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Predation and food-weather interactions drive colony collapse in a managed metapopulation of Arctic Terns (*Sterna paradisaea*)

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Predation and food-weather interactions drive colony collapse in a managed metapopulation of Arctic Terns (*Sterna paradisaea*). L. C. Scopel and A. W. Diamond.

Abstract

Seabirds are considered bioindicators of bottom-up ecosystem processes, owing to seabirds' dependence on marine prey. However, ground-nesting seabirds are susceptible to predation, which can limit their use as bioindicators. Machias Seal Island (MSI) supported the largest colony of Arctic Terns (*Sterna paradisaea* Pontoppidan, 1763) in the Gulf of Maine metapopulation, but prolonged breeding failure led ~90% of terns to abandon the colony in 2006. We analyzed twelve years of food, weather and predation data using logistic regression models to determine which had the strongest influence on breeding success. Food-weather interactions were important; under low rainfall, more euphausiids (*Meganyctiphanes norvegica* Sars, 1857) in the diet increased breeding success, but euphausiids had a negative effect as rainfall became moderate or high. Predation by Herring Gulls (*Larus argentatus* Pontoppidan, 1763) increased following the cessation of lethal predator control; we identified a predation threshold of 25%, beyond which terns could not breed successfully. The collapse of MSI's tern colony can be attributed entirely to gull predation. The breeding success of terns at MSI cannot be used as a bottom-up ecosystem bioindicator without accounting for predation. Managers of ground-nesting seabirds should consider predation and food as equally valid potential causes of population or reproductive declines.

Keywords: predator management, bioindicator, bottom-up ecosystem control, topdown ecosystem control, Arctic Tern, *Sterna paradisaea*, conservation

44 Introduction

45 Seabirds are regarded as important bioindicators or sentinels of changes in marine ecosystems, owing to
46 seabirds' dependence upon marine prey (Bost and Le Maho 1993; Piatt et al. 2007). Aspects of seabird
47 foraging and demography may serve as a proxy for ecosystem processes if the relationship between them
48 is strong (Durant et al. 2009). The quality of seabird species as bioindicators varies based on their size
49 and foraging ecology, where small, surface-feeding seabirds like terns and kittiwakes are less able to
50 overcome poor foraging conditions to support their young (Pearson 1968; Furness and Tasker 2000), and
51 thus provide an honest signal of foraging quality. In the North Atlantic, terns and kittiwakes are thus
52 likely to be the first seabirds to show a negative response in their breeding success when foraging
53 conditions deteriorate (Monaghan 1992; Frederiksen et al. 2008). Sudden negative responses in tern or
54 kittiwake reproduction or abundance may therefore indicate negative changes in the local marine
55 environment (Monaghan 1992; Wanless et al. 2007).

56 Breeding Arctic Terns (*Sterna paradisaea* Pontoppidan, 1763) cannot compensate for food shortage;
57 both adults in a pair must spend most of their time budgets foraging for chicks (Pearson 1968; Kirkham
58 1986), and may abandon a breeding attempt mid-season if there is insufficient food (Langham 1968;
59 Monaghan et al. 1989). Food shortage can manifest as a lack of high quality prey early in the breeding
60 season, leaving adults with fewer energy reserves (Monaghan et al. 1989; Wendeln and Becker 1999), or
61 as insufficient energy density in the available prey to sustain chicks during rearing (Dunn 1975; Massias
62 and Becker 1990; Wanless et al. 2005). The highest quality prey are fish with a high lipid content (e.g.
63 Atlantic herring (*Clupea harengus* L., 1758), Budge et al. 2002), but Arctic Terns feed their chicks lower
64 quality invertebrate prey at high rates when higher quality prey are not available (Hawksley 1957;
65 Kirkham 1986). For Common Tern chicks (*S. hirundo* L., 1758), invertebrate prey can result in a net loss
66 of chick mass if fed for a long period of time (Massias and Becker 1990), but Arctic Terns can fledge
67 chicks successfully on a diet composed primarily of invertebrates in spite of the higher foraging cost
68 (Schubel 1992; North 1994).

In addition to their sensitivity to changes in prey, small-bodied ground-nesting species like terns are particularly vulnerable to predators (Lavers et al. 2010), which can confound their use as bioindicators (Furness and Tasker 2000). When terns cannot deter predators, they will abandon a breeding attempt, and sometimes disperse permanently from a colony if predation is severe (Austin 1940; Donehower et al. 2007). Further complicating matters, food and predation can have interactive effects on seabird populations and exacerbate poor conditions (Regehr and Montevecchi 1997).

