Institute for Seabird Research and Conservation

Middleton Island Seabird Research and Monitoring

2019 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 2019 season marked the third 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.

Additional lines of research in 2019 were possible by way of research personnel and financial support contributed by McGill University (NSERC, National Science Education and Research Council of Canada), Bucknell University, Queen's University (CA), the University of Ottawa, and Swansea University (UK). Those efforts included instrumentation of several species with GPS trackers and accelerometers and extensive research on the physiology and behavioral ecology of black-legged kittiwakes. Cooperators from the Prince William Sound Science Center (PWSSC) deployed GLS trackers on tufted puffins to ascertain the winter movements of that species, with financial support from the North Pacific Research Board (NPRB). With the partial exception of GPS tracking results for kittiwakes and rhinoceros auklets, the outcomes of those special investigations are not included in this report.

In 2019, the Middleton research station was occupied by members of the field crew from 5 April 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 field crew were Shannon Whelan (Interim Camp Leader), Hannes Schraft, Catherine Lee-Zuck, Frederique Tremblay, Jenna Schlener (Interim Camp Leader), Emily Choy, and Kyle Elliott from McGill University, Sierra Pete and Morgan Benowitz-Fredericks (Bucknell University), Drew Sauve (Interim Camp Leader) and Emma Lachance Linklater (Queen's University), Ethan Hermer (University of Ottawa), Baptiste Garde (Swansea University), Akiko Shoji (University of Tsukuba), Naya Sena (University of Hokkaido), Jon Green (University of Liverpool) and ISRC volunteers Hannah Weipert, Abe Turner, Dan Netti, Scott Hatch, and Martha Hatch. Kristen Gorman and Anne Schaefer (PWSSC) joined the effort for several weeks in July and August for telemetry studies of tufted puffins. Thanks also to Shawn and Kelly Pummill for assistance with facilities renovation and camp set up during April. 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, and their population is increasing (currently ~20,000 individuals). At 0.61 chicks/egg laid (Table 1), production in 2019 was a little lower than the long-term average of 0.66 (n = 23 years, 1995-2019). The installation of nest boxes for rhinoceros auklets (n = 57) on the property this season will greatly facilitate productivity measures and other research on this species in future years (Appendix Fig. 1).

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 five 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 0.32 chicks per egg in 2019 continued that trend, 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 1.43 fledglings per nest built) is relatively constant (Table 2). Production in 2019 (0.84 fledglings/nest) was similar to the previous year and only a little beneath the long-term average of 1.05 fledglings/nest. On average, about 90 nests are constructed annually by cormorants on the tower, versus 75 nests in 2019. 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—Among 73 fed pairs of kittiwakes on the Middleton tower, production was 0.93 fledglings/nest in 2019, whereas 326 unfed pairs produced 0.35 chicks/nest (Table 3). The difference between groups indicated poor foraging conditions in 2019 for surface-feeding kittiwakes, as contrasted with divers such as rhinoceros auklets and pelagic cormorants. This season extended 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. In 2018, there were signs of a nascent return to more normal foraging conditions, but see below.

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 4). 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 5).

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. 1). 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. 2).

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. 1). 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. 2). 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. 2).

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. 3) and May (Fig. 4). 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. 3 & 4). 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. 3 & 4). 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. 3). 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. 3), 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. 2). 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. 3 & 4). However, myctophids seemed to be largely unavailable during that time, when the main constituents of the fish diet were Pacific 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. 2). 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.

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 2019 yielded 319 bill loads and ground samples, comprising about 11 kg of auklet prey in total (Table 6). 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. 5). 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. 6).

Since 1978, nearly 135 kg of auklet prey samples have been collected on Middleton (Table 6), 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. 6). The appearance of about 30% sand lance in the auklet diet in 2016-2017, and more than 50% by weight in 2018 is consistent with a known association of sand lance with warm-water conditions (Hatch 2013). While herring appear superficially to have benefitted from the recent warming of surface waters (Fig. 7), 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). Also 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. 7).

The juxtaposition of time series for kittiwakes and rhinoceros auklets since 1978 (Fig. 6) 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. 6). In 2019, the trade-off appeared to occur primarily between herring (more prevalent in kittiwake diet) and juvenile greenlings (taken mainly by auklets).

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. 8). Foraging tracks give the impression of birds sampling intermittently the pelagic zone off the continental shelf, but not staying and 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 virtual absence this year of deep-ocean foraging (Figs. 8 & 9). 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 former year, spring foraging occurred almost exclusively in the pelagic zone, then shifted to the continental shelf prior to egg-laying (Fig. 9). 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, more recently (2015-2019, to our knowledge) such parents have made regular trips to coastal waters from Montague and Hinchinbrook islands to Cape St. Elias (Fig. 9), where presumably they obtained the Age 1+ herring that appear in the diet (Fig. 2).

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).

As in 2018, 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. 10). That would seem to be the location where age-0 greenlings and gadids were unusually abundant in 2019. We remain a bit 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 7, Fig. 11). 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 have remained a relatively minor component of the spring diet through 2019, April 2018 being a partial exception. Although indications in 2018 were of a gathering return to normal conditions in the Gulf, patterns in recent months portend another heatwave, prompting references in the popular media to "Son of Blob" (e.g., Yulsman 2019). The continued large effect of supplemental feeding on laying dates, clutch sizes, and productivity in 2017-2019 (Table 8) confirms the continued difficulty kittiwakes are having in acquiring sufficient energy for breeding.

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. 12). The events of 2014-2019 have only increased the strength and predictive power of relations among the PDO, prey dynamics, and kittiwake breeding performance (Table 9). As of fall 2018, 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, the effects of which still linger in the Gulf of Alaska, is 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 2015-2019.

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

Table 2. Breeding performance of pelagic cormorants on the Middleton tower, 2002-2019.[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
Totals	1,419	149.8	0.98	8.63	1,512	3.2	0.13	1.180	1,512	1.1	0.12	1.048

[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, 1996-2019.[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	0.3	5.471	368	1.61	0.04	0.691	368	0.35	0.03	0.511	73	150	0.46	3.921	73	1.99	0.04	0.312	73	0.93	0.09	0.805

[a] Mean clutch size includes zero-egg nests, reflecting both breeding propensity and egg production by laying pairs

Table 4. Temporal distribution of diet samples from black-legged kittiwakes on Middleton Island, 1978 – 2019.

	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
Total	114	1004	770	323	168	491	451	2280	2731	93	623	716	5826

Table 5. Numbers of prey types identified in kittiwake food samples—the basis for computations of relative occurrence—by month on Middleton Island from 1978 through 2019.

