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WHAT MAKES AN ISLAND GREEN? PLANT COMMUNITIES AT MULTIPLE SPATIAL AND TEMPORAL SCALES

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WHAT MAKES AN ISLAND GREEN?

PLANT COMMUNITIES AT MULTIPLE SPATIAL AND TEMPORAL SCALES

Eric M. Danner

Abstract

I investigated the spatiotemporal dynamics of plant communities on islands in the Aleutian archipelago, Alaska, using small scale plots and landscape level remote sensing. Islands of the Aleutian archipelago are a model system for vegetation studies: there is no significant variation in island size, geology, soil type, or plant composition for hundreds of islands spanning 1600km of longitude. There is variation in two important factors: nutrients and climate. Past fox introductions onto some of the islands substantially reduced seabird populations that formerly vectored nutrients from the sea to land. Previous field studies have documented significant differences in vegetation composition and biomass between fox-infested and fox-free islands using small scale field measurements. I examined the landscape level vegetation response to nutrient subsidies on individual islands and to a regional climate gradient across the entire archipelago. There was also evidence of a climate gradient of gradual cooling from east to west. In order to capture the full extent of the spatial and temporal variation in the system, I developed a method of using high temporal frequency, moderate spatial resolution remote sensing data to measure the landscapes of entire islands across the archipelago through time. Using this technique I calculated the seasonal phenological profiles of every island, including descriptive parameters such as length, width, and peak of the growing season. With this information I was able to show that the plot level results scaled-up to the landscape level. I documented difference in the vegetation dynamics between nutrient subsidized and non-subsidized islands, demonstrating the landscape level

impact of an apex predator. I also documented a regional cooling trend in climate and associated trends in vegetation dynamics. Overall, there was lower production from east to west on fox-infested islands. However, this longitudinal trend was not always present for the vegetation parameters on fox-free islands. This suggests that the significant nutrient subsidies can override the effect of climate in this system; a pattern that is driven by an introduced apex predator.

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Introduction

The factors that structure plant communities are diverse and complex. They range from abiotic factors such as light, water, temperature, and nutrients, to biotic factors such as herbivory, pollination, and commensalism. Much of the research addressing the importance of these factors has been done at the scale of small study plots (Kareiva 1990), occasionally at the landscape scale, but rarely at both. This is an important issue because the mechanisms that structure biological communities often operate at more than one scale (Levin 1992). In addition, the importance of these mechanisms often changes over time. Processes that have strong effects at the local scale may show weak effects or no effect at all at the regional scale. Likewise, processes that are important during one season may be insignificant during a different time of year. Yet field biologists are commonly limited to choosing between measuring communities at small scales through time or large scales at a single point in time.

One of the reasons for these limitations is the methodological constraints brought about by the requirements of an appropriate experimental design. In order to have properly replicated units some of the factors must be held constant while others are varied through space, time, or both. These requirements can usually be met at small scales but are rarely met at large scales. For example, while it is possible to hold environmental conditions constant in the laboratory or at a small scale field site, this requirement becomes increasingly more challenging with increasing spatial scope of the study area. As a result, our ability to make stronger inferences about ecological processes is often limited to smaller scales.

One solution to these limitations is to use naturally occurring large scale replicates. Islands are often good choices because they represent clearly defined units (Vitousek et al. 1995).

Island archipelagos are particularly well suited for ecological studies because of the often great abundance of islands and the similarities in physical and biological factors among islands. In the correct context, islands can serve as replicates in large scale ecological experiments. Variation in factors of interest among islands across archipelagos can thus be used to test specific hypotheses (Vitousek 2004).

Until recently, the principal limitation in conducting large-scale ecological experiments has been in the difficulty of measurement. Our ability to measure vegetation at large scales has been greatly enhanced through recent advances in remote sensing. A commonly used and powerful metric, the Normalized Difference Vegetation Index (NDVI) is a measure of vegetation greenness that is highly correlated with plant biomass. Collected at frequent intervals, the NDVI can provide valuable information about seasonal vegetation dynamics. While the shear volume of these measurements is breathtaking (complete global satellite vegetation measurements are being cataloged every two days), until recently they have rarely been applied to interesting ecological questions (Kerr and Ostrovsky 2003, Pettorelli et al. 2005).

In the following three chapters I describe how I used remote sensing combined with detailed field data to provide insight into the factors that are important in structuring plant communities at both landscape and regional scales. I used islands within the Aleutian archipelago, Alaska, to determine the importance of nutrient input at the landscape scale and the importance of climate and the regional scale. In the first chapter I describe the study system and the remote sensing approach I have developed to measure entire island landscapes through time. In the second chapter I show that these techniques can be used to measure the response of the plant communities to nutrient input driven by a multi-species interaction pathway. In the final chapter I address a regional climate gradient that affects vegetation dynamics across the 1900km east-west range of the archipelago.

The Aleutian archipelago is well-suited for studying the factors that structure plant communities. There is little variation in the plant species composition or soil type across the archipelago. Island size ranges widely but the distribution of island shapes and sizes is also preserved across the Aleutian archipelago. Further, the introduction of Arctic foxes to many of the islands has provided an opportunity to examine the impacts of a top-level predator on the vegetation dynamics. Before the introduction of foxes, millions of seabirds likely provided substantial nutrient subsides to all or most of the islands in the form of guano. The introduced foxes significantly reduced or eliminated these nutrient subsides by reducing the seabird populations on various islands. Intensive field studies were done to measure the plant community response to the presence of foxes by taking on-the-ground measures of soil and plant chemistry and plant community structure and composition. There has been considerable debate in ecology about the indirect impacts of top-level predators on the vegetation dynamics of terrestrial systems (Pace et al. 1999, 2000, Schmitz et al. 2000). Croll et al. (Croll et al. 2005) and Maron et al (Maron et al. 2006) have shown striking differences in plant communities between island with and without introduced foxes. However, the supporting data were obtained from a relatively small number of small plots, obtained at a single point in the growing season. As with many ecological field studies, it was not known if the plot-level results would "scale-up" to the landscape level.

I addressed this issue of scale by using remote sensing to complement the field studies described above. This was problematic, however, because the Aleutian region has high levels of cloud cover making many forms of satellite remote sensing ineffective. Further the archipelago is isolated from any major human settlements, making it difficult to survey using airborne remote sensing platforms. I solved these problems by using a high temporal frequency satellite platform: 250m NDVI data from the Moderate Resolution Imaging Spectroradiometer (MODIS) satellite. By sampling the region on a daily basis MODIS can provide enough data to generate high quality NDVI composite images every 16 days throughout the year. From these images I was able to observe the islands on the few cloud-free days, and thus to characterize the landscape of each island on a monthly basis. This approach provided a view of the landscape-level response by the vegetation community that was not confounded by spatial autocorrelation. By simultaneously measuring all the islands across the entire 1600km archipelago on a monthly basis I could then generate seasonal phenological profiles of each island that were comparable across space. I was able to measure the precision of these phenological profiles by quality of the fit to a two-term Fourier function.

Once I had established the effectiveness of the MODIS landscape level measurement approach I was able to contrast the results with the vegetation patterns that had been established using traditional field methods. Multispecies interaction pathways can be very complex, and top-level predator driven plant community responses have never been measured at the landscape level. By using this approach, I was able to show that the seasonal vegetation dynamics were significantly different between fox-infested and fox-free islands at the landscape level.

The vegetation differences between fox-infested and fox-free islands were the result of a localized effect (at the scale of individual islands) of nutrient input. Islands could be classified as subsidized or not subsidized and this was independent of their location throughout the archipelago. At the regional scale there was a significant cooling trend from east to west. Eastern islands tended to warm earlier, and to have less snow and cloud cover. These regional patterns provided a rare opportunity to examine the interactions between climate and community ecology. As a result of the climate patters, there were significant trends in the seasonal NDVI parameters for non-subsidized (fox-infested) islands from east to west across the Aleutian archipelago. In contrast, many of the same parameters did not have significant trends for the fox-free islands. These results indicate that the input of nutrients, as a function of the presence or absence of a top-level predator, nullify the effect of the climate gradient.

In summary, the Aleutian archipelago is a model system for conducting research on plant community dynamics. I was able to examine the impacts of nutrient subsidies controlled by a top level predator across entire landscapes in a replicated manner. Because of the distribution of fox-infested islands throughout the archipelago, I was able to measure these patterns while holding climate constant. Likewise, by excluding islands with significant numbers of seabirds I was able to measure the landscape-level response of vegetation communities to a significant gradient in climate while holding nutrients constant. Finally, I was able to test for significant interactions between climate and nutrients by including both parameters in the analysis.

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Chapter 1. Assessing the use of MODIS Normalized Difference Vegetation Index (NDVI) data to measure seasonal vegetation phenology over a range landscape sizes

Introduction

The Normalized Difference Vegetation Index (NDVI) has long been a standard remote sensing metric for measuring terrestrial vegetation (Pettorelli et al. 2005). Generated from the ratio of red (~650 nm) and near infrared (~850 nm) bands [(NIR-RED) / (NIR+RED)] the NDVI is an optical measurement of "greenness" that correlates strongly with plant biomass (Myneni et al. 1995), and above ground net primary productivity (Tucker and Sellers 1986). Satellites such as the Advanced Very High Resolution Radiometer (AVHRR) that acquire NDVI data at frequent intervals can thus be used to generate precise measurements of seasonal vegetation dynamics. These phenology curves serve as baselines from which informative quantitative parameters can be extracted regarding the timing and magnitude of seasonal events (Jonsson and Eklundh 2002, Schwartz 2003, Zhang et al. 2003). This information is fundamental for the studies of net primary production, climate change, trophic interactions, habitat loss, and many other ecological issues that require assessment on large spatial scales (Schwartz 2003). A significant limitation of these studies is the coarse spatial resolution (8km) of the AVHRR pixels. Although there are other higher resolution platforms available such as Landsat (30m pixels), these sensors are not specifically designed to produce an NDVI product and require critical atmospheric correction to produce consistently accurate results (Ouaidrari and Vermote 1999, Song et al. 2001). The launch of the Terra satellite and the production of Moderate Resolution Imaging Spectroradiometer (MODIS) NDVI data starting in 1999 greatly increased the spatial resolution and quality of NDVI data available to the scientific community. With a 250m atmospherically corrected NDVI product, MODIS is the newest generation of satellites for measuring vegetation dynamics at regional to global scales (Pettorelli et al. 2005). While studies are just beginning to take advantage of the higher resolution MODIS products, there have been few attempts to date to use these products to measure the seasonal phenological patterns of small landscapes. Thus the smallest landscape size at which MODIS NDVI can be used effectively has not yet been determined. This study makes use of a natural system, the Aleutian Island Archipelago, Alaska (Figure 1.1), that is uniquely suited to evaluate the effectiveness of the MODIS 250m NDVI for measuring the seasonal vegetation phenology across landscapes that range in size from tens to thousands of hectares.

