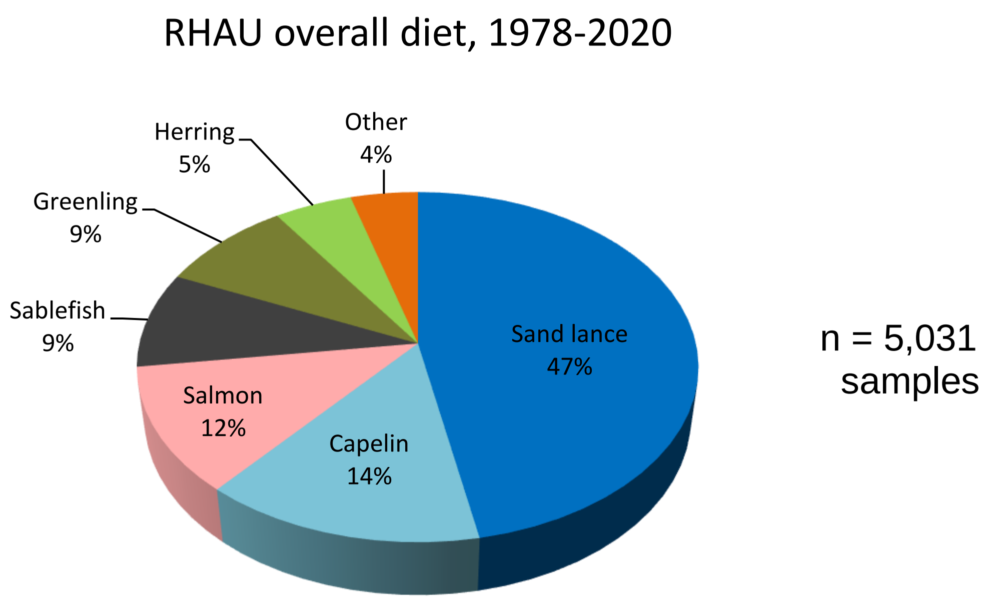
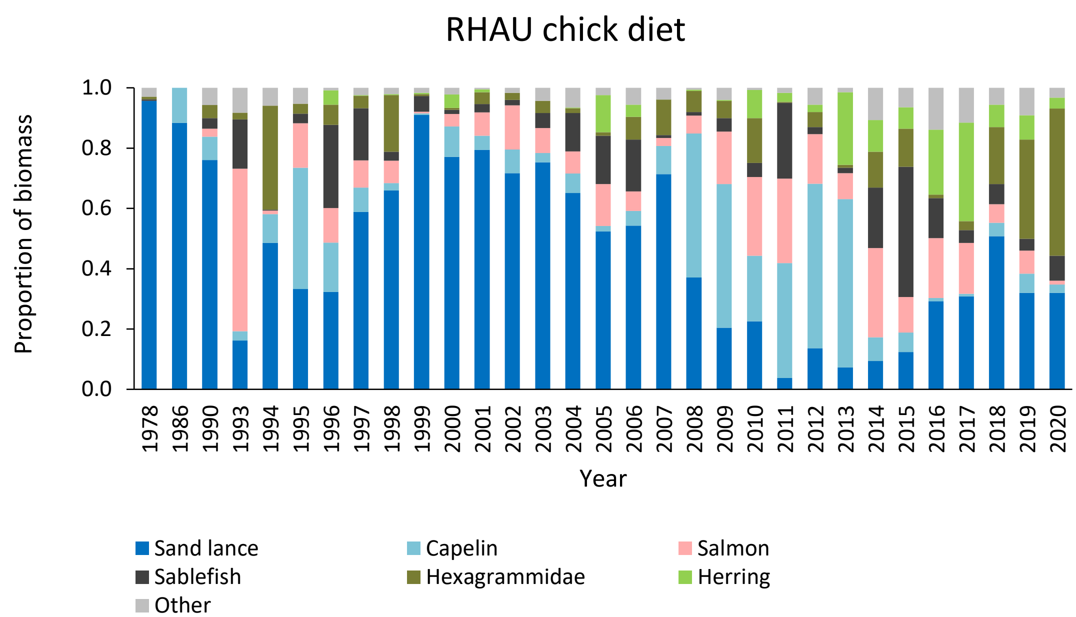


Figure 8. Overall composition of food samples obtained from chick-rearing rhinoceros auklets (% biomass, July-August) on Middleton Island from 1978 through 2020.