	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
Total	129	1422	883	594	3507	946	7481

Table 6. Food samples (bill loads, partial bill loads, and ground samples) obtained annually from rhinoceros auklets on Middleton Island from 1978 through 2019.

Year	No. samples	TotalMass (g)
1978	72	3109.2
1986	4	97.7
1990	17	199.4
1993	70	1407.2
1994	190	3680.1
1995	146	2217.1
1996	78	1488.0
1997	138	1707.6
1998	315	7816.6
1999	100	2688.3
2000	106	2537.8
2001	126	3888.6
2002	95	2706.7
2003	121	3461.6
2004	107	2889.9
2005	95	2749.3
2006	113	4393.8
2007	100	2470.0
2008	130	4514.9
2009	111	3079.4
2010	175	6297.6
2011	115	3430.8
2012	260	7011.6
2013	248	8732.3
2014	180	5920.0
2015	334	9351.0
2016	306	8988.5
2017	328	10,056.8
2018	210	6,989.0
2019	319	10785.9
All years	4709	134,666.7

Table 7. Time series of kittiwake productivity, dietary capelin and PDO index during the breeding season on Middleton Island from 1978 through 2019.

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	0.35	0.1820

Table 8. 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	0.58
Mean	-3.76	0.33	0.43

Table 9. 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*	0.691	---
	P (2-tailed)	<0.001	---
	n (years)	26	---
PDO (Jun-Aug)			
	Pearson's *r*	-0.594	-0.692
	P (2-tailed)	<0.001	<0.001
	n (years)	40	26

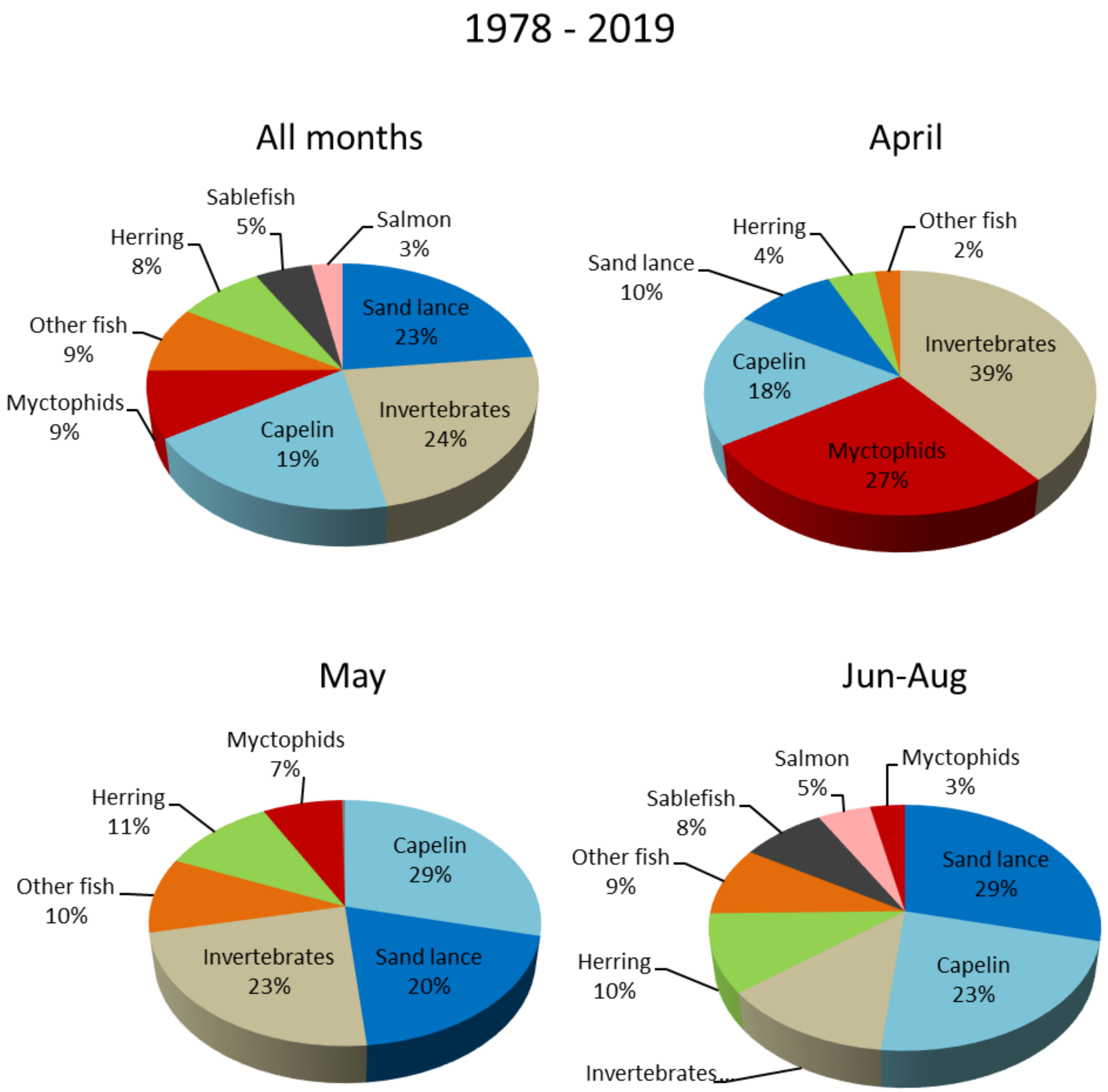

Figure 1. Overall composition of food samples obtained from black-legged kittiwakes (relative occurrence, April – August) on Middleton Island from 1978 to 2019.