The Aleutian Islands consist of hundreds of islands that mark the boundary between the North Pacific Ocean and the Bering Sea. There are three principle reasons the Aleutian Islands are appropriate for evaluating the effectiveness of MODIS NDVI for measuring vegetation phenology: (1) the dynamics of the Aleutian vegetation community are relatively simple with a single, clearly defined growing season; (2) the spatial boundaries of each island (landscape) are clearly defined; and (3) even though the archipelago spans 1900km longitude and 500km latitude, there is remarkably little variation in most of the biotic and abiotic factors of each island. The vegetation is maritime tundra, dominated by grasses, dwarf shrubs, lichens, and forbs (Amundsen 1977). There are no trees or large shrubs and the maximum vegetation height rarely exceeds 1m (Danner, pers. obs.). The phenological patterns are simple, consisting of a spring green-up, summer peak, and fall brown-down. There is little variation in plant species diversity (Maron et al. 2006), and geology (Gard 1977) among the islands.

The clearly defined island boundaries and the spatially homogeneous nature of the island chain are critical issues in terms of the statistical analysis and the appropriate replication of suitable spatial units (Hurlbert 1984, Underwood 1997). Psuedoreplication can be a significant problem for large scale remote sensing studies because the analysis is confounded across space due to spatial variation in habitat and climate that is driven by tangential factors such as rainfall, temperature, and sunlight. With the Aleutian Islands system however, islands can be used as statistical samples for comparisons. The islands range in size from <1ha to 400,000ha and cover a large geographic area (1900km longitude and 500km latitude). These factors make the Aleutian Island system well suited for a large-scale analysis of remotely sensed phenology data.

Here I evaluate the effectiveness of MODIS 250m NDVI data for precisely measuring the seasonal phenology of relatively small landscapes. My approach was to measure successively smaller islands throughout the Aleutian Archipelago to determine the minimum landscape required to measure vegetation phenology with a reasonable level of precision. First, I compared a suite of plant growth related factors among all the islands in the archipelago. From this I could establish that for each vegetation factor the archipelago was (a) largely invariant or (b) had inherent geographic trends in its vegetation and/or physical characteristics. Second, I quantified the effectiveness of the MODIS sensor in terms of how well the NDVI data for each landscape fit a theoretical seasonal phenology curve. I accomplished this by taking a four year time-series of MODIS data (2001-2004) and fitting it to a two-term Fourier curve. I then calculated the goodness of fit (adjusted r^2) for each island. I inferred the capacity of the MODIS data to precisely measure the vegetation dynamics from the goodness of fit value: the higher the r^2 the more precise the measurement.

Finally, I extracted pertinent seasonal parameters from the fitted curves. I contrasted these parameters with static physical descriptors of the islands such as island area, shape, latitude, longitude and elevation to see if they matched the general predictions based on the island characteristics (e.g. the relationship between longitudinal patterns in NDVI and plant growth factors).

Methods

Study Area - Aleutian Islands

The Aleutian Archipelago, as defined for this study, ranges from Attu Island (172°56' E, 52°00' N) to Caton Island (162°25' E, 54°23'N) covering ~1900km from east to west and ~500km from north to south. There are >450 islands and offshore rocks ranging in size from 1ha to >400,000ha. To compensate for duplication of pixels due to the projection of high latitude landscapes (approximately 20% of pixels), I reprojected the MODIS NDVI data (MOD13AQ1) from their native sinusoidal to Albers Alaska projection using the MODIS Reprojection Tool (LP DAAC User Services, U.S. Geological Survey) and filtered duplicated pixels from the analysis. For each remaining pixel I calculated the distance from shore (from the center of the pixel to the nearest edge of the island). I determined the mean elevation of each pixel from 1 arc second (30 meter) Shuttle Radar Topography Mission (SRTM) digital elevation model (DEM). I excluded islands with fewer than 8 pixels from the analysis. The final set of islands (n=90) ranged in size from 51 to 409,149 ha (Appendix A).

I compiled a suite of biotic and abiotic factors useful in tracking vegetation dynamics and regressed each factor against latitude and longitude for each island to test the assumption of archipelago-wide homogeneity as well as to determine the magnitude and direction of any spatial gradients that may be present (Table 1.1). These factors included: (1) dimensional descriptors of each island, including planar surface area (log transformed), the perimeter to area (P/A) ratio (log transformed), and mean elevation (log transformed); (2) data on soil and plant characteristics; and monthly rainfall data. I used polygon shapefiles and Digital Elevation Models (DEMs) in ArcGIS (ESRI, v 9.1) to generate the physical descriptors of each island. For some of the analyses I used plant and soil data that were collected from 19 islands as part of a separate study (Croll et al. 2005, Maron et al. 2006). Ten of these islands had high densities of seabirds (>0.1 bird/m^2) which have significantly altered the soil and plant chemistry (Croll et al. 2005, Maron et al. 2006), and were therefore excluded from the analyses. Rainfall data are monthly means from 4 field stations spanning the archipelago (Amaknak, Adak, Shemya, and Attu islands), and were analyzed using analysis of variance (ANOVA) on the mean values of the growing season months (between the spring and fall equinoxes: March 20, and September 23).

<u>MODIS Satellite Data</u>

To measure the spatiotemporal patterns in plant production and their relationship to climate, I used four datasets from the MODIS Terra satellite platform, including one vegetation dataset: the NDVI; and three climate datasets: snow/Ice cover, cloud cover, and land surface temperature (LST). The NDVI, snow/ice, and cloud data were all from the 250m 16-Day Vegetation Indices (MOD13Q1) product. The LST was from the 1km 8-Day Land Surface Temperature/Emissivity (MOD17A3) product. These products are all components of the MODIS Terra satellite and are integrated and designed to be used together. The processing and analysis of each dataset are discussed below.

Fourier fitting

The NDVI data used for the analysis were MODIS Terra NDVI 16-day composites (MOD13Q1) from 2001 through 2004 (Table 1.2). The quality of the NDVI data in the Aleutian region can be highly variable due to the atmospheric effects (primarily cloud cover), snow and ice, shadows, and satellite viewing angles. To reduce the amount of variability in the data, I restricted per-pixel VI quality (MODLAND) values to 0 or 1 ["VI produced, good quality" and "VI produced, check QA quality", (Huete et al. 1999)] and removed pixels with snow or ice. I then used these values to generate mean NDVI values for each island across the 16-day sample period. These values were then averaged to produce monthly means. With NDVI data smoothing functions are often used to remove extreme high and low values from time series data (Pettorelli et al. 2005). I fit the mean monthly values from each island from four consecutive years, 2001-2004, to a two-term Fourier function (MATLAB Curve Fitting Tool, version 1.1.3) using the following equation:

$$y = a_0 + a_1\cos(xp) + b_1\sin(xp) + a_2\cos(2xp) + b_2\sin(2xp)$$

where $p = 2\pi/(\max(x)) - (\min(x))$, or 0.53 for each island. This is a nonlinear least squares fit with the assumption of normally distributed errors. I used the adjusted r^2 value from each island as the measure of the goodness of fit of the data to the Fourier equation. I then extracted four seasonal parameters from the NDVI fitted line (Figure 1.2): NDVI at peak of growing season (Max NDVI), NDVI at lowest point in winter (Min NDVI), the date of peak of growing season (Date of Max NDVI), the season integral (iNDVI). To test for cross-correlation, I regressed the four seasonal parameters (dependent variables) against six island parameters (independent variables: surface area, P/A ratio, latitude, longitude, mean elevation, and Date of Max Temp) in a Multivariate Analysis of Variance (MANOVA). I then tested only dependent variables with significant Wilks' Lambda values against the independent variables using simple regression. To determine if the quality of the fit (as measured by the adjusted r^2) introduced any bias into the values of the seasonal NDVI parameters I tested the residual values from the MANOVA for each parameter against the adjusted r^2 using linear regression. I interpreted significant relationships as an indication of bias. To determine the relationship between the quality of the fit and islands size, I used regression to evaluate the relationship between the adjusted r^2 and island area for each island. I further examined the relationship between island size and cloud cover by categorizing each island into two sizes (sizebin = large for islands >1200ha, n = 38, or sizebin = small for islands <1200ha, n = 35) using r^2 as the independent variable, island size as the main effect and cloud cover as a covariate in an ANCOVA.