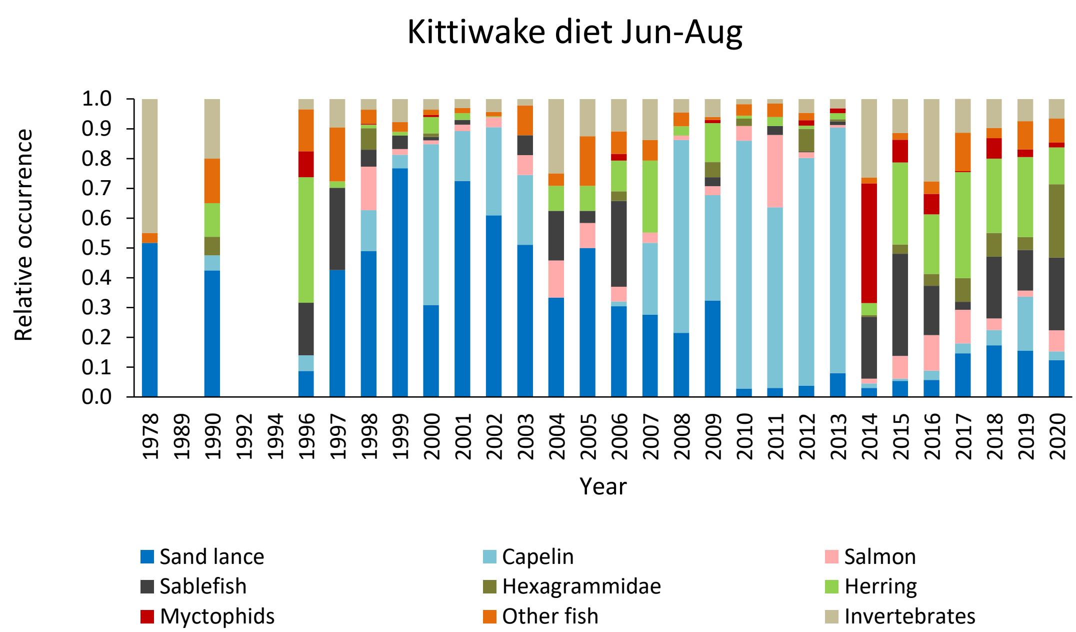


Figure 9. Interannual variation in diet composition of chick-rearing rhinoceros auklets on Middleton Island, 1978 to 2020, with a similar time series for black-legged kittiwakes (lower panel) for comparison. Sample sizes as listed in Tables 5, 6 and 7.