The influence of food on breeding success is the quintessential interaction between seabirds and the marine environment, and is the focus of studies investigating seabirds as bioindicators (Cairns 1987). A common criticism of using of seabirds as bioindicators is that the relationship between ecosystem processes and seabird responses must be simple, clear and strong to be useful (Durant et al. 2009; Grémillet and Charmantier 2010). Although high predation pressure can indicate increased food stress for predators of seabirds, top-down influences on seabirds obfuscate the interaction of interest between seabirds and forage fish communities. Exclusive focus on food may lead the impact of predation on breeding success to be overlooked, to the point of recommending the removal of high predation colonies or years from a dataset (Parsons et al. 2008). Predation is often dismissed without quantitative assessment of its impact at a colony, even though some consider predation to be the most important determinant of breeding success (Côté and Sutherland 1997; O'Connell and Beck 2003; Kress and Hall 2004). Although bottom-up and top-down factors have been identified as major forces affecting seabird populations, they are rarely considered together in quantitative analyses (but see Suryan et al. 2006; Oro and Pradel 2012). The lack of attention given to predation in the context of other aspects of seabird ecology makes the impact of predation difficult to estimate (but see Lavers et al. 2010).

The Gulf of Maine (hereafter GOM) supports a well-studied metapopulation of Arctic Terns (Devlin et al. 2008). This metapopulation was stable throughout the 20th century, largely owing to three colonies that were historically protected by lighthouse keepers (Drury 1973; Anderson and Devlin 1999). Although the increase of large *Larus* gulls limited the breeding habitat for small seabirds during the mid and late 1900s,

the persistence of these three colonies protected the Arctic Tern metapopulation from sharp declines that were observed in the other seabird populations in this region (Drury 1973; Korschgen 1979). Since the initial expansion of the large gull populations and ranges in the 1920s, smaller seabirds like terns have been forced into nesting at the few managed sites (Drury 1973); in 2014, 98% of Common Terns and 100% of Arctic Terns nested at managed colonies owing to a lack of suitable gull-free tern habitat in the GOM. While the lack of unoccupied alternative sites is unusual, gull management has been performed since the early 1900s in the GOM, and represents the most effective way to protect terns in this region (Kress and Hall 2004).

Machias Seal Island (MSI) represented the largest Arctic Tern colony in the GOM, and was the largest Arctic Tern colony in North America (Gaston et al. 2009). Notes from lighthouse keepers indicate that the colony was large and generally stable, but breeding was negatively affected by bad weather, food shortage, predation by Herring Gulls (*Larus argentatus* Pontoppidan, 1763), and human interference (MacKinnon and Smith 1985). In spite of these setbacks, breeding failure (<0.1 chicks fledged per nest) was rare, and abandonment of the colony was recorded only once, in 1944. In spite of the stability of this colony and increases projected by Devlin (2006), MSI experienced breeding failure for nine consecutive years (2005-2013); 90% of the tern colony abandoned in 2006 (Gaston et al. 2009). Given that chronic low productivity can trigger dispersal in many birds (Greenwood and Harvey 1982; Burger 1984; Danchin et al. 1998), we consider the crash in breeding success to be the impetus for the terns' dispersal. Although the MSI terns initially dispersed to other monitored colonies in the metapopulation (especially Petit Manan Island, Fig. 1), the number of Arctic Terns in the GOM has declined by 56% since 2004. In light of changing oceanographic conditions in this region (Greene and Pershing 2007; Nye et al. 2009), the sudden loss of this colony may signal that environmental conditions in the GOM have reached a critical threshold where terns can no longer breed successfully.

The collapse of MSI's tern breeding success was attributed to some combination of poor food, poor weather, and high predation (Diamond 2009; Gaston et al. 2009), but the individual contributions of these

factors were unclear. The virtual disappearance of herring from the tern diet on MSI was suspected to be a major contributing factor (see Fig. S1 in Supporting Information¹). Our objective was to determine the relative contributions of food, weather, and predation to the decline in breeding success at MSI's tern colony. We developed three hypotheses:

- 1.) Breeding success declined because of a loss of high-quality fish from the tern diet.
- 2.) Breeding success declined because of more frequent bad weather.
- 3.) Breeding success declined because of increased predation by gulls.

Materials and Methods

MSI is a 9.5 ha island located ~20 km southwest of Grand Manan Island, New Brunswick, Canada. A.W.D. has conducted seabird monitoring on MSI since 1995 (Diamond and Devlin 2003, protocol available at <http://www.unb.ca/research/alar/msi-seabirds/protocol-methods.html>, data summaries available at <http://www.unb.ca/research/alar/msi-seabirds/data-summaries.html>). Field work was approved annually by the Animal Care Committee at the University of New Brunswick. The island has operated as a lighthouse station for the Canadian Coast Guard since 1832, and permanent buildings and boardwalks are located at the centre of the colony to permit year-round occupation. Terns have nested at the colony since at least 1873 (Kress et al. 1983; MacKinnon and Smith 1985). Researchers arrived on the island in early May and departed in mid- to late August. Temporary research blinds were erected around the island for the duration of the monitoring season. In addition to the terns, there were other seabird species on the island, totaling roughly 10,000 pairs of birds.