Mixed pixels (pixels that include both land and ocean) tend to have lower NDVI values than pixels of pure vegetation. There was potential for this to cause spurious results, particularly for smaller islands because of the inverse relationship between island area and the proportion of mixed pixels. I examined the impact of mixed pixels by determining the mean NDVI value as a function of distance from the shoreline. I binned pixels from all islands into 100m bins as a function of their distance from shoreline from 0 to 1000m, and calculated the mean NDVI for each bin. I classified distance bins from 0 to 300 as "mixed" as they were within the approximate width of a single MODIS 250m pixel, and bins from 400 to 1000m as "non-mixed". I tested mean differences between mixed bins using one-way ANOVA with planned comparison contrast for linear trend. I tested mean differences between non-mixed bins using one-way ANOVA.

Snow/Ice and Cloud Cover

I used the MODIS NDVI quality data to estimate the monthly percent cloud cover and the percent snow/ice cover for each island. MODIS NDVI datasets include associated quality data that separately identify the presence of clouds and snow/ice on an individual pixel basis (presence = yes or no). I calculated the percent cloud cover for each island as the proportion of pixels that were positive for clouds for each time period. From these data I then calculated an annual mean percent cloud cover. I used the same process in the calculation of the percentage of snow/ice cover.

Land Surface Temperature

I generated the mean monthly land surface temperatures (LST) for each island from MODIS MOD11A2 1km Land Surface Temperature/Emissivity data. I averaged the 8-day values into monthly means and then fit these means to a two-term Fourier function following a similar protocol as the NDVI analysis described above. I restricted the analysis to daytime temperatures and per-pixel quality values equal to 0 ["LST produced, good quality" (Wan 1999)]. I extracted two seasonal parameters from the LST curves: the annual integrated temperature (iLST), and the date of peak temperature (Date of Max LST).

Results

Characteristics of the Aleutian Islands

Despite spanning 1900km in longitude, the Aleutian Islands are spatially homogeneous for most of the factors tested. There were no significant differences in island area, P/A ratio, or mean elevation with latitude or longitude (Table 1.3). There were no significant spatial or island dimensional trends in the biotic and abiotic vegetation parameters (Table 1.4). While the plant and soil characteristics were invariant across the archipelago, there were significant trends in some of the climate variables. There were no significant spatial trends in the iLST, but the eastern islands reached their maximum temperature significantly earlier than western islands (Date of Max Temp was negatively related to longitude, $r^2 = 0.27$, $P < 0.001$). In addition, cloud cover was positively related to island area (Figure 1.3) and negatively related to longitude ($r^2 = 0.35$, $P < 0.001$, $P = 0.047$, respectively). Snow cover was also positively related to island area, latitude, and longitude ($r^2 = 0.38$, $P = 0.002$, $P < 0.001$, and $P < 0.001$, respectively). Finally, there was no difference in rainfall between the four field stations throughout the archipelago during the growing season (ANOVA, $F_{3,20} = 1.88$, $P = 0.1662$).

Fourier fitting

Overall, the seasonal MODIS 250m NDVI data fit the two-term Fourier function better for larger islands than smaller islands. There was a wide range in the goodness of fit to the Fourier curve for the 73 study islands as measured by the adjusted r^2 values (0.32 to 0.95, Figure 1.4). While there was a positive relationship between the r^2 values and island area ($P < 0.001$; $r^2 = 0.31$), there was increasing variation in r^2 values with decreasing island size (Figure 1.5). This pattern is likely related to cloud cover. The results of the ANCOVA of the adjusted r^2, island sizebin, and cloud cover indicated that there was a significant *island sizebin* x *cloud cover* interaction (ANCOVA, $F_{1,69} = 7.79$, $P = 0.0068$). Separate regressions for adjusted r^2 against island area for each sizebin indicate there was no relationship between island size and cloud cover for large islands ($r^2 = 0.07$, $P = 0.106$), but there was a negative relationship between island size and cloud cover for small islands ($r^2 = 0.14$, $P = 0.027$, Figure 1.6). Thus cloud cover has a significant negative effect on the quality of the fit for islands smaller than 1200ha and no effect on islands larger than 1200ha.

The majority of the seasonal parameters generated from the Fourier fit were not significantly related to the physical island parameters (Table 1.5, only values with significant results are included). The minimum NDVI and the iNDVI were negatively related to longitude (decreasing from east to west, $P = 0.007$ and $P = 0.025$ respectively) and negatively related to cloud cover ($P = 0.006$ and $P = 0.007$ respectively). There were no significant relationships between the residuals and the adjusted r^2 values for any of the seasonal NDVI parameters, indicating that the quality of the Fourier fit did not introduce any significant bias to the results.

There was a clear negative relationship between mixed pixels and mean NDVI (Figure 1.7). Mixed pixels caused a decline in the mean NDVI that diminished with each distance bin from shore up to 300m inland ($F_{1,342} = 20.5$, $P < 0.001$). Past the 300m distance (slightly larger than the width of a single 250m MODIS pixel) the mean NDVI values for each distance bin were not significantly different ($F_{6,380} = 0.62$, $P = 0.72$). Finally, to test how the mixed pixels impacted the precision and accuracy of the Fourier fit I calculated adjusted r^2 values, Max NDVI, and GSI from two revised datasets: one with only mixed pixels and one excluding mixed pixels from each island. Mixed pixels were not the cause of any loss of precision as there was a significantly greater mixed pixels mean adjusted r^2 of 0.80 compared to a non-mixed pixel mean adjusted r^2 of 0.76 (paired t-test, $t = -3.175$, $P =$

0.0022). Mixed pixels did cause a significant decrease in the Max NDVI (6974 and 7136 mixed vs. non-mixed mean NDVI, paired t-test, t = -2.4067, P = 0.0185). Finally, the contrast between mixed and non-mixed pixels had no effect on the GSI (32167 and 31547 respectively, paired t-test, t = -1.069, P = 0.2887).

Discussion

While MODIS NDVI data has been successfully used to measure global and regional vegetation dynamics, the minimum spatial dimensions over which it can be used to detect landscape level variation in seasonal vegetation phenology had not been fully explored. Because vegetation assemblages are highly variable entities, both spatially and temporally, the scale at which they are measured is of critical importance. With this study, I establish the utility of using MODIS 250m NDVI, a high-temporal, moderate-spatial resolution sensor, for examining vegetation dynamics at across a range of landscape sizes.

The Aleutian Island chain is an ideal system for a comparative remote sensing study for a number of reasons. First, the spatially consistent nature of the suite of plant growth related factors allow for valid comparisons and contrasts among islands. There were few spatial trends in any of the variables measured – a remarkable result considering that the archipelago spans 1900km of longitude and 500km of latitude. Second, the growing season consists of a simple, nearly symmetrical unimodal curve. This is critical because complex, multiple, or unclear growing seasons often complicate and confound satellite based studies of vegetation phenology (Reed et al. 2003). Third, the boundaries of each island are clearly defined. Unlike the often gradual transitions that occur across regional landscapes, the transitions on islands allow for the clear definition of statistical replicates. Finally, the biotic communities on the Aleutian Islands are relatively simple. There are few complex trophic interactions that might generate unexplained variation. For example, there are no native mammalian predators and no significant herbivores. One significant biotic influence on the vegetation communities is seabirds through the input of nutrients (Croll et al. 2005, Maron et al. 2006). Most of the anthropogenic disturbances occurred many decades in the past (the establishment of military bases during and after World War II) and, with the exception of a few known islands, should no longer be a source of variation in the current vegetation dynamics.

With this study I demonstrate that MODIS 250m NDVI data can be used to precisely measure the phenology of relatively small landscapes. The vast majority of the study islands fit the Fourier distribution well: 78% of the r^2 values were greater than 0.70 (57 of 73 islands, Figure 1.4). While there was a significant positive relationship between adjusted r^2 and island area, there was no point in the relationship, such as a sudden change in the shape of the curve that might signify a minimum landscape size required for a precise measurement. Instead, the range of r^2 values increased with decreasing island area in a linear fashion (Figure 1.5), indicating that as islands get smaller, predicting the quality of the fit becomes more difficult. This increased variation is most likely driven by cloud cover. While cloud cover is positively related to island size ($r^2 = 0.20$, $P < 0.001$), the greater surface area on larger islands likely counteracts the negative effect of the cloud cover.

Regardless of the exact form of the island size–fit relationship it may be beneficial to discard the islands with adjusted r^2 values below some threshold. Due to the large pool of islands (n=73) it is possible to exclude all the islands below $r^2 = 0.60$ (n=10) while maintaining a large sample size. For example, the island area x cloud cover interaction is not significant when the minimum r^2 value is >0.60. The use of data smoothing techniques such as the Fourier fitting is a standard procedure for NDVI time-series data (Vandijk et al. 1987, Jonsson and Eklundh 2002, Zhang et al. 2003, Pettorelli et al. 2005), and there are more complex curve fitting models available that may be more suitable for different systems (e.g. semiarid systems with multiple rainy seasons and multiple growth cycles).

For the results presented here I make the assumption that the precision of the Fourier fit (as measured by the r^2 value) is directly related to accuracy of MODIS NDVI product in measuring the true vegetation dynamics. Validating this assumption is problematic because measuring vegetation phenology on the ground is very difficult (Reed et al. 2003). Two sources of bias that may affect the accuracy of this method are rapid, short-term vegetation change, and inter-annual variation. Rapid short-term vegetation change can be defined as significant one-time departures from the growth trajectory, both positive and negative in direction. These spikes and drops are likely not the result of real variation in plant dynamics, particularly rapid decreases in primary production during the spring and rapid increases during the fall. As discussed above, there are few sources of rapid vegetation change in this system such as disturbance, or pulses in rainfall or temperature. Therefore extreme short-term vegetation change is more likely the result of satellite measurement error. Inter-annual variation is another source of bias because Fourier analysis does not take into account inter-annual variation (Vandijk et al. 1987). As with short-term variation, there is little reason to assume there is any substantial year-to-year variation in vegetation growth in the Aleutian Islands system. While other fitting methods may incorporate short-term and inter-annual variation, the choice of smoothing method often does not alter the extracted seasonal parameters significantly (Pettorelli et al. 2005).