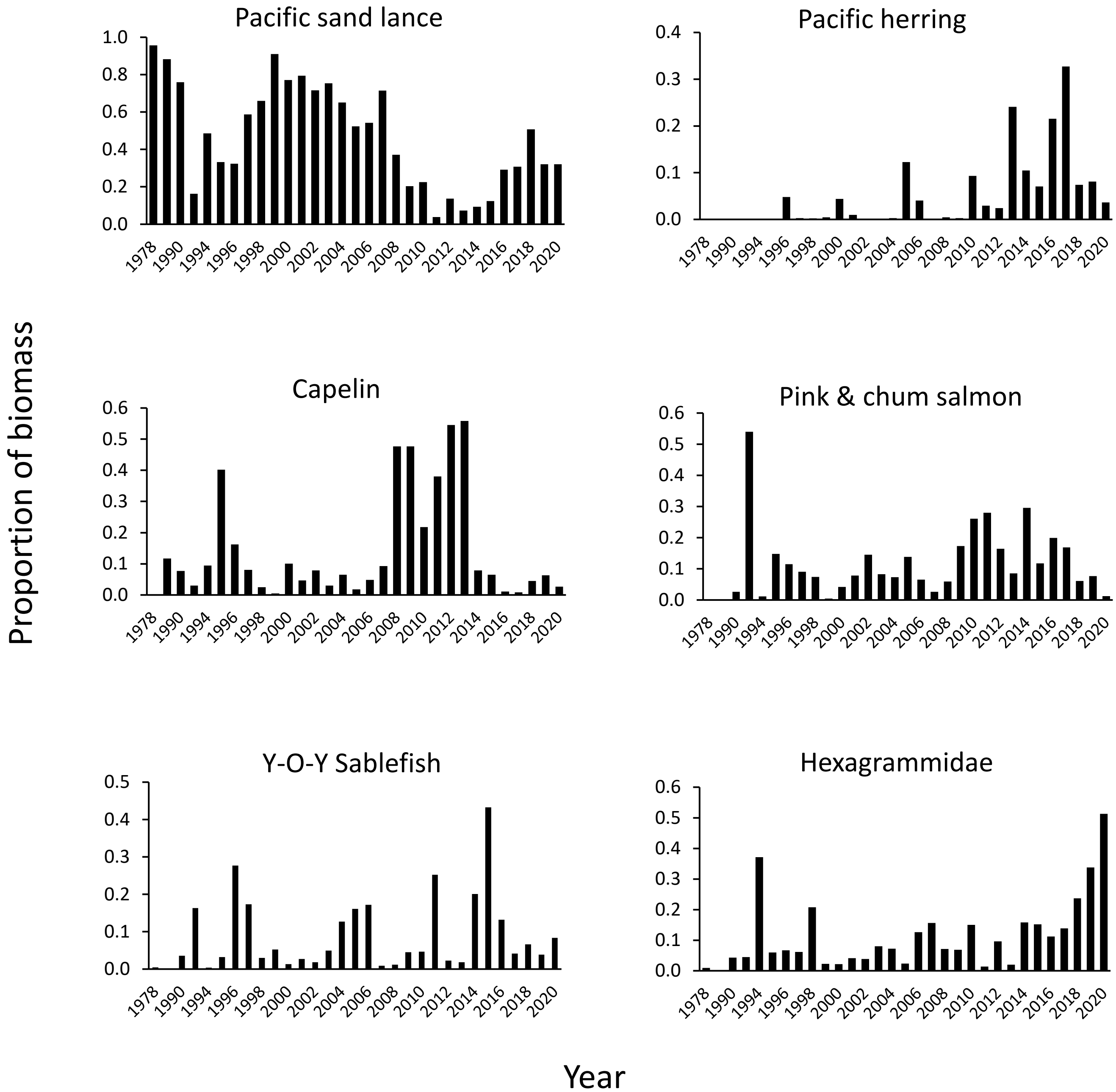


Figure 10. Indices of prey species occurrence in the nestling diet of rhinoceros auklets on Middleton Island from 1978 through 2020.