Food

Arctic terns bring food to their chicks one item at a time, carried visibly in the bill. Prior to hatch, a subset of nests at two or more research blinds was selected for feeding observations, based on their

¹ Please see supporting information for more information.

proximity and visibility from research blinds. Observers watched up to eight nests for 3 hour periods, recording the number of feedings, the species of prey, the length of the item relative to the adult's bill length, and the number of hours each chick was observed. Prey specimens were collected opportunistically to determine length-mass relationships for each prey species; these conversions were retroactively applied to prey deliveries to estimate the wet mass (g) of each prey sample. For frequently observed species (herring, white hake (*Urophycis tenuis* Mitchell, 1814), butterfish (*Poronotus triacanthus* Peck, 1804), sand lance (*Ammodytes* spp. Bonaparte, 1832), euphausiid (*Meganyctiphanes norvegica* Sars, 1857), haddock (*Melanogrammus aeglefinus* L., 1758), and larval fish), annual wet masses were estimated to compile metrics of prey quality and quantity for each season. Taxon estimates were represented as annual rates (mass (g) feeding⁻¹ and mass chick-hour⁻¹) and as a proportion of total diet. Since few or no chicks hatched during 2006-2013, feeding observations were not performed, and no prey data were collected. Feeding data from coexisting Atlantic Puffins (*Fraterecula arctica* L., 1758) were collected during all years, and serve as a qualitative estimate of prey abundance from 2006-2013 (Table S1¹). Please see Table S2¹ and Appendix SA¹ in SI for more detail about provisioning data, including methods and prey conversion formulae¹.

Prey abundance, prey quality, and foraging behaviour have all been identified as important aspects of seabird diet (Wanless et al. 2005; Jodice et al. 2006; Olsson et al. 2008). To account for these different aspects of diet, we compiled several prey metrics: good quality food, poor quality food, quantity of food, and feeding rate. Herring, sand lance, and hake were considered "good quality" food, encompassing metamorphosed fish that have high energy density. Euphausiids, larval fish, and butterfish were considered "poor quality" food. Invertebrates and larval fish have lower energy density and are smaller than metamorphosed fish, requiring a higher feeding rate to sustain chicks. Butterfish, although high in energy density, are too deep-bodied to be consumed by most tern chicks. Haddock were observed only in 2014. An independent estimate of numbers of juvenile herring in the Bay of Fundy was provided from the Department of Fisheries and Oceans virtual population analysis (hereafter VPA).

Weather

Researchers collected weather data daily at 9:00 and 21:00 during each breeding season. Data included air temperature, wind speed, and precipitation. We divided weather metrics into three periods of the breeding season: pre-lay (May), incubation (June), and chick rearing (July). Two additional time periods were included for the first and second weeks post-hatch, when chicks are unable to thermoregulate (week 1) or are too large to be brooded by their parents (week 2) and thus may be more susceptible to exposure (Langham 1968; Dunn 1975; Paquet 2001). Many studies report most chick mortality during the first 5-10 days of life (e.g. Hawksley 1957; Langham 1972).

Predation

The history and rationale of MSI's predator control regime is described in Scopel and Diamond (2017). During 1995-1999, the Canadian Wildlife Service performed targeted lethal control of predatory large gulls as needed during the breeding season. During 2000-2012, lethal control was suspended and only nonlethal control (scaring and nest destruction) was permitted. Limited lethal control was resumed in 2013-2015. These different approaches to predator management serve as an inadvertent experiment to investigate the importance of lethal control at MSI.

Individual gulls vary in their propensity to depredate tern eggs, because only 1-4% of gulls specialize in seabird prey (Spear 1993; Hario 1994; Guillemette and Brousseau 2001). Consequently, gull abundance is a poor predictor of predation intensity. Instead, we measured the proportion of eggs that were depredated or disappeared from our monitored productivity plots (Fig. S2¹); MSI has no other predators of tern eggs. We could not estimate chick predation accurately, and so our models use estimates of egg predation only.

Response variables

Breeding success of Arctic Terns was recorded in all years in fenced and unfenced plots in different vegetation types on the island. Fenced plots around the periphery of the island were not erected after