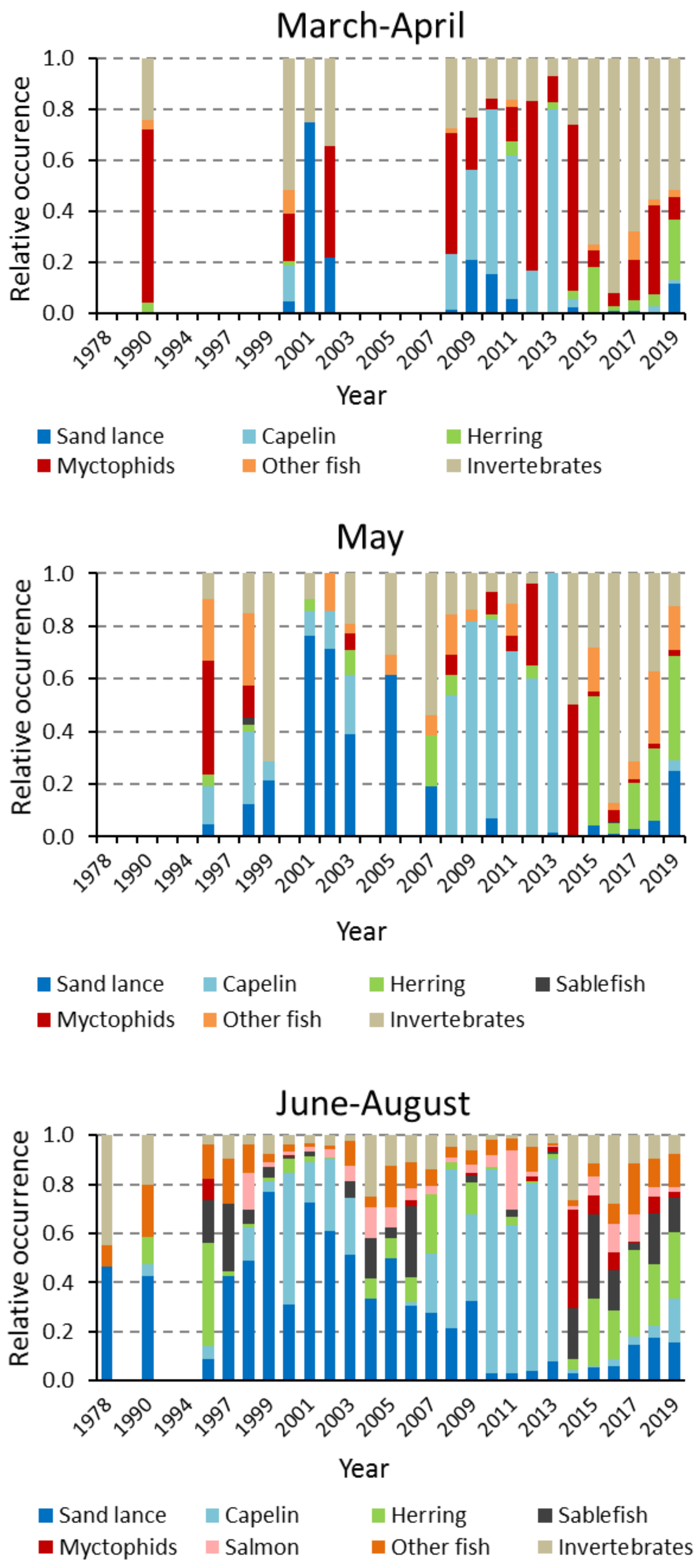

Figure 2. Interannual variation in kittiwake diet composition at three stages of breeding on Middleton Island, 1978 to 2019. Sample sizes as listed in Tables 4 and 5.

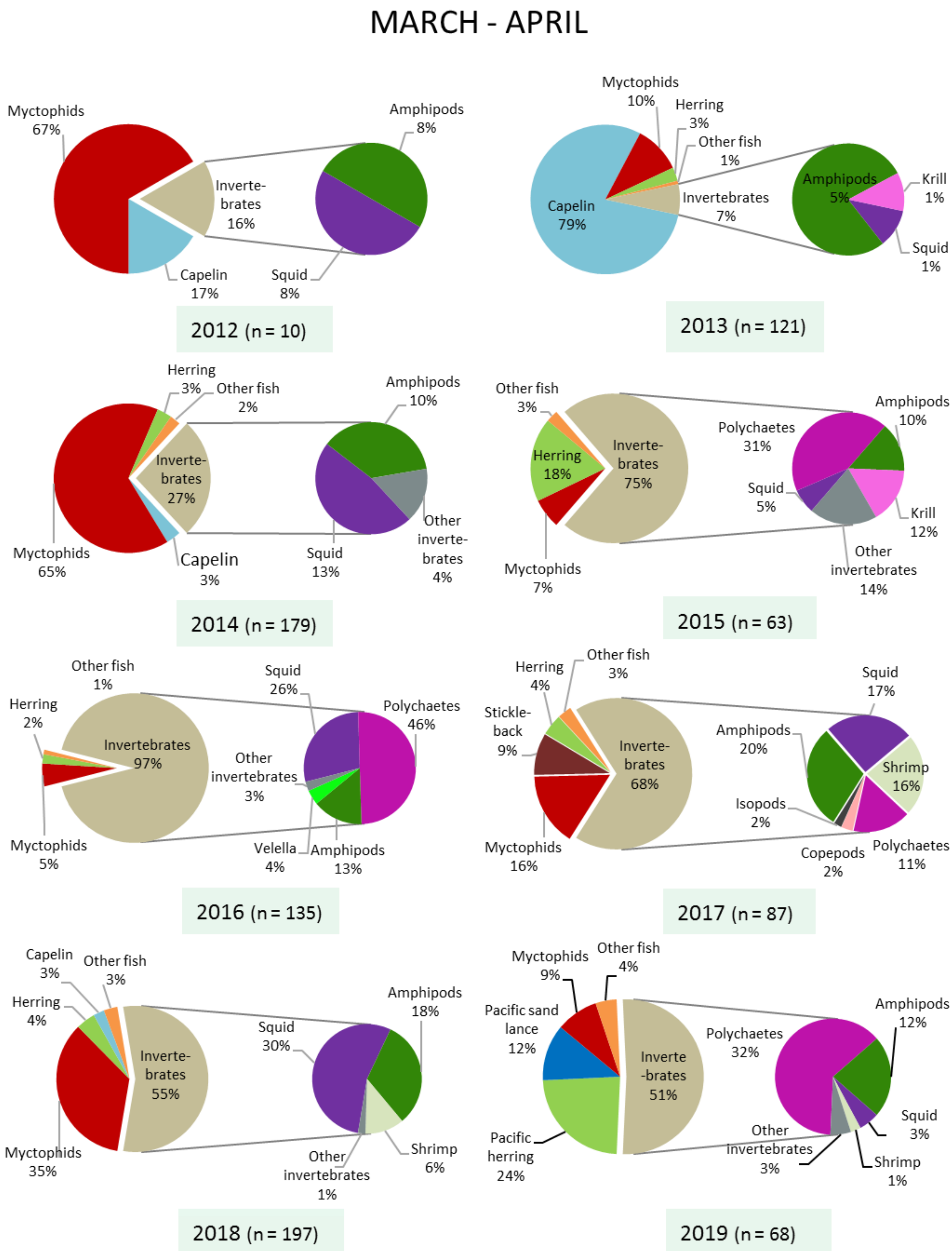

Figure 3. Variation in the relative occurrence and composition of fish and invertebrates in the diet of black-legged kittiwakes on Middleton Island from spring arrival through April in 2012-2019.