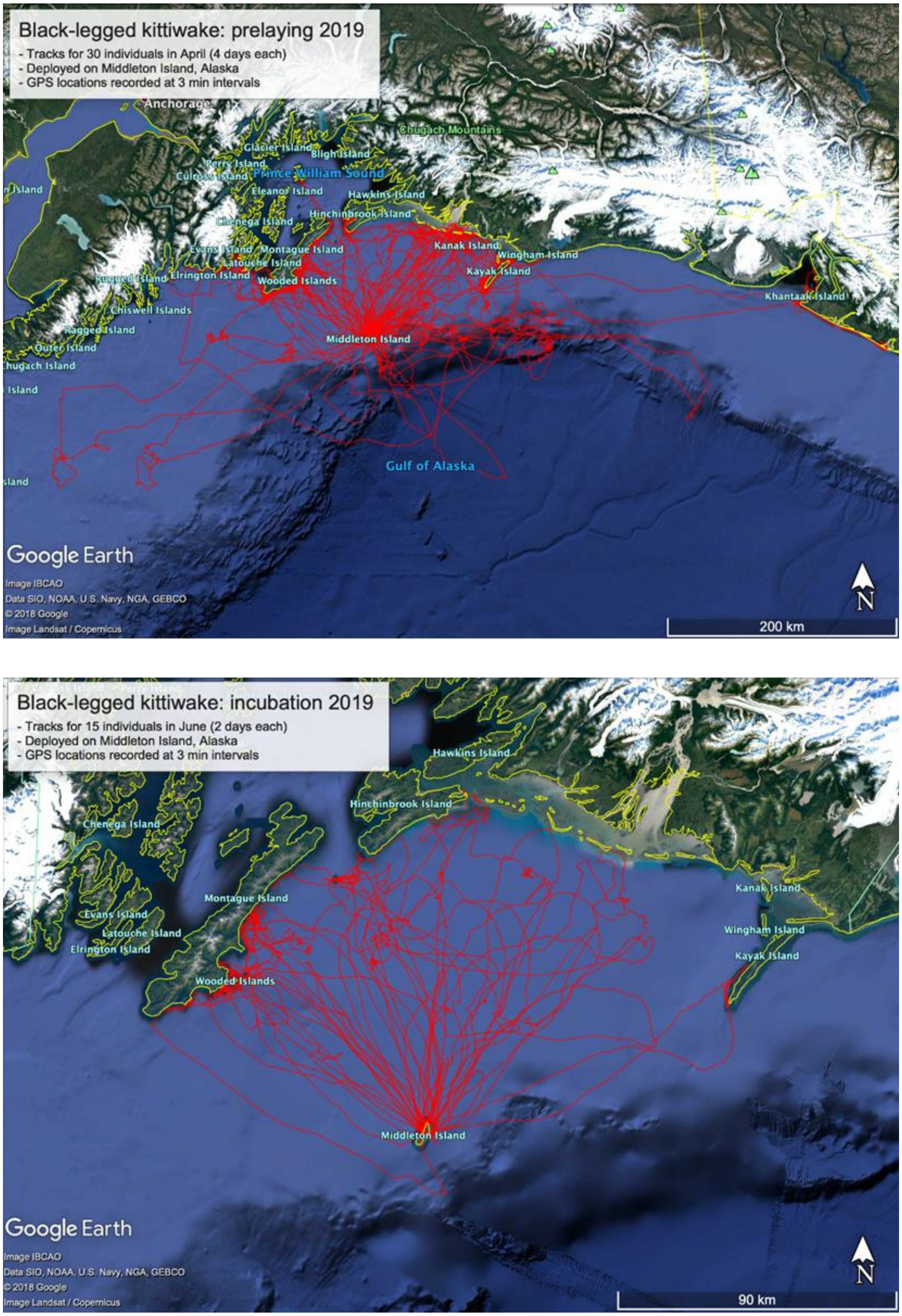


Figure 11. Foraging areas of Middleton Island kittiwakes during the prelaying period (upper panel) and incubation (lower panel) as revealed by GPS tracking devices deployed on 45 individuals in 2019.