For the Aleutian Island system a significant source of measurement error are mixed pixels (pixels that include both land and water). This type of error is less problematic than the sources discussed above for two reasons: (1) individual mixed pixels can be identified and remain static through time; and (2) mixed pixels have consistently lower NDVI values than pixels of pure vegetation. For these reasons the bias introduced by mixed pixels can be estimated. While there are small interior lakes on many of the islands, the vast majority of the mixed pixels occur at the island perimeters, making the impact of mixed pixels increasingly important with decreasing island size. Vegetation is consistently thick and lush at the perimeters of islands in the Aleutians chain (Maron et al. 2006), yet this pattern is not apparent when viewing MODIS NDVI as a function of distance from shore (mean NDVI binned by 100m increments, Figure 1.7). Within the first 250 meters (the width of a single MODIS pixel) the shoreline influence of water has the effect of lowering the mean NDVI values. Each successive distance bin has a higher NDVI value due both to the smaller proportion of each individual pixel that has water in it and the smaller proportion of mixed pixels within each distance bin. NDVI values past the 250m distance do not show the effect of mixed pixels and remain statistically constant between each bin. In terms of the effect of mixed pixels on the fitted NDVI parameters, the results are inconclusive. While there was a significant decline in the Max NDVI per island when comparing mixed and non-mixed pixels there was not a significant difference in the GSI. Furthermore, the fit to the Fourier curve was better for mixed-pixels than for non-mixed pixels. These results suggest that some of the extracted seasonal parameters are more susceptible to distortion from mixed pixels than others.

I found two significant patterns in the seasonal NDVI parameters: the minimum NDVI and the iNDVI decreased from east to west, and both decreased with increasing cloud cover. The trend in lower minimum NDVI values from east to west is likely related to the associated cooling climate patterns as measured by the increase snow cover and later Date of Max Temp with longitude. These patterns, along with the negative relationship between cloud cover and both the iNDVI and the Min NDVI show the effect of external variables on plant dynamics. These results illustrate that the relationships between the NDVI and large scale patterns can be modeled using the methods described in this chapter. Further, the utility of MODIS-measured NDVI phenology curves in detecting important patterns in vegetation dynamics at small scales is illustrated in a comparison of two islands: Bogoslof and Bird (Figure 1.8). Both of these islands are approximately 60 acres, are represented by 12 and 11 pixels respectively, and are less than 30km apart from each other. However, Bogoslof is unique from the rest of the islands in that it is geologically young and volcanically active. Due to recent eruption events, Bogoslof has more bare rock and less vegetation cover than other Aleutian Islands. As a result Bogoslof has significantly lower max NDVI values than Bird Island (4037 and 6879 respectively), as well as GSI (13986 and 27477 respectively) and spring slope (70.0 and 147.6 respectively) values.

These results indicate that MODIS 250m NDVI data can be used to effectively measure vegetation dynamics at various scales, but precision of the measurements becomes variable with smaller landscapes. While the Aleutian archipelago is a region of extremely high cloud cover (Figure 1.3), which affects the quality of the data, is it also a relatively simple system with consistent and predicable vegetation dynamics. Other systems with multiple growing seasons and stochastic variation in plant growth may be more difficult to measure, yet environments such as arid systems with lower levels of atmospheric disturbance should have substantially less variable phenology curves. A better understanding of the capabilities of MODIS data to characterize smaller landscapes will emerge with ground validation through time. Nonetheless, with the continuous collection of quality NDVI data since mid 2000, MODIS represents a valuable but underutilized source fine scale phenological data.

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Table 1.1. Biotic and abiotic factors addressed in the analysis.

Factor	Source
Dimension descriptors	
Surface area	Shapefiles [1]
P/A ratio	Shapefiles [1]
Mean Elevation	DEMs [2]
Soil and plant characteristics	
Soil total N	Maron et al. (2006)
Soil total C	Maron et al. (2006)
Soil total P	Maron et al. (2006)
Plant %C	Maron et al. (2006)
Plant %N	Maron et al. (2006)
Forb Cover	Maron et al. (2006)
Grass Cover	Maron et al. (2006)
Moss Cover	Maron et al. (2006)
Shrub Cover	Maron et al. (2006)
Climate variables	
Monthly rainfall data	Global Historical Climatology Network [3]
Land Surface Temperatur	MODIS (MOD11A2) [4]
Percent snow / ice cover	MODIS (MOD13Q1) [5]
Percent cloud cover	MODIS (MOD13Q1) [5]

[1] Shapefiles were generated by hand using orthorectified 15m Landsat ETM+ mosaics from the Global Land Cover Facility: http://glcf.umiacs.umd.edu/index.shtml

[2] http://srtm.usgs.gov/

[3] http://www.ncdc.noaa.gov/oa/ncdc.html

[4] http://edcdaac.usgs.gov/modis/mod11a2.asp

[5] http://edcdaac.usgs.gov/modis/mod13q1v4.asp

Table 1.2. Characteristics of the Moderate Resolution Imaging Spectroradiometer (MODIS) 250m Normalized Difference Vegetation Index (NDVI) dataset (MOD13Q1). Pixel size is 250m and temporal frequency is 16-days.

		wavelengths	Range	Version
Band 1	Red	620 - 670 nm	0 - 10,000	
Band 2	NIR	841- 876 nm	0 - 10,000	
NDVI	(NIR-RED) / (NIR+RED)		-2,000 - 10,000	V004 SIN

Table 1.3. Multiple linear regressions results for the geographic distribution of island physical parameters: island area (log ha), perimeter to area ration (P/A ratio), and mean elevation (log meters) against latitude and longitude.

Variable	N	Latitude	Longitude
Area (log hectares)	90	0.161	0.127
P/A ratio (log meters)	90	0.111	0.093
Mean elevation (log meters)	90	0.912	0.790

Table 1.4. Multiple linear regressions results for the geographic distrubition of island vegetation parameters: variables by island area (log ha), perimeter to area ratio (P/A ratio), latitude and longitude. Plant values are the means of grass and forb values. Significant results are in bold.

Variable	N	Area	Latitude	Longitude
Soil total N	9	0.551	0.160	0.165
Soil total C	9	0.562	0.101	0.067
Soil total P	9	0.356	0.094	0.554
Plant %C	9	0.249	0.473	0.078
Plant %N	9	0.654	0.192	0.381
Forb Cover	9	0.184	0.596	0.159
Grass Cover	9	0.122	0.874	0.125
Moss Cover	9	0.191	0.657	0.327
Shrub Cover	9	0.762	0.176	0.667
iLST	73	0.116	0.234	0.515
Date of Max Temp	73	0.835	0.990	**0.001**
Cloud cover (percent)	73	**>0.001**	**0.047**	0.386
Snow cover (percent)	73	**0.002**	**>0.001**	**>0.001**

Table 1.5. Results of MANOVA on the islands seasonal parameters. Independent variables with non-significant Wilks' Lambda values were not displayed. Significant results are in bold.

	Longitude	Cloud Cover
Wilks' Lambda	**0.039**	**0.050**
Min NDVI	**0.007**	**0.006**
Max NDVI	0.278	0.399
Date Max NDVI	0.223	0.584
iNDVI	**0.025**	**0.007**

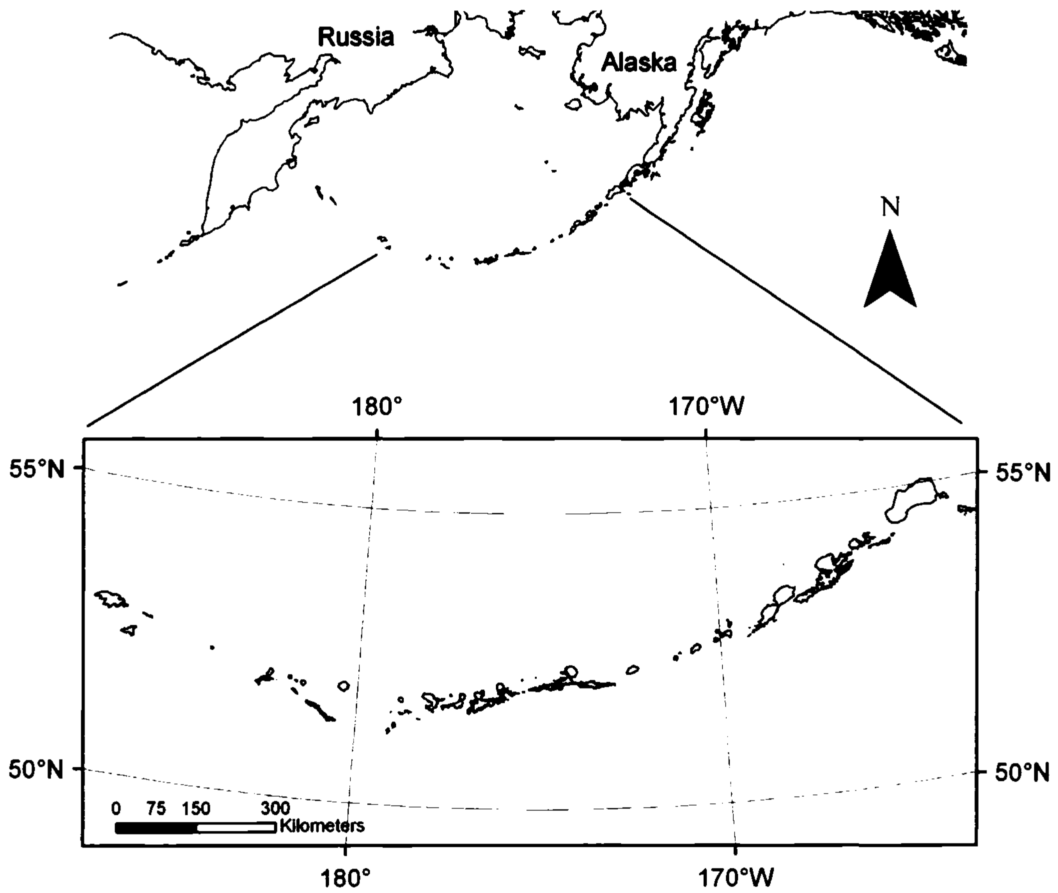


Figure 1.1. The Aleutian Islands, Alaska. The islands included in the analysis are listed in Appendix A.