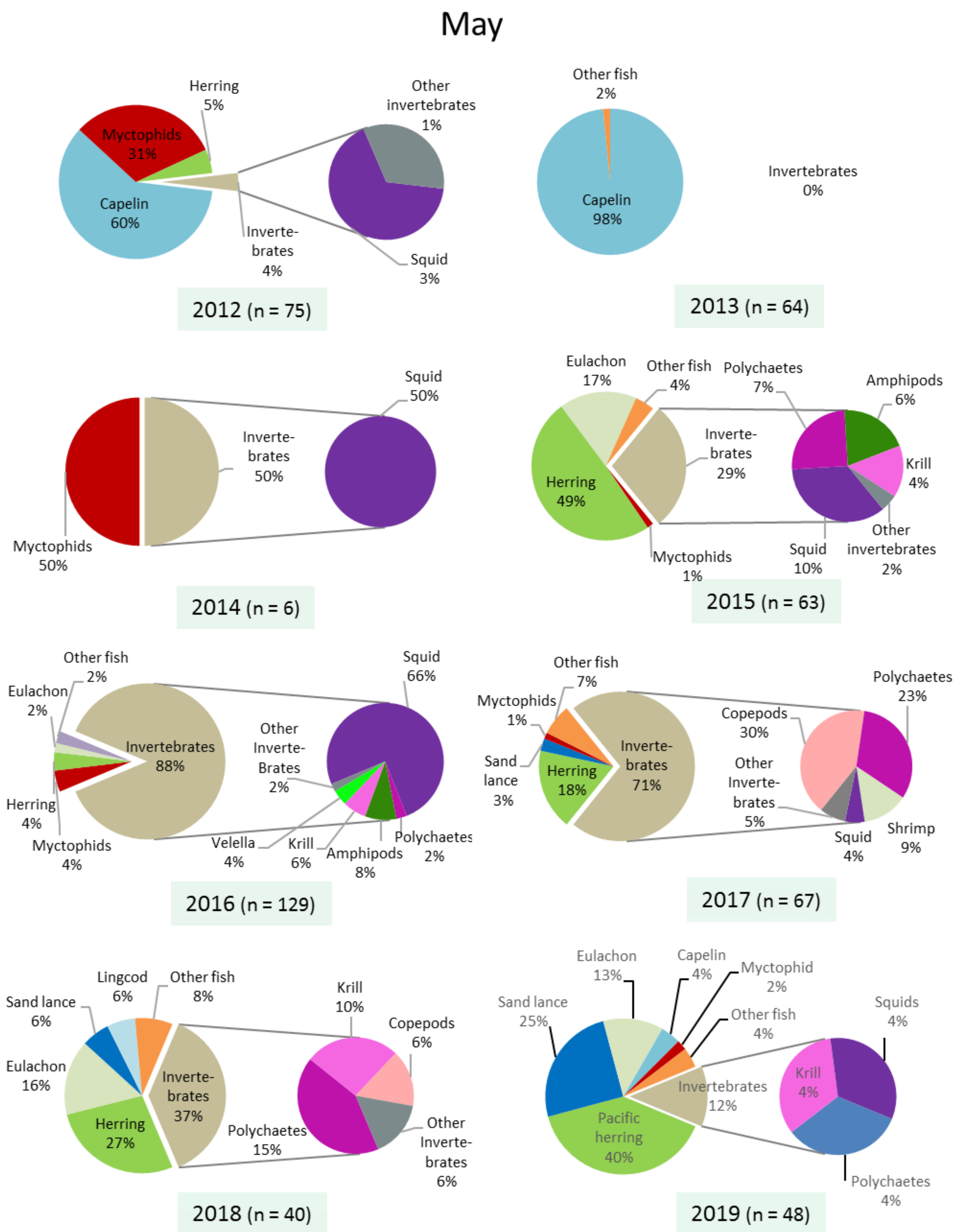

Figure 4. Variation in the relative occurrence and composition of fish and invertebrates in the diet of black-legged kittiwakes on Middleton Island during May in 2012-2019.

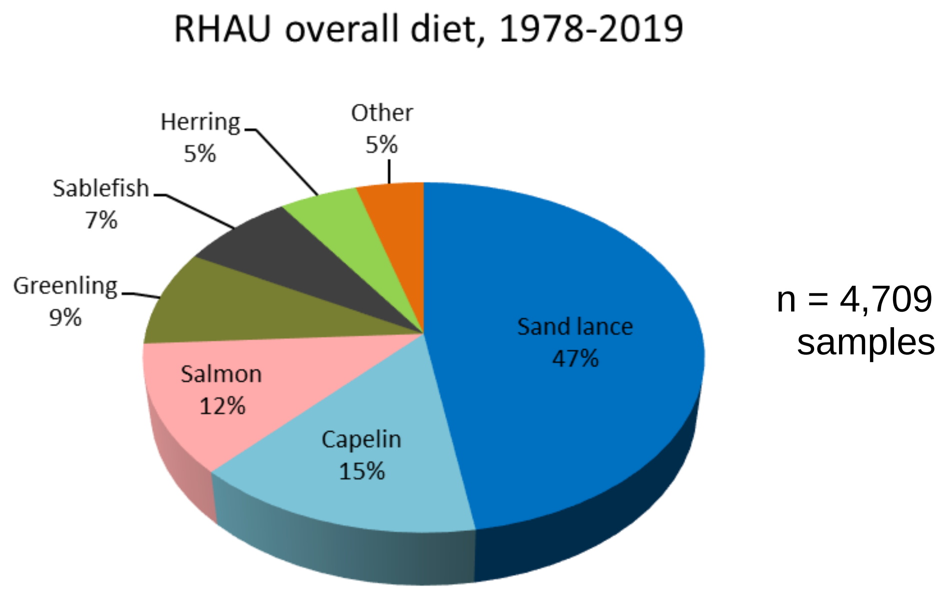

Figure 5. Overall composition of food samples obtained from chick-rearing rhinoceros auklets (% biomass, July-August) on Middleton Island from 1978 through 2019.