2006 because the area of the tern colony decreased following abandonment, and thus these plots had no terns nesting in them. Plots were checked daily beginning in late May of each year, and followed at least through mid-July to check for clutch initiations and egg predation. After hatch, plots were checked every 1-3 days, depending on weather. Each egg laid was followed to determine its fate (failed, hatched, fledged). Chicks that hatched were also banded at hatch and measured for wing chord and mass at least twice during their linear growth period (day 5-15). Chicks seen alive through day 15 were considered fledged, subtracting any later found dead. Chicks that disappeared before day 15 were considered dead. Two metrics of breeding success were compiled: the proportion of nests that fledged at least one chick (nest success), and the number of chicks that each nest fledged successfully (productivity: zero, one, or two). We were interested in the decrease of successful nesting by terns after 2000, and a binary response was the simplest way to investigate the predominant change in reproduction on MSI. However, Arctic Terns on MSI rarely fledge two chicks in a season, and we hypothesized that exceptional years may lead to higher productivity per nest, which may be overlooked when using a binary response variable. Adults may change their foraging effort at hatch depending on their perception of their ability to raise more than one chick, and second- or third-hatched chicks may be left to starve early in rearing, in spite of low energetic requirements then (Langham 1972; Safina et al. 1988; Monaghan et al. 1992). We thus performed a second analysis using a trinomial response for number of chicks fledged to investigate conditions that led to greater production. We treated each response group as an independent outcome by allowing the slopes for each response to vary to account for potential behavioural differences between adults at 1- and 2-chick nests.

Breeding success on MSI was 0 (complete breeding failure) from 2006-2013, precluding analysis of these years. Please see Table S3¹ for a complete summary of reproductive data used in these analyses.

Analyses

We hypothesized that food, weather, and predation each contributed to the collapse of MSI's tern colony, and thus wanted to compare these hypotheses directly using Akaike's Information Criterion corrected for small sample sizes (AICc). A preliminary set of predictor variables was developed, for relevant food, weather, and predation data (Table S4¹). Clutch size data were also included to correct for annual variations in clutch size. Data were normalized. Correlations between predictor variables were checked for multicollinearity and were noted if >0.5 and flagged if >0.7 (Tabachnick and Fidell 2013). Flagged variable pairs were not included in models together.

We used logistic regression models to assess changes in annual breeding success (hereafter "nest analysis"). Individual covariates were not available for all nests, so the response data were grouped by year into counts of successful (1) or unsuccessful (0) nests for 12 years of data (1995-2005, 2014). We used multinomial logistic regression to assess changes in the number of chicks fledged per nest for these 12 years of data (hereafter "productivity analysis").

We developed a series of global models following a consistent pattern of food, weather, and predation influences on breeding success:

Breeding success ~ good food + poor food + weather1 + weather2 + predation + interaction

We hypothesized five *a priori* two-way interactions between food, weather, and predation (Table S4¹), but included only one interaction per model for ease of interpretation. For further details on the rationale behind included interactions, see Appendix SB¹. We hypothesized two quadratic relationships: feeding rate and wind speed (Dunn 1975). All models with interactions or quadratic terms included the associated main effects (Aiken and West 1991). Goodness of fit was assessed using our hypothesized best global model, including herring, euphausiid, predation and rain metrics. Goodness of fit was estimated by G^2 and was 2.4912 ($P=0.78$, $df=5$) and 9.1913 ($P=0.51$, $df=10$) for the nest and productivity analyses, indicating a reasonable fit and no overdispersion (Agresti 2007). Tolerances for global models were checked following Quinn and Keough (2002 p. 128), and variable pairs <0.2 were flagged. Tolerance is

237 calculated by computing $1-r^2$ of predictor X_i against the other predictor variables in a model; it represents
238 the overlap in explained variance between predictors included in the same model.

239 For the nest analysis, global models were developed using the `glm()` function in R 3.1.2 ([http://cran.r-](http://cran.r-project.org)
240 [project.org](http://cran.r-project.org)). Global models were run using the dredge function (package MuMIn v.1.10.5, Bartoń 2014)
241 to include all subsets of these global models. Dredge results were collated and redundant models were
242 removed. For the productivity analysis, global models were developed using the `vglm()` function
243 (multinomial family) in package VGAM (Yee 2015). Results of all models were collated and ranked
244 (Appendix SC¹). Model fit of highly ranked models was checked *a posteriori* by comparing the residual
245 scaled deviance to the residual df (Agresti 2007).

246 Our confidence set of models was cut off at 95% of cumulative model weight (Burnham and Anderson
247 2002, p. 169), but we reported results up to $\Delta 15$ AICc. Models were further examined for pretending
248 variables (Anderson 2008, p.65) and potential outliers by examining residuals, leverage, and influence
249 (Fox and Weisberg 2011). If no interactions were present in the confidence set, parameters were model
250 averaged. Confidence sets with interactions were not model averaged, but interactions were plotted to
251 illustrate the shape of the interaction. Parameter coefficients (log-odds) were plotted to estimate the effect
252 size of each predictor. The log-odds were also converted into Cohen's *d* for a standardized estimate of
253 effect size (Borenstein et al. 2009). After the confidence set was generated, 2015 data were input into the
254 model set to assess its predictive ability. Observed data in 2006-2013 could be used as a test set of data,
255 using puffin data if the model included either no food parameters or euphausiids only, but models with
256 other food parameters could not be predicted, owing to poor correlations between puffin and tern diet data
257 (Table S1¹).