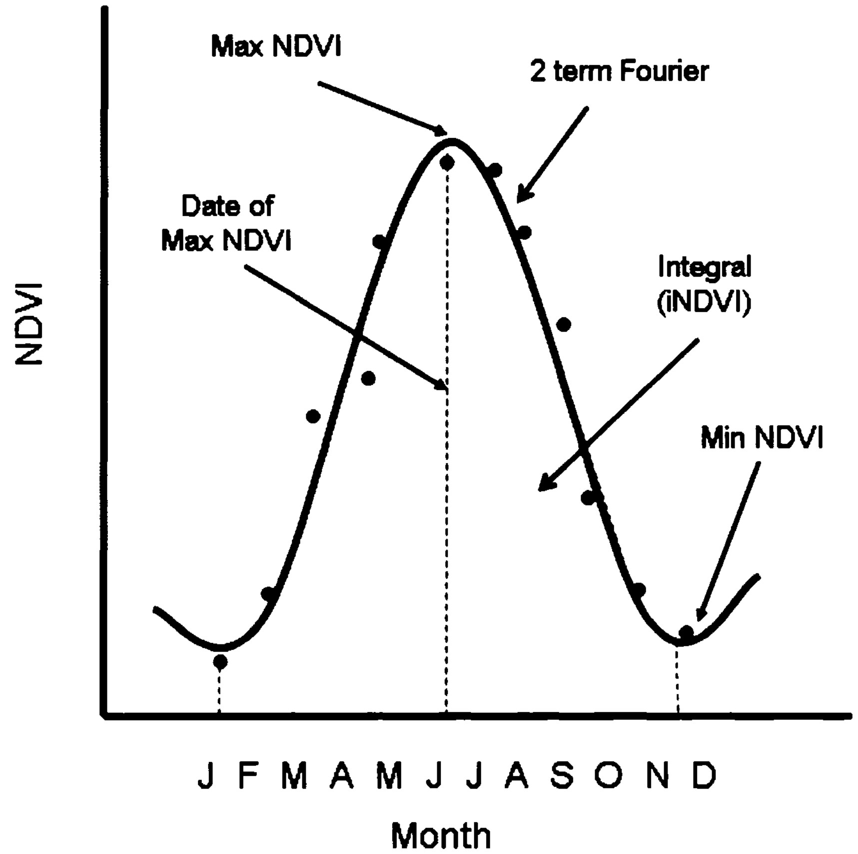


Figure 1.2. Hypothetical Fourier fitted curve and extracted seasonal parameters. The blue dots represent monthly mean NDVI values for a single island. The red line represents the fitted Fourier curve. The four extracted seasonal parameters are: the maximum and minimum NDVI values during the growing season (Max NDVI and Min NDVI); the date at the peak of growing season (Date at Max NDVI); the growing season integral of the (GSI).

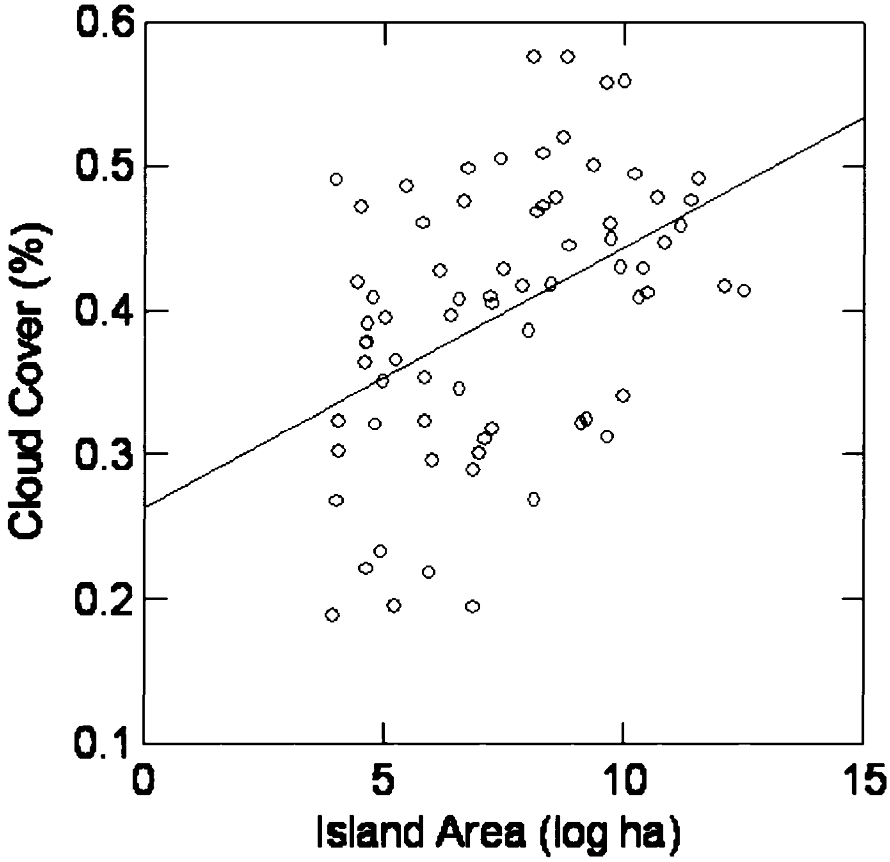


Figure 1.3. Relationship between cloud cover and island size. Cloud cover is annual percent and island size is hectares (log transformed).

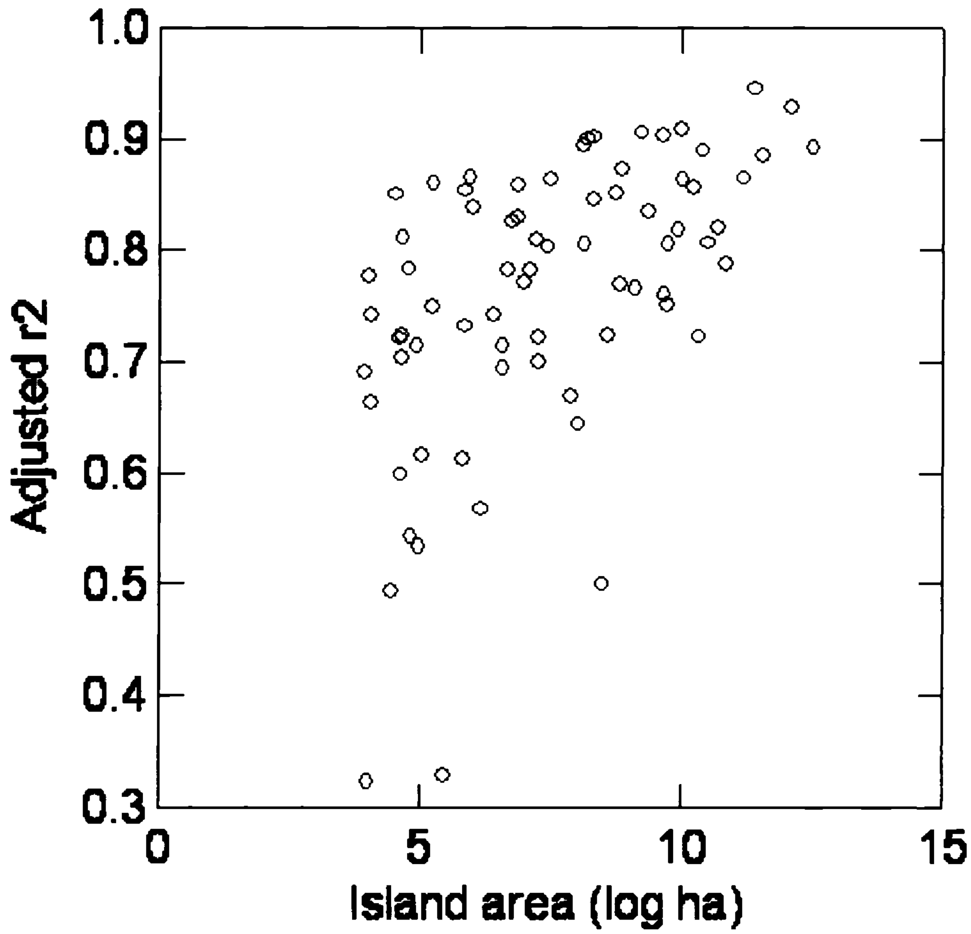


Figure 1.4. Relationship between island size and quality of the Fourier fit. Island size is hectares (log transformed) and Fourier is adjusted r^2.