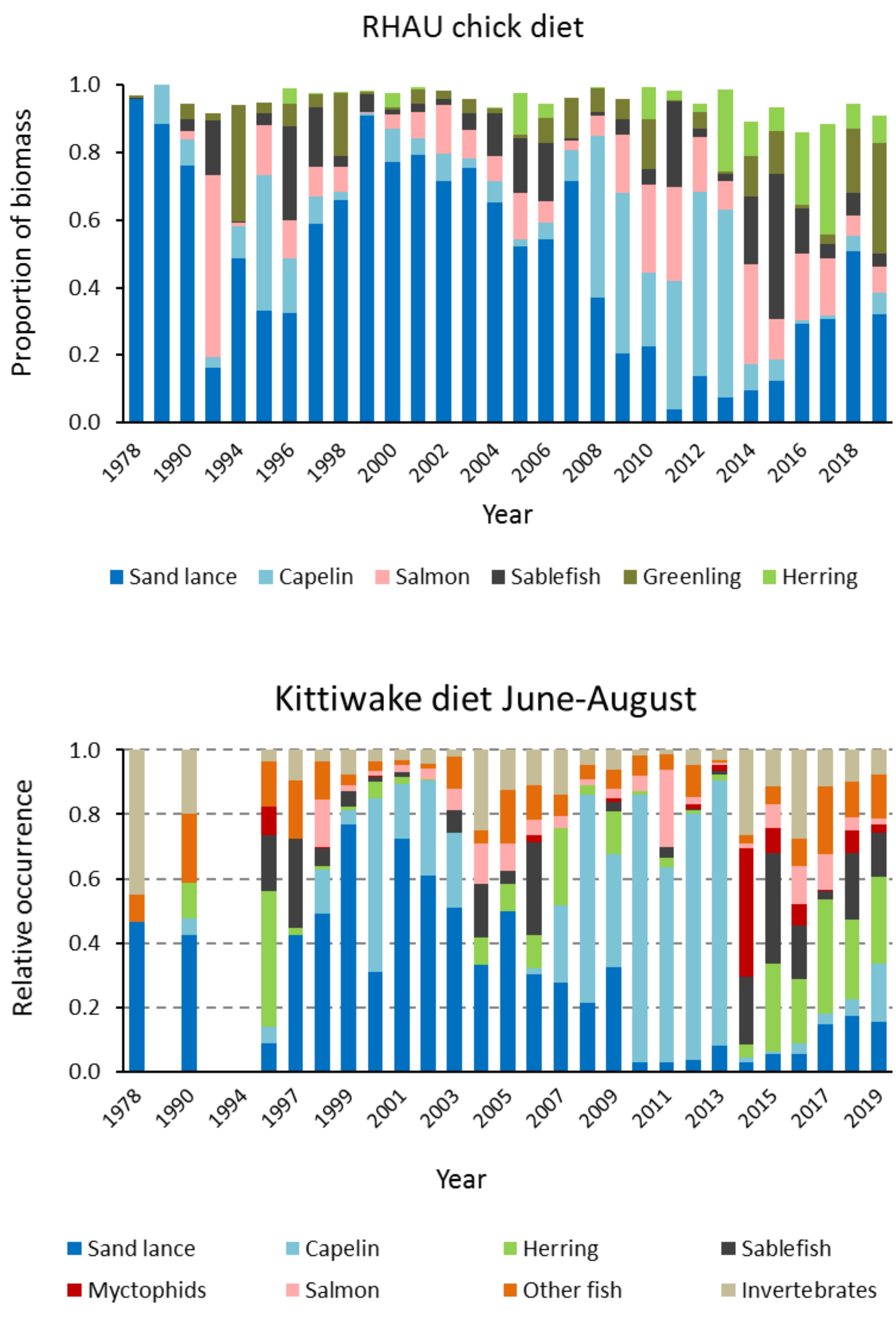

Figure 6. Interannual variation in diet composition of chick-rearing rhinoceros auklets on Middleton Island, 1978 to 2019, with a similar time series for black-legged kittiwakes (lower panel) for comparison. Sample sizes as listed in Tables 4, 5 and 6.