258 Although Burnham and Anderson (2002) caution strongly against trying many models relative to a small
259 sample size, we put much *a priori* thought into model structure to minimize the chance of spurious
260 results. Furthermore, the implications of the collapse of the MSI tern colony were grave for the
261 conservation of Arctic Terns in the GOM; rather than risk the chance of a Type II error by keeping the

number of potential models low, we instead chose to create models from our large dataset to fully investigate potential leads regarding the collapse of the MSI tern colony. To account for potential prediction error, we performed a leave-one-out cross-validation on well-supported models to examine potential prediction outliers.

Results

Variable selection

A list of variables was removed from consideration owing to redundancy between metrics, high correlations, or lack of relevance (Table S4¹). June and July weather data were highly correlated, and were thus not included together in models. A strong negative correlation was also discovered between clutch size and predation (Table S5¹), which precluded the use of clutch size in the analyses. Moderate correlation was also observed between good food and predation parameters, but was not strong enough to preclude the usage of either; we do take these correlations into consideration when interpreting the results.

Nest analysis – proportion of successful nests

The final candidate set produced one model with 97% of the weight (Table 1). The 2002 data point had high influence, owing to the high incidence of euphausiid mass feeding⁻¹ that year (>2 SD). However, removal of 2002 from the dataset and re-analysis of the data with the same models still gave the top-ranked model 88% of the weight (Table S6¹) and the slopes were similar (Table S7¹). Although high incidence of euphausiids during a season is uncommon, it does occur occasionally, and we therefore kept the 2002 data in the model. Cross-validation suggested that prediction error for this model was very low, and all data points were consistent (Table S8¹), with low prediction error (Fig. S3¹).

Examination of the interaction between euphausiids and rain showed that rain was a moderating variable between euphausiids and nest success (Fig. 2). Qualitative levels of each interaction were notated using the mean $\pm$ one standard deviation for each level (mean = moderate, -1 SD = low, +1 SD = high). Under

low rainfall, more euphausiids in the diet led to greater breeding success, but euphausiids had a negative effect on breeding success at moderate or high levels of rain.

Owing to the high weight attributed to the top-ranked model, we extracted coefficients from only this model (Fig. 3) instead of for a larger model set following Burnham and Anderson (2002) for models with >90% model weight. Data from 2006-2013 (using puffin euphausiid data as a proxy) and 2015 were input into the model to examine its predictive ability (Fig. S4¹).

Productivity analysis - number of chicks fledged

The final confidence set included four models, where the top-ranked model received 40% of the weight (Table 2). Three models included interactions and the fourth included a quadratic term, so model averaging was not appropriate. We instead included the effect sizes for terms in each model (Figs S5-S12¹), plots of the interaction or quadratic term (Fig. S13-S16¹), and a comparison of model-predicted and real values (Figs S17-S20¹); all models had complex food parameters, so 2006-2013 data could not be predicted. The 2015 data were poorly predicted by three of the four models.

Diagnostics showed that 2000 was an outlier in three of the four top-ranked models. However, removal of 2000 data made parameter estimates for the two-chick level unstable. All years were thus retained, but results are interpreted qualitatively only and are not suitable for quantitative prediction. Given this issue with outliers, prediction error was likely very high, and we did not perform cross-validation.

Discussion

The high rank of food, weather, and predation parameters indicates that all contribute to breeding success on MSI. The presence of interactions supports the idea that relationships between indicator species and their environment are not simply linear (Durant et al. 2009; Lepetz et al. 2009).

Food quality, rain, and their interactions

The interaction between euphausiids and rain during early chick rearing was highly ranked in both

analyses. We suggest that this interaction illustrates an effect of parental foraging behavior on chick survival. Chicks are unable to thermoregulate well during the first week of life and are brooded frequently (Klaassen 1994), yet parents delivering a high proportion of euphausiids must feed their chicks more frequently to sustain their chicks, leaving little time for brooding. In periods of good weather, leaving the chick alone for long periods will have little effect on chick survival; chicks are cryptic and will hide in vegetation beginning at a few days of age. As cold or rainy weather increases, however, chicks left alone at the nest are more susceptible to chilling and death by exposure (Langham 1968). On MSI, rain elicits a brooding response from adult terns, and rain was the only environmental variable of five that led terns to alter their time budgets to incorporate more brooding (Paquet 2001). Inclement weather also makes foraging more challenging for adults (Hawksley 1957; Langham 1968; Becker and Specht 1991), and can reduce their foraging efficiency. It is thus not food quality that is problematic for chicks receiving euphausiids in poor weather, but impossible demands on parental time budgets. It is possible that increased metabolic costs during rainy weather require more energy than euphausiids can provide (Dunn 1975; Becker and Specht 1991), but chicks at this stage of rearing have low energy demands (Klaassen et al. 1989). Arctic Terns are capable of raising multiple chicks on a primarily euphausiid diet, as was observed during 2002, when euphausiids represented 70% of the diet by mass. The assessment of food quality as a function of weather is therefore important to consider – although herring are considered the best available prey for seabirds in the GOM (Diamond and Devlin 2003), our results suggest that for terns, food quality becomes relevant only when foraging conditions are poor; euphausiids should not always be considered poor quality prey for Arctic Terns. An examination of this relationship in further detail would elucidate its mechanism, which is only speculated here.