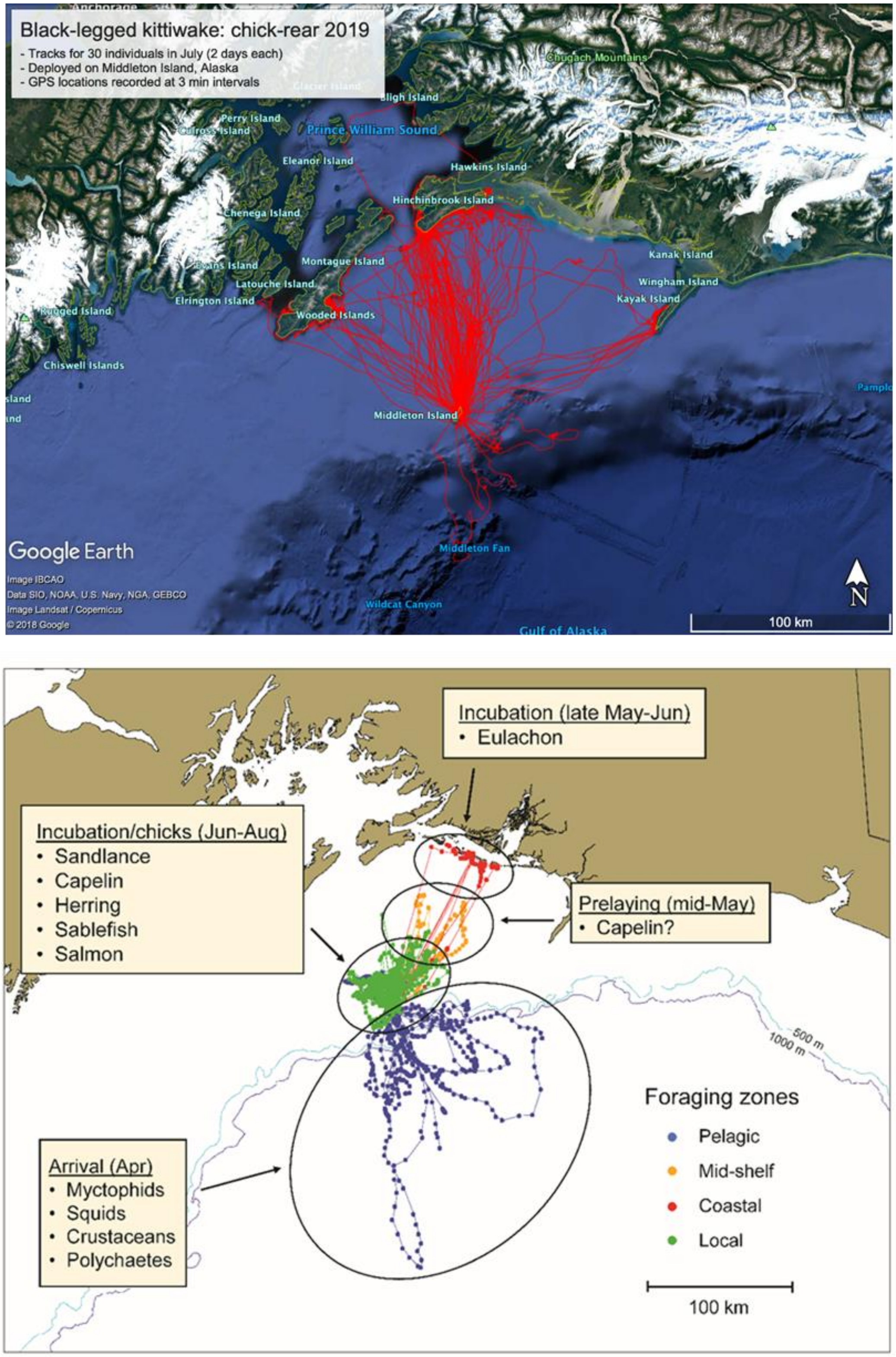


Figure 12. Foraging areas of Middleton Island kittiwakes during chick-rearing in 2019 (upper panel), and for comparison, use of pelagic and neritic foraging habitats by Middleton kittiwakes according to stage of breeding in 2008 (lower panel).