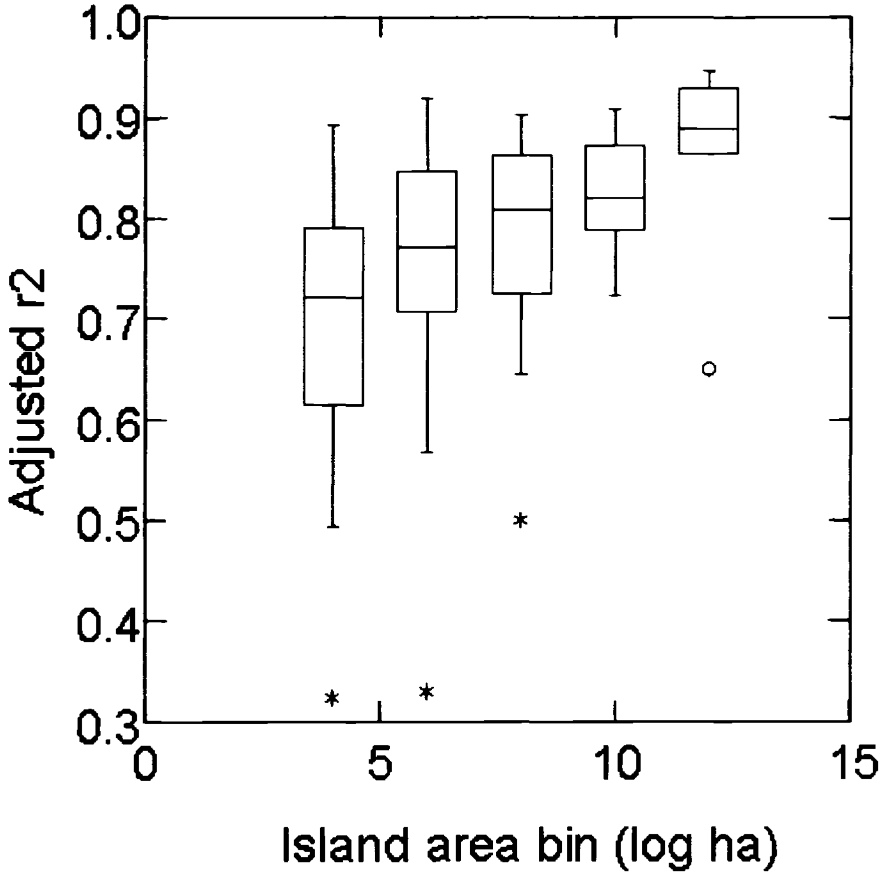


Figure 1.5. Relationship between island size (binned by log ha) and fit to Fourier (adjusted r^2)

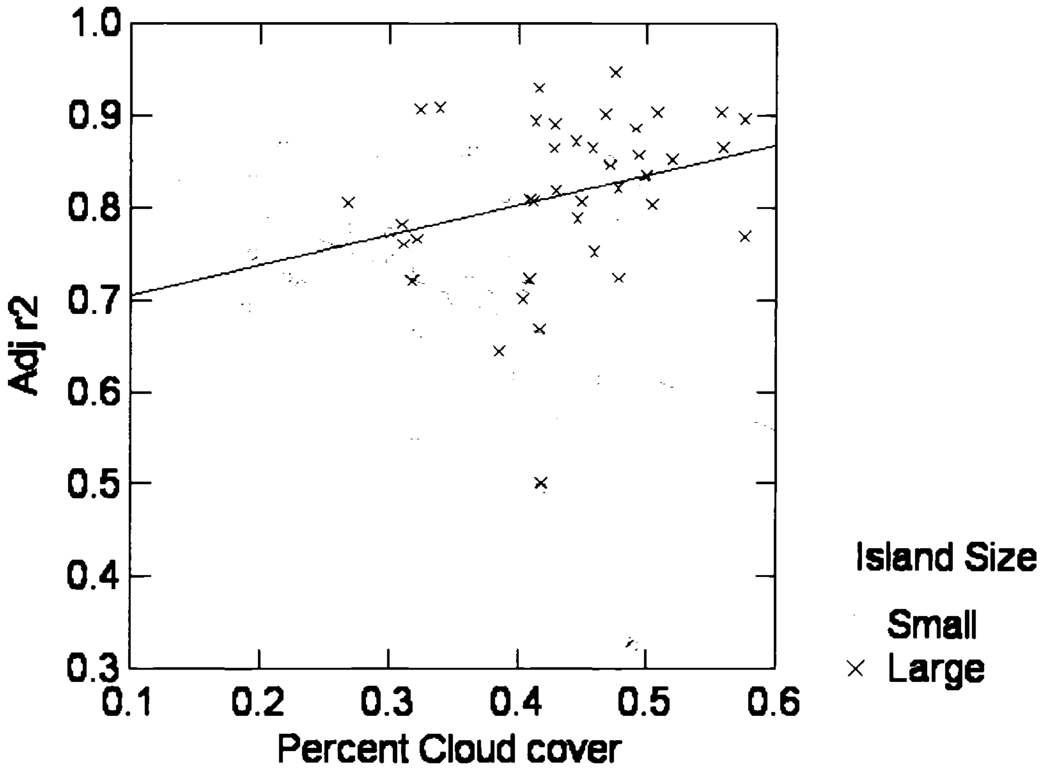


Figure 1.6. Relationship between island size (small island < 1200 > large islands) and cloud cover (annual percent cover).

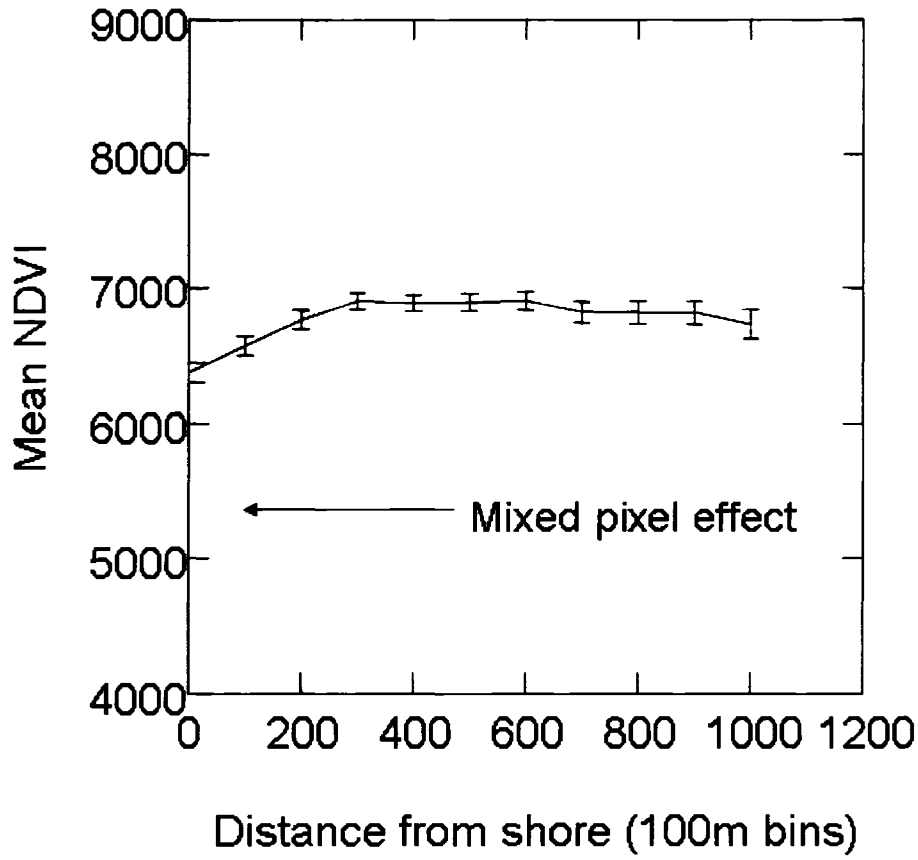
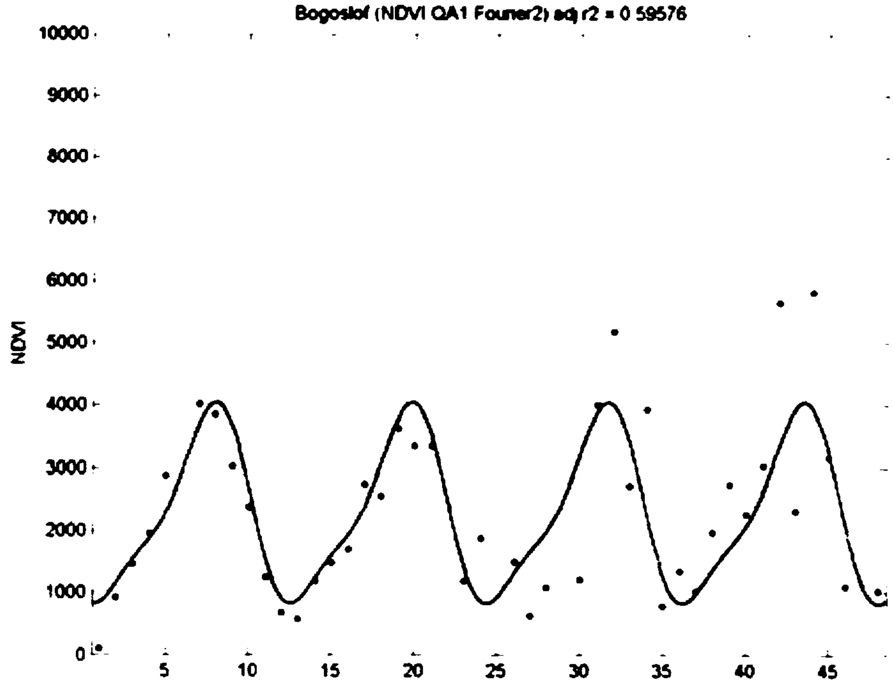


Figure 1.7. Mean pixel values as a function of distance from shore (by 100m distance bins). The shaded area represents the width of a single MODIS 250m pixel.