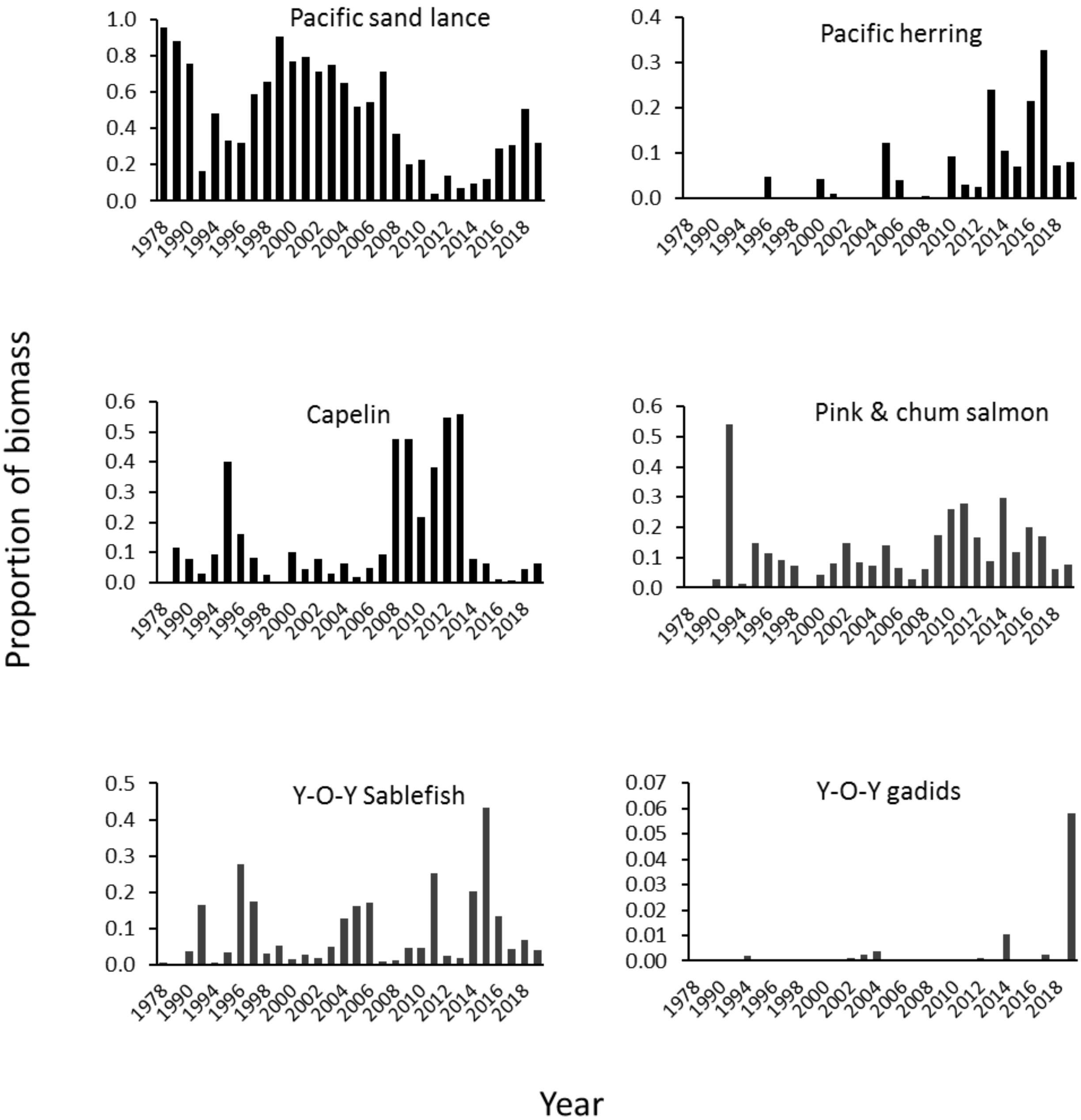

Figure 7. Indices of prey species occurrence in the nestling diet of rhinoceros auklets on Middleton Island from 1978 through 2019.

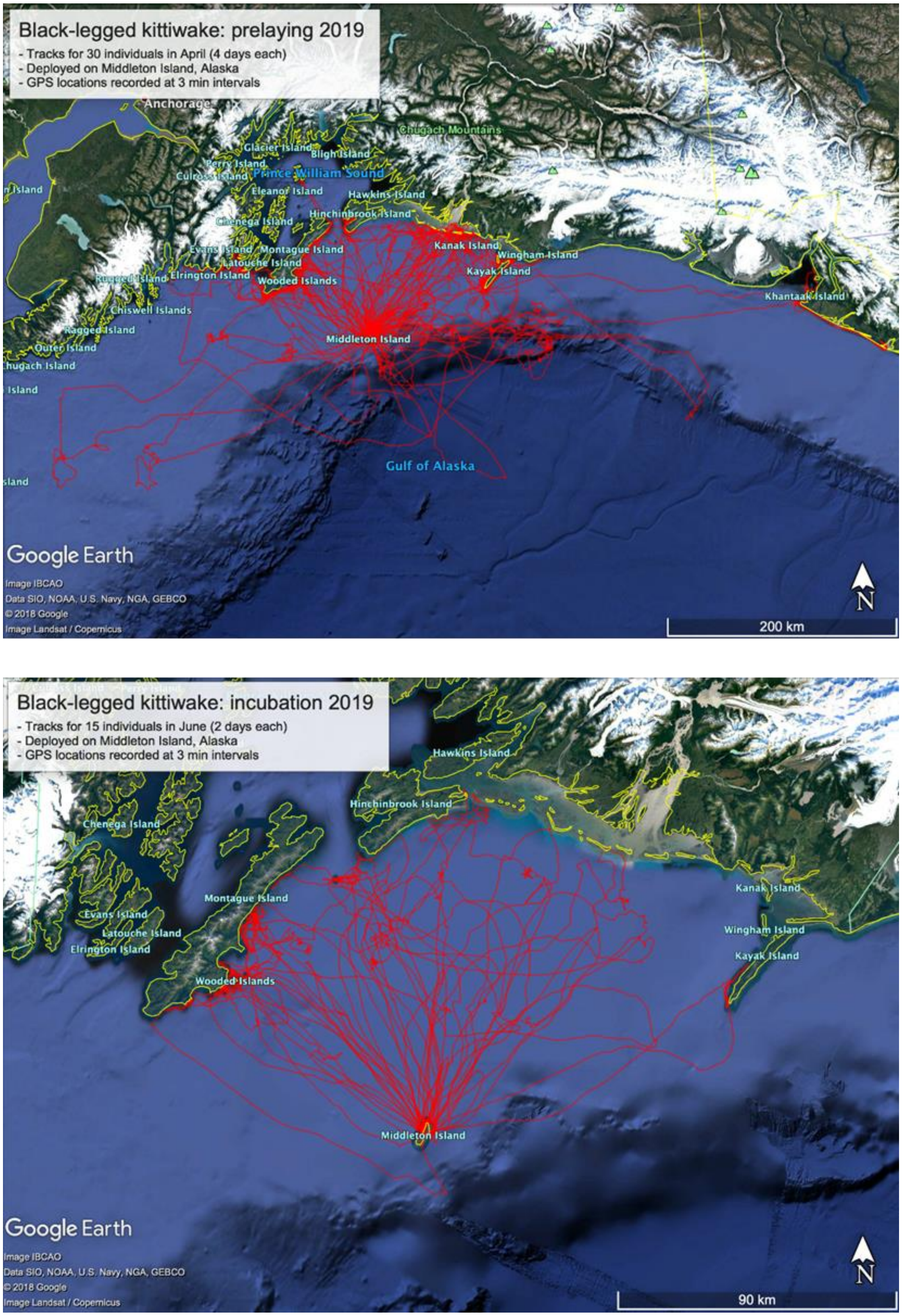

Figure 8. Foraging areas of Middleton Island kittiwakes during the prelaying period (upper panel) and incubation (lower panel) as revealed by GPS tracking devices deployed on 45 individuals in 2019.