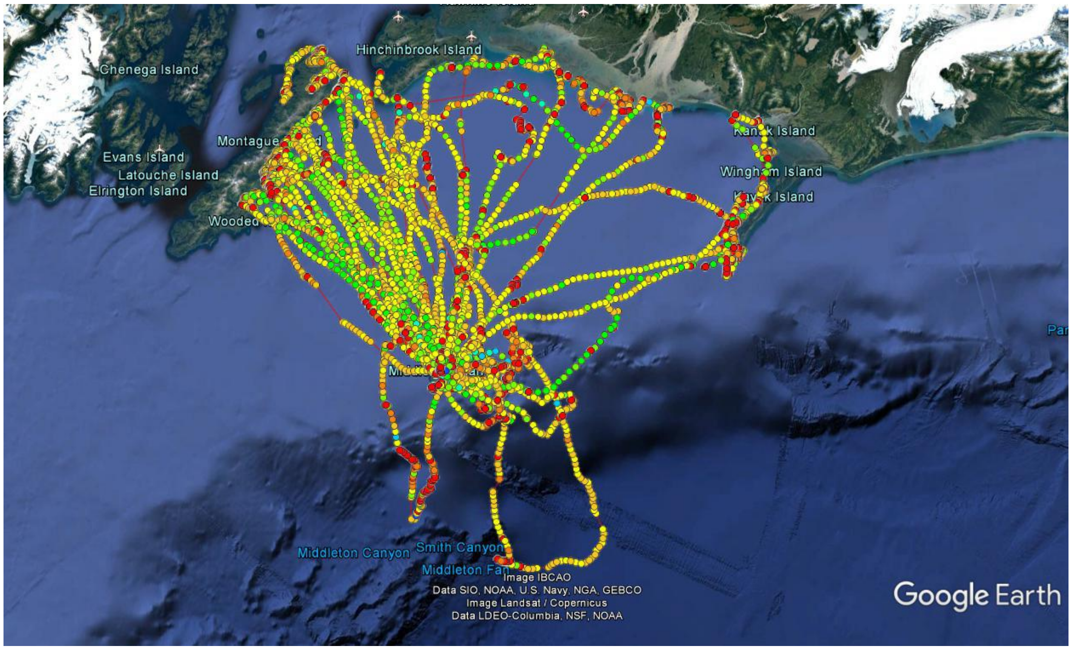


Figure 13. Foraging areas of Middleton Island kittiwakes during late incubation and chick-rearing as revealed by GPS tracking devices deployed on 11 individuals in 2020.

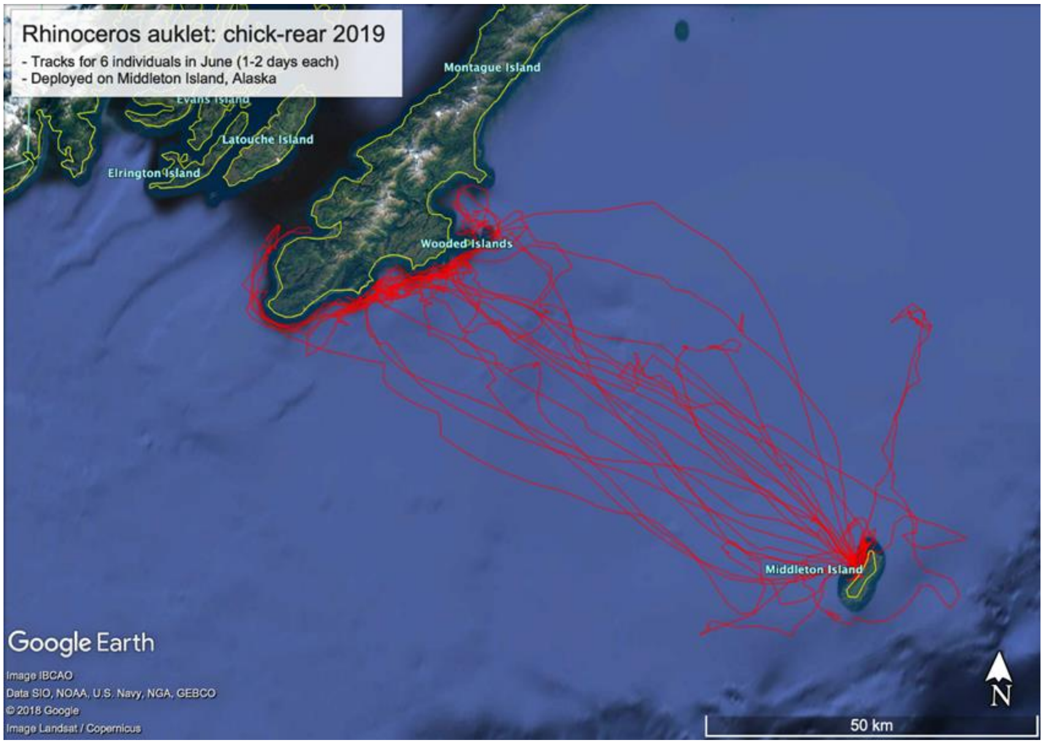


Figure 14. Foraging areas of rhinoceros auklets during chick-rearing as revealed by GPS tracking devices deployed on 6 individuals in 2019.