A



B

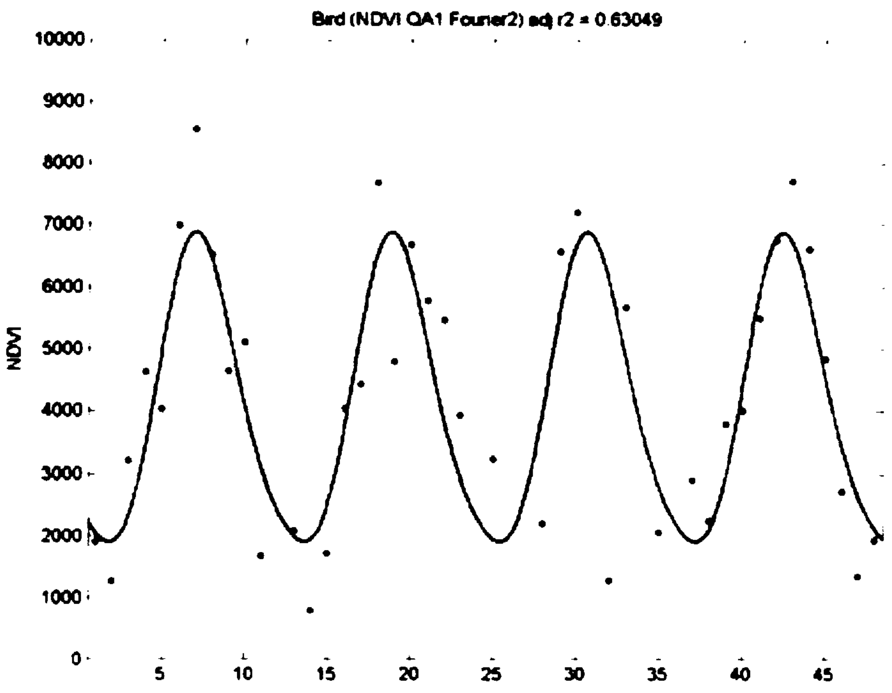


Figure 1.8. Comparison of fitted curves between two similar size islands: (A) Bogoslof Island (62ha, 12 pixels), (B) Bird Island (60ha, 11 pixels).

Chapter 2. Introduced predators and spatial subsidies: plant community patterns in space and time

Introduction

There has been considerable debate in ecology about the indirect impacts of top-level predators on the vegetation dynamics of terrestrial systems (Pace et al. 1999, Polis et al. 2000, Schmitz et al. 2000). Under the classic "Green World" hypothesis, predators can have strong indirect effects on plants by controlling the abundance of herbivores (Hairston et al. 1960). Recently, alternative interaction pathways have also been demonstrated in systems where predators have substantial indirect impacts on plants that are not exclusively trophic (Maron et al. 2006). One such alternative interaction pathway involves spatial subsidies—the movement of nutrient resources between systems. Such subsidies can significantly influence the structure and dynamics of the recipient system (Polis et al. 1997, Maron et al. 2006). Croll et al. (2005) and Maron et al. (2006) have established that predators have had significant indirect impacts on vegetation communities on islands in the Aleutian Archipelago of Alaska via a spatial subsidy. More specifically, foxes introduced to individual islands have caused shifts in plant community composition by severely reducing the number of seabirds that formerly vectored nutrients from the ocean onto the islands in the form of guano (while guano is the principle material source, other sources include seabird carcasses, uneaten food, and broken eggs). Islands without introduced foxes had significantly greater biomass and percent cover of grasses, while islands with foxes had significantly greater biomass and percent cover of dwarf shrubs. In addition, plant, soil, and higher trophic level organisms had significantly higher $\delta^{15}N$ signatures on fox-free islands, indicating they were utilizing marine derived nutrients (MDN) as opposed to internally derived sources.

While the results of Croll et al. (2005) and Maron et al. (2006) showed striking differences in vegetation between fox-infested and fox-free islands, their conclusions were based upon small samples (30 X 30m plots and 1m subplots) regularly distributed across the islands, collected at a single point in the growing season. Thus their work did not test the full temporal and spatial extent of the predator impacts in this system. Mechanisms that drive observed patterns often operate at different scales (Levin 1992). The logistical constraints of on-the-ground sampling often limit the spatial scale and level of detail at which communities and ecosystems can be characterized (Kareiva 1990), and it is important to understand if the same patterns measured at smaller scales are translated to the landscape level. Remote sensing provides a tool for measuring vegetation dynamics over large spatial and temporal scales and can be used in combination with detailed field sampling to rigorously evaluate if processes occurring on the scale of meters can be translated to the landscape level. To date there are no published studies that rigorously document the landscape-wide effects of top-level predators on vegetation communities.

Here I test for differences in the satellite measured phenological characteristics of the dominant plant communities across the entire Aleutian archipelago, comparing islands infested with foxes to those that are fox-free. From the optical remote sensing perspective, the primary difference between fox-infested and fox-free islands is the percent cover and biomass of two important community types: grasses and dwarf shrubs. Through extensive field surveys, Maron et al. (2006) showed: 1) that the mean biomass of grasses is ~3x higher and mean cover is 14 percent higher on fox-free than fox-infested islands, and correspondingly, the cover of dwarf shrubs is significantly greater on fox-infested than fox-free islands (30% and 6% respectively); but that 2) that the <u>total</u> community biomass is only marginally higher on fox-free islands. Remote sensing offers the opportunity to examine differences in seasonal dynamics of these two plant classes that can be used to better separate fox-infested and fox-free islands and to test the importance of any temporal differences in productivity. In other words, remotely sensed phenological patterns can provide critical data to add to our understanding of the temporal dynamics of the plant communities on each island type. This approach can provide temporally detailed information across large scales that is logistically difficult or impossible to obtain using tradition ground based methods (Schwartz 2003).

In addition to understanding growing season plant dynamics at the landscape and regional (i.e., across an entire island chain) levels, a more precise depiction of the effects of top-level predators includes examining the within-island spatial variation in the response of the plant communities to nutrient subsidies. These subsidies are indirectly mediated by foxes preying on seabirds. Seabird colonies in the Aleutian Islands are generally located close to the shoreline (J. Williams, USFWS personal communication) and the amount of nutrient deposition likely decreases with distance from shore. Thus, it is important to determine the distance that the nutrient subsidies extend inland in order to evaluate the total spatial extent of the impact of introduced foxes on the plant communities.

In this chapter I examine effects of introduced foxes on the insular vegetation of the Aleutian Archipelago. This work expands the smaller scale study done by Croll et al. (2005) and

Maron et al. (2006) by sampling entire islands on a monthly basis. Using this approach I demonstrate the indirect effects of a top predator on plant communities at both the landscape level and across seasons. Specifically, I address two patterns: (1) the differences in seasonal vegetation dynamics between fox-free and fox-infested islands, and (2) the spatial extent of the nutrient subsidy within islands. I examine these patterns by analyzing the seasonal dynamics in the satellite derived vegetation parameters across 30 islands in the Aleutian Archipelago (20 fox-infested, 10-fox-free) from 2001-2004.

Methods

Remote sensing technology has rapidly improved over the past two decades and the use of the Normalized Difference Vegetation Index (NDVI) remains a simple yet powerful remote sensing metric for measuring plant community dynamics (Kerr and Ostrovsky 2003, Pettorelli et al. 2005). The NDVI is generated from the ratio of red and near infrared bands [(NIR-RED) / (NIR+RED)] and is an optical measurement of "greenness" that correlates strongly with plant biomass and seasonal production (Myneni et al. 1995). The NDVI has been applied successfully in studies of land cover changes (Fung and Siu 2000), global increases in terrestrial productivity due to climate change (Nemani et al. 2003), and regional effects of drought and fire (Leblon 2005). Although satellites capable of providing NDVI parameters have been available for several decades, there has traditionally been a tradeoff between spatial and temporal resolution, such that there have been no good platforms for studying ecosystems such as the Aleutian Archipelago. Spectral data from the most recent generation of satellites such as the Moderate Resolution Imaging Spectroradiometer (MODIS) acquire NDVI data at frequent intervals and reasonable (250 m) spatial resolution, and can therefore be used to generate precise measurements of seasonal vegetation dynamics. These phenology curves serve as baselines from which informative quantitative parameters can be extracted regarding the timing and magnitude of seasonal events (Jonsson and Eklundh 2002, Schwartz 2003, Zhang et al. 2003). Thus, remotely sensed phenological patterns can provide critical, temporally detailed information across large scales that is logistically difficult to obtain using tradition ground based methods (Schwartz 2003).

Danner (Chapter 1), in a study of the Aleutian Islands, Alaska, demonstrated that MODIS 250m NDVI data can be used to precisely measure seasonal vegetation phenology of a range of landscape sizes. The NDVI is commonly used as a covariate in ecological studies (Pettorelli et al. 2005), but in this study I explicitly test for differences in plant community composition on islands using the NDVI (and parameters derived from it) as the dependent variables. The foundation of this technique is based on generating the mean NDVI value across an entire island on a monthly basis. The variation across vegetation communities and habitats is averaged out and the NDVI for an island at any given point in time represents the mean of all the plant communities across the entire landscape. Thus, this approach provides for each island an estimate of how the vegetation is responding to a given factor of interest at the landscape level.

Study Islands

I defined the Aleutian Archipelago as ranging from Attu Island (172°56' E, 52°00' N) in the west to Caton Island (162°25' W, 54°23'N) in the east, an area covering ~1900km of longitude and ~500km of latitude (Figure 2.1). The archipelago contains >450 islands and offshore rocks ranging in size from 1ha to >400,000ha. The vegetation is maritime tundra, dominated by grasses, dwarf shrubs, lichens, and forbs (Amundsen 1977). There are no trees or large shrubs and the maximum vegetation height rarely exceeds 1m (Danner, personal observations). Even though the archipelago spans a large geographic range, the islands share similar geological origins and histories and have plant communities that are relatively homogeneous in species composition (Maron et al. 2006). The island sizes and shapes are not different across the archipelago, nor is the amount of rainfall (Danner Chapter 1). There are, however, significant longitudinal trends in the percent cover of snow, ice, and clouds which affect the timing of some of the phenological events measured using the NDVI (Chapter 1). The maximum and minimum seasonal NDVI and the integrated NDVI values were all lower from east to west, indicating lower overall production due to colder climate (Chapter 1).