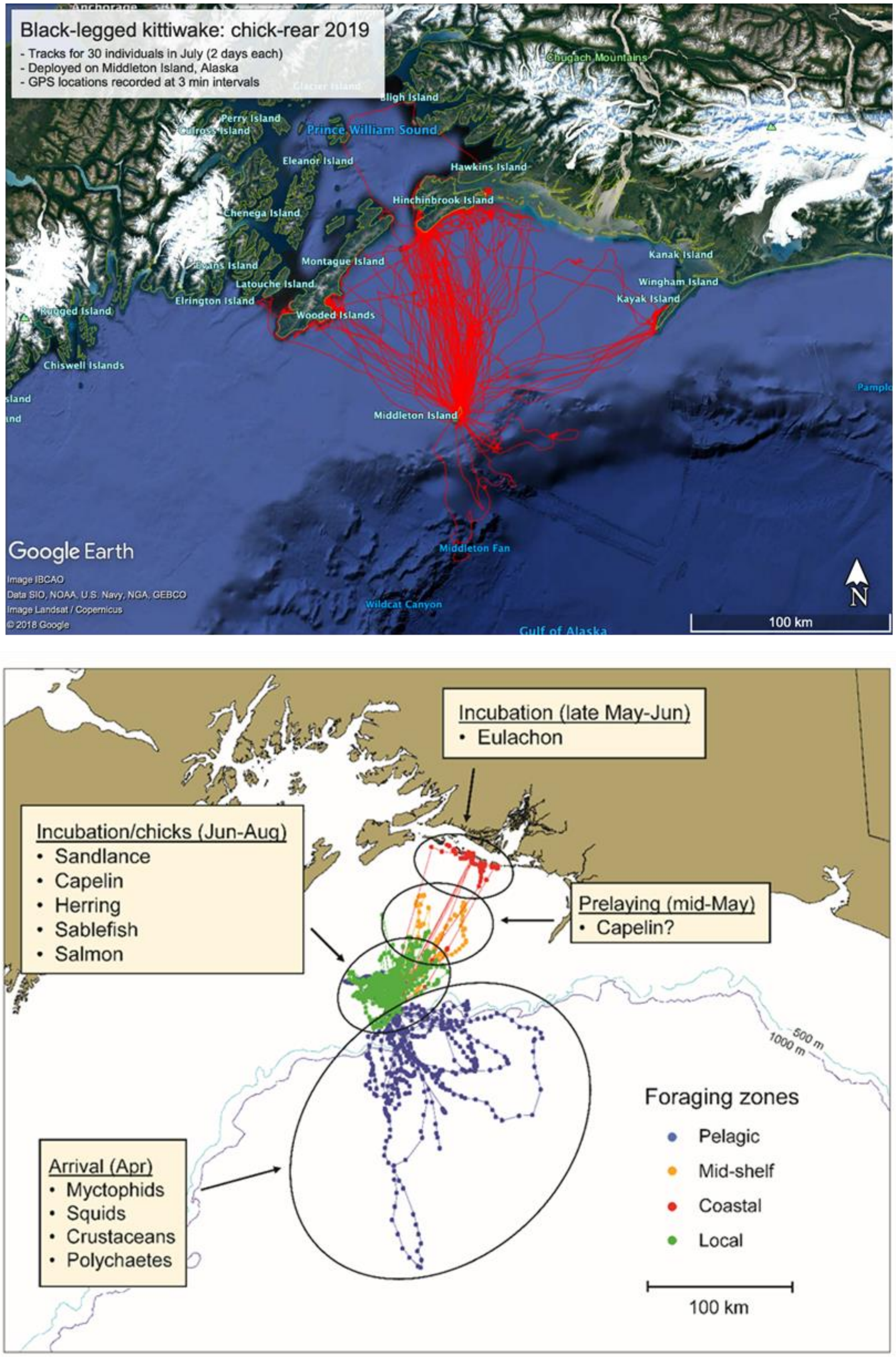

Figure 9. Foraging areas of Middleton Island kittiwakes during chick-rearing in 2019 (upper panel), and for comparison, use of pelagic and neritic foraging habitats by Middleton kittiwakes according to stage of breeding in 2008.

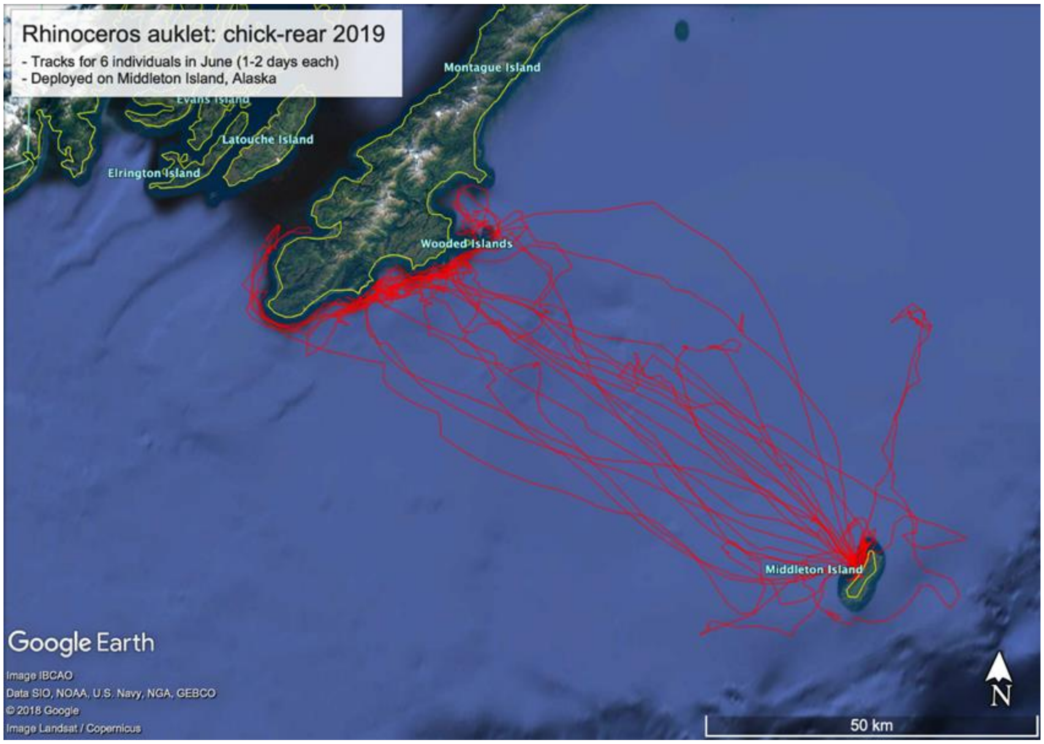

Figure 10. Foraging areas of rhinoceros auklets during chick-rearing as revealed by GPS tracking devices deployed on 6 individuals in 2019.