The weak support for herring and other high quality food was unexpected. In the productivity analysis, although high quality food was part of the top-ranked model, the effect size of good food was small relative to weather and predation, indicating that food quality is important only when poor weather and predation are minimal. Furthermore, high quality food had no effect on nest success or on one-chick

333 nests, indicating that food quality will determine only how many additional chicks can be fledged. This is
334 consistent with observations of tern productivity in the GOM, where first-hatched chicks are
335 preferentially fed higher quality items (North 1994) and later-hatched chicks usually die of starvation
336 (Hawksley 1957). Given that the top-ranked models in both analyses show a positive effect of
337 euphausiids when weather is good, our results suggest that Arctic Terns on MSI do not always require
338 prey with a high energy density. The moderate correlation between predation and good food metrics may
339 mask the importance of good food, but even quantitative measures of diet were not well supported. High
340 quality food may be especially important prior to breeding – in the nest analysis, although none of the
341 seabird-derived “good food” metrics ranked highly, the availability of herring regionally (from the VPA)
342 performed much better. This could indicate that food quality for adults – a variable not measured in these
343 analyses – is a key factor in their breeding performance, and may be linked more strongly to reproductive
344 metrics from earlier in the breeding season, such as clutch size or adult mass (Langham 1968; Evans and
345 McNicholl 1972; Monaghan et al. 1992). We conclude from our results that food is a secondary factor to
346 Arctic Tern breeding success, and was not the main cause of colony abandonment at MSI.

347 If herring availability is important to adult tern condition, future oceanographic changes could be a major
348 cause for concern. Copepods make up the majority of the juvenile herring diet (Last 1989; Pedersen and
349 Fossheim 2008), but increasing temperatures in the GOM could affect the timing of their emergence from
350 winter diapause, and lead to trophic mismatches (Johnson et al. 2011). Predicting the effects of climate
351 change on fish population dynamics is difficult, and cod provide a cautionary tale for fisheries (McQuinn
352 2009; Pershing et al. 2015); future quotas for the herring fishery in the GOM should be extremely
353 cautious, in light of potential effects on seabirds in the GOM (Breton and Diamond 2014). A variety of
354 potential marine prey – rather than one essential prey species – is likely one of the most important factors
355 to seabird success in the GOM.

356 Weather during the first week of chicks’ lives was included in each of our highest ranked models. Rain
357 during chick rearing has increased at MSI (Fig. S21¹). This has major implications for young chicks, but

it is also a natural phenomenon to which terns can adapt. A higher frequency of storm events, as is expected in climate change projections (Stocker et al. 2013), could leave terns with less resilience to environmental stochasticity, but alone is unlikely to cause abandonment. Our results indicate that rain can contribute significantly to chick mortality, can influence the relationship of food to nest success, and can severely hinder the likelihood of successful two-chick nests; for ground nesting species, then, weather is a critical consideration for breeding success.

Predation

Predation was also included in each of our highest ranked models. In the nest analysis, every 10% increase in predation leads to a 4.09 odds increase of nest failure. Based on the model, exceeding ~25% depredation at MSI leads to colony breeding failure under most scenarios, regardless of weather. This is consistent with observations by Austin (1940) at large tern colonies in Cape Cod, and is likely related to a loss of synchronized anti-predator response under chronic predation (Monaghan et al. 1989; Becker 1995). Furthermore, our results indicate that the collapse of breeding success at MSI can be attributed to just the effects of gulls: during the failure years from 2006-2013, years of low rainfall and good food (for alcids) were observed, yet predation consistently exceeded 50% in all years, well beyond the tolerable threshold of 25%. The hypothesis that gull predation alone was responsible for the colony collapse was confirmed following the resumption of lethal predator control on MSI in 2013 and 2014, which was followed immediately by reduced predation, better attendance behaviour, and a successful breeding season in 2014, the first since the collapse (L. Scopel and A. Diamond, unpublished data). We therefore identify predation as the definitive cause of the collapse of the MSI tern colony, and reduction of predation to pre-abandonment levels was the impetus for colony recovery at MSI. The initial increase in predation at MSI in 2000 can be attributed to the cessation of lethal control that year, and is consistent with studies following the cessation of lethal control at other sites (Côté and Sutherland 1997; Anderson and Devlin 1999).