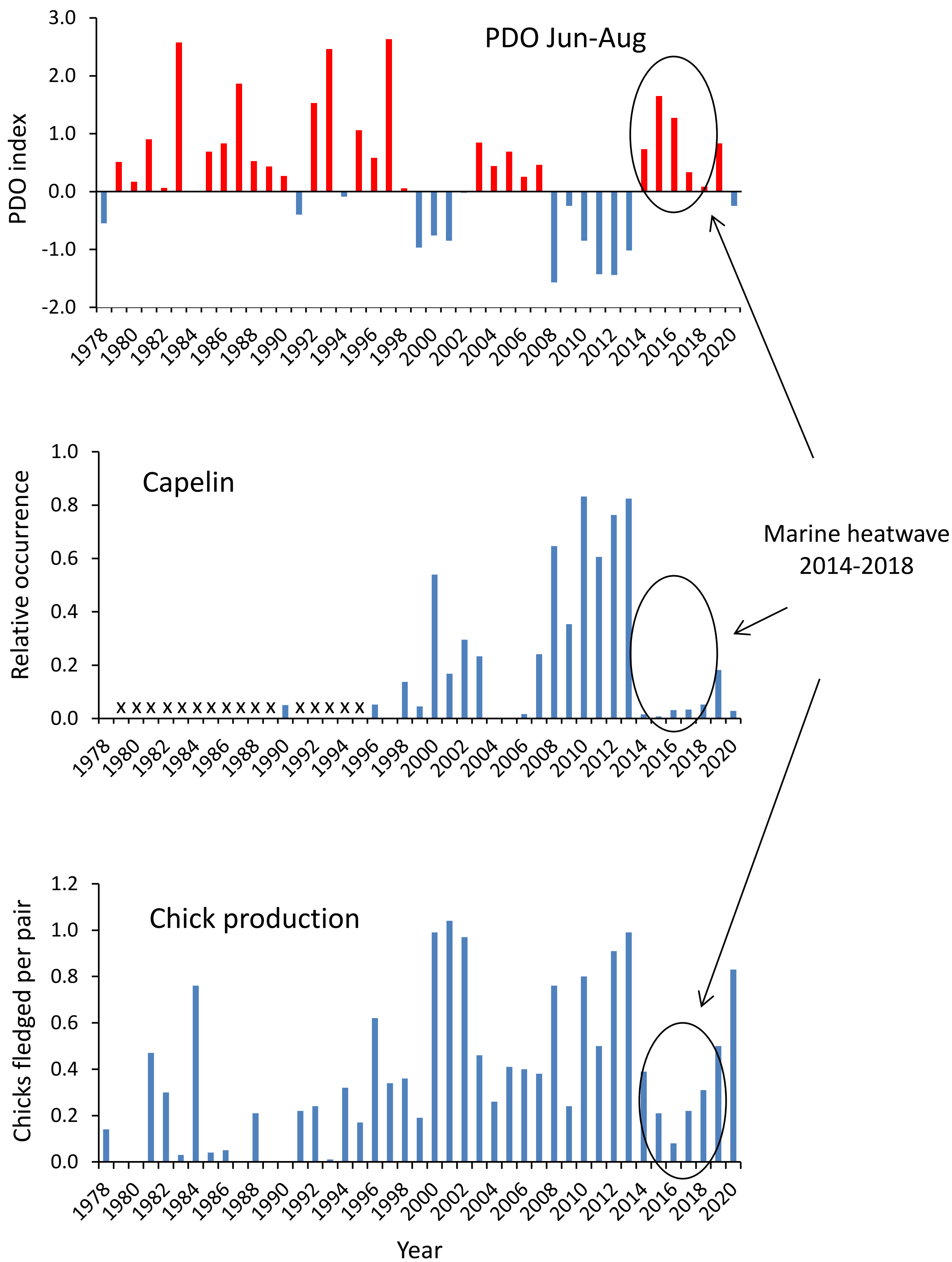


Figure 15. Relations among the Pacific Decadal Oscillation (PDO) index (June – August), the relative occurrence of dietary capelin, and the annual production of chicks by kittiwakes on Middleton Island, 1978 to 2020. Missing data denoted by ‘x’.