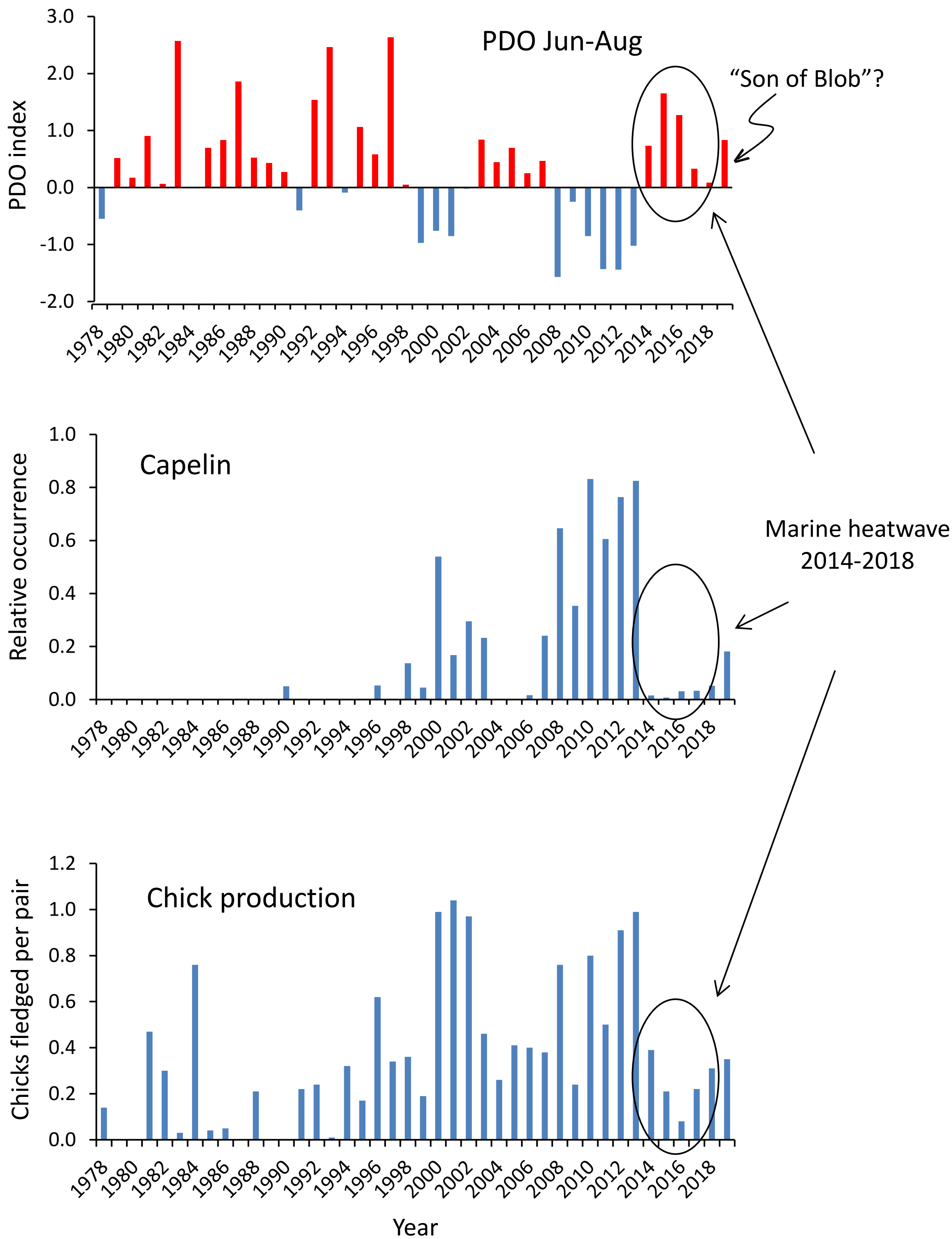

Figure 11. Relations among the Pacific Decadal Oscillation (PDO) index (June – August), the relative occurrence of dietary capelin, and the annual production of chicks by kittiwakes on Middleton Island, 1978 to 2019. Missing data denoted by ‘x’.

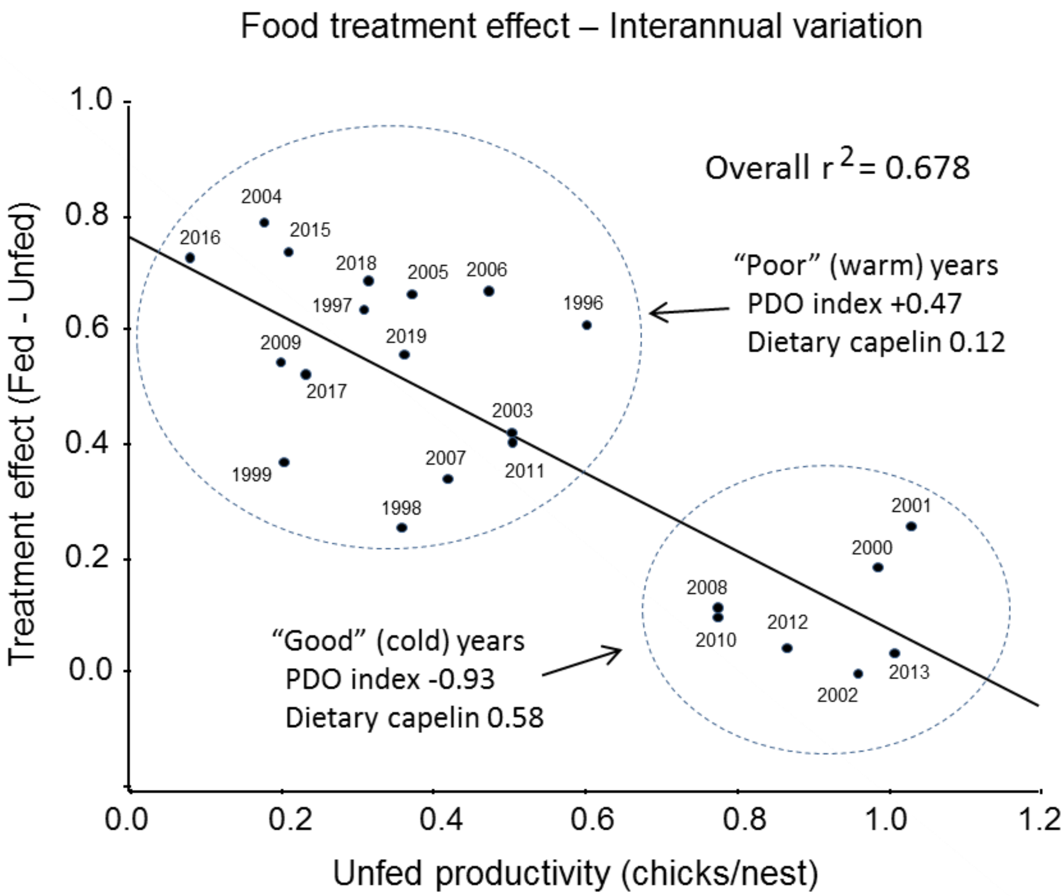

Fig. 12. Effect of supplemental food treatment on kittiwake breeding performance on Middleton Island in 23 years since 1996. Productivity of unfed pairs is a proxy for quality of the foraging environment. Treatment effect is the difference in productivity between supplementally fed and unfed pairs. "Poor" 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.

Appendix Fig. 1. Nest boxes for rhinoceros auklets and tufted puffins are being installed at the Middleton station to facilitate future research and monitoring of these species.