382 Although natural predators are rarely the sole cause of population declines in their prey (Burger and
383 Gochfeld 1994; Côté and Sutherland 1997), the effects of gull predation are enhanced in the GOM.
384 Although terns naturally disperse from sites where predation is chronic, viable alternative sites no longer
385 exist in this region owing to displacement from preferred nesting habitat by gulls (Nisbet et al. 2013).
386 Persistent tern colonies attract chronic predation (Burger 1982; Jackson and Jackson 1985), and thus face
387 reduced breeding success in perpetuity. Furthermore, declines in the regional population of the *Larus*
388 gulls are attributed to declining sources of anthropogenic food (Cotter et al. 2012; Nisbet et al. 2013).
389 Generalist predators may switch to seabird prey in the absence of preferred natural or anthropogenic prey
390 (Regehr and Montevecchi 1997; Votier et al. 2004), which would further increase predation at existing
391 colonies. In the GOM, the only effective way to reduce predation pressure is to perform selective lethal
392 control of specialist individuals (Kress and Hall 2004). The success of lethal control in restoring breeding
393 success to MSI is encouraging, but requires implementation indefinitely, and does not address the
394 regional problem of gull overpopulation.

395 Increased predation and precipitation during early chick rearing represent crucial future issues for terns in
396 the GOM. Our models indicate that MSI terns have reduced nesting success if predation and rain are
397 high, and these terns cannot fledge more than one chick if moderate levels of either occur. Our models
398 also indicate that food quality becomes an important consideration when weather during chick rearing is
399 poor, meaning that breeding success of terns is increasingly dependent upon good food, good weather,
400 and low predation just to fledge one chick. The higher predation under limited lethal control and higher
401 precipitation in the past decade both leave smaller margins for the terns to succeed, leave little chance of
402 rescue by way of high production during good years, and ultimately increase the likelihood of colony
403 failures or declines. Extended periods of poor weather and high predation could further reduce the Arctic
404 Tern metapopulation in the GOM.

405 These models suffer from small sample size, but for the purposes of investigating the collapse of the tern
406 colony, we find these data to be sufficient. Further application of these models to other Arctic Tern

colonies in the GOM will improve their reliability at a broader spatial scale. For further discussion of the importance of lower-ranked interactions in this analysis, please see Appendix SB¹.

Arctic terns as bioindicators

Our results provide an important counterpoint to the use of seabirds as bioindicators of bottom-up ecosystem change. For terns in the GOM, where predation by gulls is prevalent, our ability to use tern breeding success as an indicator of bottom-up ecosystem change is called into question. MSI terns are affected much more strongly by top-down control and weather, which confounds their use as indicators of bottom-up change. The only species of 14 considered by Cury *et al.* (2011) that did not show a significant threshold response of breeding success to forage fish abundance was the Arctic Tern, consistent with our result that breeding success of Arctic Terns is determined by more than just food; the relationship of food to reproductive success is moderated by weather. We found no evidence to support the hypothesis that MSI's tern colony collapsed because of a decline in herring availability.

Evidence of strong top-down control does not preclude bottom-up control, however, and predatory gulls are likely also affected by bottom-up forcing. Interactions between terns and gulls in this region are complex, and would not be represented adequately by a simple indicator metric. In spite of these complexities, we highlight the importance of considering both top-down and bottom-up forcing on a potential indicator species; a desire to ignore "extraneous" factors like predation in order to provide a cleaner indicator metric can misrepresent ecological relationships. For small, ground-nesting seabirds, we recommend that the importance of predation is given equal *a priori* consideration to the importance of food in the case of population or reproductive declines.

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Draft

641 Figure 1. Map of the five major Arctic Tern (*Sterna paradisaea*) colonies in the Gulf of Maine metapopulation.
642 Colonies include Metinic Island, Maine (MI), Matinicus Rock, Maine (MR), Seal Island, Maine (SI), Petit Manan
643 Island, Maine (PMI), and Machias Seal Island, New Brunswick (MSI).

644

645 Figure 2. Interaction plot of nest success as a function of euphausiid mass feeding⁻¹ in the Arctic Tern (*Sterna*
646 *paradisaea*) chick diet and rain during the first week of a chick's life. Data are normalized; 0 represents the mean.
647 Qualitative rain categories designate mean ("Medium") and +/- 1 SD ("High"/"Low") values. Plots represent low (A),
648 moderate (B), and high (C) predation, based on mean (B) +/- 1 SD (C,A). Dashed lines represent 95% confidence
649 intervals.

650

651 Figure 3. Effect sizes for coefficients in the top ranked model from the analysis of nest success of Arctic Terns (*Sterna*
652 *paradisaea*) at MSI – log odds (A) and Cohen's *d* (B). Error bars represent 95% CIs.

Main text tables for:

Predation and food-weather interactions drive colony collapse in a managed metapopulation of Arctic Terns (*Sterna paradisaea*)

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Table 1. Final AICc output table for analysis of nest success of Arctic Terns (*Sterna paradisaea*); the confidence set is shaded, but results report up to $\Delta 15$.