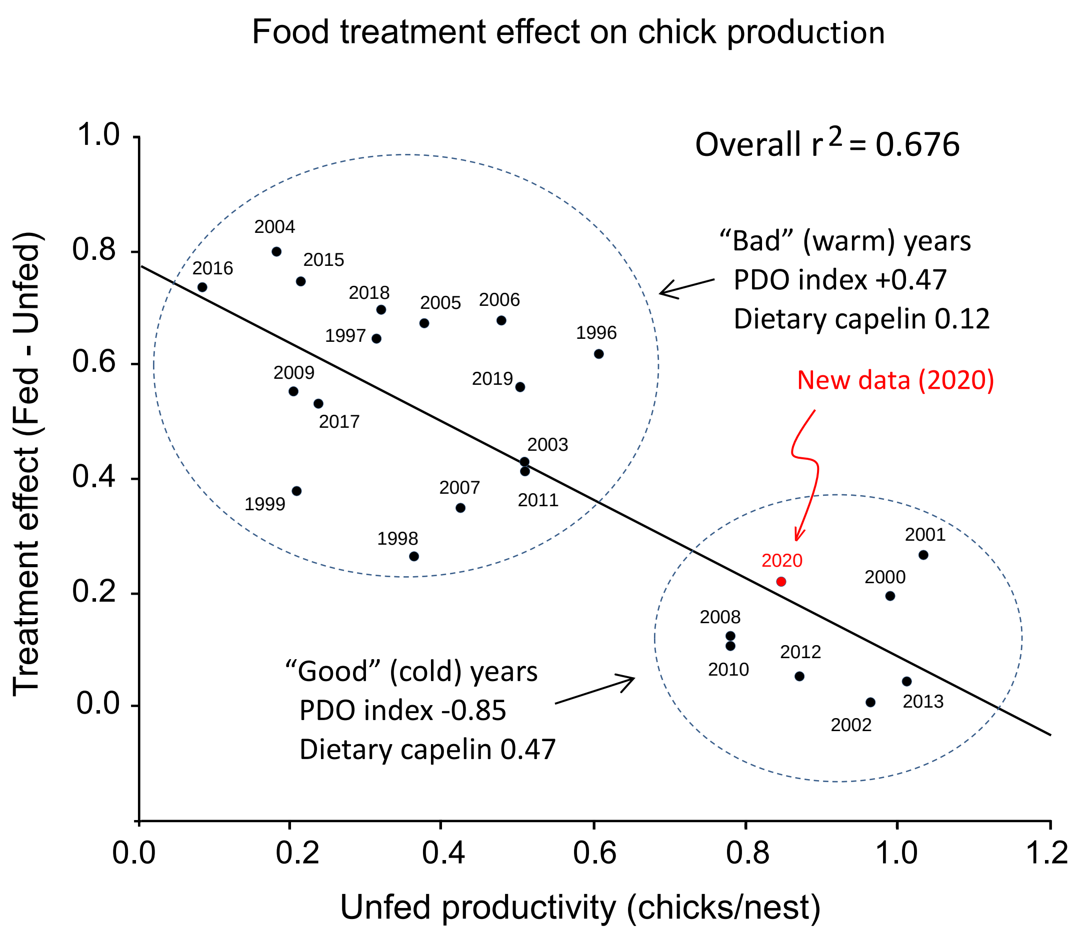


Fig. 16. Effect of supplemental food treatment on kittiwake breeding performance on Middleton Island in 24 years since 1996. Productivity of unfed pairs is a proxy for quality of the foraging environment. Treatment effect is the difference in productivity between supplementally fed and unfed pairs. "Poor" years are characterized by warm ocean conditions (PDO index June-August), a low proportion of capelin in the diet, and a marked effect of food treatment on kittiwake production. "Good" years have cool ocean conditions, a higher proportion of dietary capelin, and reduced or no difference in breeding performance of fed and unfed pairs.