ID	<i>k</i>	AICc	Δ AICc	Weight	Log-Lkhd	R^2	Good food	Bad food	Weath. 1	Weath. 2	Pred.	Interaction
2	5	79.71	0.00	0.970	-29.85	0.98		Euph feed ⁻¹	Rain Wk1		Y	Euph-Rain
4	5	88.37	8.66	0.013	-34.18	0.95			Rain Wk1	Rain Wk2	Y	Pred-Rain
5	6	89.43	9.72	0.008	-30.31	0.98	Feed rate ²		Wind Wk1	Rain Wk2	Y	
6	6	92.04	12.33	0.002	-31.62	0.97	VPA		Rain Wk1	Rain Wk2	Y	Pred-VPA
7	5	92.62	12.91	0.002	-36.31	0.93	VPA		Rain Jun.		Y	Pred-VPA
8	5	93.33	13.62	0.001	-36.66	0.93		Euph feed ⁻¹	Wind Wk1		Y	Euph-Wind
10	5	94.09	14.38	0.001	-37.04	0.93	Her. length	Bad food hr ⁻¹		Rain Wk 2		Bad food-Rain
9	5	94.11	14.40	0.001	-37.05	0.93		Euph feed ⁻¹	Rain Wk1		Y	Pred-Rain
11	5	94.42	14.71	0.001	-37.21	0.93		Bad food hr ⁻¹	Rain Wk1		Y	Pred-Rain
12	4	94.45	14.74	0.001	-40.37	0.90			Rain Wk1		Y	Pred-Rain

Note: Column headings include ID# of the model, the number of parameters, model weight, log-likelihood, and representations of good food, bad food, weather, predation, and interactions between parameters. Parameters include feeding rate (feed rate), estimated number of herring recruits from the virtual population analysis (VPA), euphausiid mass (g) feeding⁻¹ (Euph feed⁻¹), mass of bad food hr⁻¹ (Bad food hr⁻¹), average wind speed during the first week of chick rearing (Wind Wk1), total rain during the first week of chick rearing (Rain Wk1), total rain in June (Rain June), total rain during the second week of chick rearing (Rain Wk2), and the proportion of eggs depredated (Y).

54

55 Table 2. Final AICc output table for analysis of productivity of Arctic Terns (*Sterna paradisaea*); the confidence set is
56 shaded, but results report up to $\Delta 15$.

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ID	<i>k</i>	AICc	Δ AICc	Weight	Log-Lkhd	R^2	Good food	Bad food	Weath. 1	Weath. 2	Pred.	Interaction
1	12	-204.68	0.00	0.401	-41.66	0.97	Good Food hr ⁻¹	Euph feed ⁻¹	Rain Wk1		Y	Euph-Rain Wk1
2	12	-203.98	0.70	0.282	-42.01	0.97		Euph feed ⁻¹	Rain Wk1	Rain Wk2	Y	Euph-Rain Wk1
3	12	-203.75	0.93	0.251	-42.13	0.97	Feed rate ²		Wind Wk1	Rain Wk2	Y	
6	12	-200.02	4.66	0.039	-43.99	0.95		Euph feed ⁻¹	Rain Wk1	Rain Wk2	Y	Pred-Rain Wk1
7	12	-197.28	7.40	0.010	-45.36	0.95	VPA	Euph feed ⁻¹	Rain Wk1		Y	Euph-Rain Wk1
8	12	-196.94	7.74	0.008	-45.53	0.94	Feed rate ²		Wind Wk1		Y	Pred-Wind Wk1
9	12	-196.93	7.75	0.008	-45.53	0.94	VPA		Wind Wk1	Rain Wk2	Y	Pred-VPA
12	12	-190.22	14.47	0.000	-48.89	0.92		Bad food hr ⁻¹	Rain Wk1	Rain Wk2	Y	Bad food-Rain Wk2
13	12	-189.85	14.84	0.000	-49.08	0.92	VPA	Bad food hr ⁻¹		Rain Wk2	Y	Pred-VPA
14	12	-189.76	14.92	0.000	-49.12	0.92	Feed rate		Rain Wk1	Rain Wk2	Y	Pred – Rain Wk1

82 Note: Column headings include ID# of the model, the number of parameters, model weight, log-likelihood, and
83 representations of good food, bad food, weather, predation, and interactions between parameters. Parameters include
84 mass (g) of good food hr⁻¹ (Good food hr⁻¹), feeding rate (feed rate), estimated number of herring recruits from the
85 virtual population analysis (VPA), euphausiid mass (g) feeding⁻¹ (Euph feed⁻¹), mass of bad food hr⁻¹ (Bad food hr⁻¹),
86 average wind speed during the first week of chick rearing (Wind Wk1), total rain during the first week of chick rearing
87 (Rain Wk1), total rain during the second week of chick rearing (Rain Wk2), and the proportion of eggs depredated (Y).

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