Arctic foxes, *Alopex lagopus*, were added to hundreds of Alaskan islands by fur trappers over the past 250 years (Black 1984). I selected a subset of 20 fox-infested islands and 10 fox-free islands for analysis (Table 2.1, Figure 2.1). Islands were selected based upon a known history of fox introductions, based upon a comprehensive survey by Bailey (1993). I assumed that foxes were only introduced to islands with high seabird densities (seabirds provided the primary food source for the foxes and very likely played an important role in the island selection process), but recognized that in some cases foxes were introduced but subsequently died off or were removed. On a small subset of these islands the seabird populations have recovered [e.g. Vsevidof, which currently supports over 120,000 seabirds, had foxes introduced in 1920 (Bailey 1993), but these died off at an undetermined date]. Because fox-free islands are relatively rare, the introduced foxes persisted only for short periods, and they have subsequently been fox-free for many decades, I consider these islands to be "fox-free" for the purposes of this study. I also selected islands that were > 50ha but <

3400ha for the analyses. The minimum size was based upon on the resolution limitations of MODIS 250m NDVI sampling (Chapter 1), while maximum island size corresponded to the largest fox-free island, Segula (3308ha). Finally, each island used in the analysis had to meet minimum remote sensing quality criteria for measurement using MODIS 250m NDVI (see below).

MODIS Analysis

The protocol for analyzing MODIS 250m NDVI data are described in detail by Danner (Chapter 1). Briefly, I used MODIS Terra 250m NDVI 16-day composites from 2001 through 2004 (MOD13Q1). For each island I calculated the mean value of all pixels for each 16-day sample period, and then averaged these two values for each month for a single monthly mean. For each island I fit the mean monthly values from four consecutive years, 2001-2004, to a two-term Fourier function (MATLAB Curve Fitting Tool, version 1.1.3) using the following equation:

$$y = a_0 + a_1 \cos(xp) + b_1 \sin(xp) + a_2 \cos(2xp) + b_2 \sin(2xp)$$

Where y = the NDVI at time x (month) and $p = 2\pi/(\max(x)) - (\min(x))$, or 0.53 for each island. This is a nonlinear least squares fit with the assumption of normally distributed errors. I checked plots of the residuals for normal distribution of errors. I used the proportion of the variance explained, the adjusted r^2 value, from each island as the measure of the goodness of fit of the data to the Fourier equation. I generated NDVI values at 3-day increments from the Fourier function and then averaged the values from each island type to generate mean seasonal phenology curves for fox-free and fox-infested islands. I used the same procedure to generate mean phenological curves for both island types combined for the western and eastern Aleutian sub-regions. For each island I then extracted six seasonal parameters that are commonly used in satellite based phenological studies from the NDVI fitted line (Figure 2.2): the maximum and minimum values of the NDVI during the growing season (Max NDVI, Min NDVI); the date of peak of growing season (Date at Max NDVI); the growing season integral (GSI); the slope of the spring green-up (Spring Slope); and growing season length [distance between the most rapid green-up during the spring (spring inflection point) and the most rapid senescence in the fall (GSL)]. I then used these parameters as the response variables for the statistical tests of fox effects (see below).

Aleutian plant communities

The effectiveness of using seasonal NDVI parameters to distinguish between fox-infested and fox-free islands depends on the magnitude of island-wide differences in plant species composition and total plant biomass. While Croll et al. (2005) and Maron et al. (2006) found that the introduction of arctic foxes caused significant shifts in plant community composition and biomass on fox-infested islands, two components of their results illustrate the limitations for detecting differences between the two island types at a single point in time compared to using the NDVI. First, the differences in community structure were due to differences in the relative abundances of plant species rather than complete changes in species composition (Figure 2.3a, J. L. Maron, J. A. Estes, and D. A. Croll, unpublished data). Second, the difference in total plant biomass between island types is only marginally significant [$F_{1,15}$ = 3.3, $P = 0.09$, Maron et al. (2006)]. These results are based on field data collected at the peak of the growing season (August). When measured over an entire season, however, the seasonal phenological patterns of the key species classes may be substantially different. Specifically, the graminoids (dominated by *Leymus mollis*, a perennial graminoid up to 120 cm tall) that make up the majority of the cover on both types of islands have strong seasonal growth patterns that are clearly detected using the NDVI (green during the growing season and brown in the early spring and late fall, Figure 2.4). In contrast, the dwarf shrub *Empetrum nigrum* (a creeping, matted, perennial evergreen shrub to 15 cm tall) is green year round and does not fluctuate substantially in biomass throughout the growing season (Chapin and Shaver 1985). Croll et al. (2005) and Maron et al. (2006) found that graminoids were more abundant on fox-free islands and dwarf shrubs were more abundant on fox-infested islands. In summary, the differences in relative abundance and biomass of the principle plant types combined with differences in phenology could result in significantly different seasonal NDVI patterns between fox-free and fox-infested islands (Figure 2.5a). Because this analysis incorporates these temporal dynamics, the NDVI may therefore be more robust at detecting differences between fox-infested and fox-free islands than the single point measurement of Croll et al. (2005) and Maron et al. (2006), despite the subtle plant community differences for any given time point.

Spectrometer Measurements

To validate the quality of the MODIS NDVI data, I generated NDVI estimates of the dominant plant classes (forbs, graminoids, dwarf shrubs, and moss, Figure 2.6) in the field using a GER 1500 hand-held spectroradiometer (GER Corporation). I used the same bands as MODIS NDVI product (620-670nm and 841-876nm) to generate NDVI estimates from the hand-held spectroradiometer data. The instantaneous field of view (IFOV) was 3 x 4.75cm at a height of 35cm, so the target area was a precise measurement of a single species.

I calibrated the instrument to ambient light conditions before every third sample or any time there was a notable change in light conditions. To contrast the island-wide satellite derived NDVI with the field spectrometer measurements I "scaled-up" the spectrometer-measured values to the landscape scale. I generated an *adjusted* NDVI for each of the major plant classes by multiplying the NDVI generated from the spectrometer measurements by the percent cover determined from the field studies (Maron et al. 2006). I summed the adjusted NDVI values for each island within each island type to generate a composite NDVI value.

Spatial extent of the subsidy

The spatial patterns of subsidies across landscapes likely result in corresponding spatial structure in the food webs (Cadenasso et al. 2004). Seabird colonies in the Aleutian Islands are generally located close to the shoreline (J. Williams, USFWS personal communication) and the amount of nutrient deposition likely decreases with distance from shore. Therefore with the exception of small islands with high densities of seabirds it is likely that nutrient subsidies diminish towards the interior portions of fox-free islands. Further, the high precipitation common in the Aleutian archipelago likely facilitates the transportation of nutrients toward the perimeter of the islands. Thus it is critical to determine the distance that the nutrient subsidies extend inland in order to evaluate the corresponding spatial extent of the impact of introduced foxes on the plant communities.

I was able to measure the differences in the NDVI between fox-infested and fox-free islands extending from the shore to 1000m inland (extending beyond 1000m from shore diminished the number of pixels available for analysis to <5% of the total number of pixels due to the small size of islands). I divided pixels from each island into 100m bins as a function of their distance from shoreline (0 to 1000m) and calculated the mean NDVI (non Fourier smoothed) for each bin. I subtracted the grand mean for all fox-infested islands from the grand mean for all fox-free islands for each distance bin to provide an NDVI differential (dNDVI). This value represents enrichment as a function of distance from shore (DS). Thus the higher the dNDVI value the greater the vegetation enrichment due to the absence of foxes (and thus the presence of seabirds). The dNDVI distance from shore (dNDVI-DS) relationship was defined by fitting the dNDVI values by distance bin to a two-term exponential function (MATLAB Curve Fitting Tool, version 1.1.3) using the following equation:

$$y = ae^{(bx)} + ce^{(dx)}$$

where y = dNDVI at distance bin x. This is a nonlinear least squares fit with the assumption of normally distributed errors. This function was selected over a simple exponential because it incorporates an initial increase followed by exponential decay.

I then calculated the theoretical area affected on each fox-infested island assuming that enrichment occurred at the rate described by the dNDVI-DS function. I limited the analysis to islands within the same size range as the study islands (between 50 and 3400 ha). This resulted in 44 islands (I did not include islands where seabirds have recovered). I used the distance from shore corresponding to the maximum dNDVI to represent 100% enrichment, with all other distances representing a corresponding percentage of that maximum based on the above function. I applied the percentage enrichment to each MODIS pixel as a function of its distance from shore (based on the center of the 250m pixel). For example, a pixel with a distance from shore value of 200m would have an enrichment value of 100%, while pixels beyond 1000m from shore would have an enrichment value of 0.

Statistical Analysis

The analyses were performed with SYSTAT 10.2 (2002). For the spectrometer data I tested for differences in mean NDVI between plant classes using one-way ANOVA with planned comparison contrast for linear trend (class order: forbs, graminoids, shrubs, moss). To compare the satellite data with the spectrometer data I used the composite NDVI values for each island type (fox-free = 10 islands, fox-infested = 8 islands) and the Max NDVI value from Fourier smoothed satellite data (fox-free n = 10 islands, fox n = 20 islands). I tested for differences between measurement type (spectrometer or MODIS) for each island type using ANOVA with planned comparisons (fox-free spectrometer vs. fox-free satellite, and fox-infested spectrometer vs. fox-infested satellite).

Due to the large geographic extent of the Aleutian archipelago there are significant gradients in climate from east to west (Chapter 1). I tested for east-west trends in the vegetation dynamics by regressing the seasonal NDVI parameters for each island against longitude. In addition I tested for sub-regional differences (eastern Aleutians vs. western Aleutians, Figure 2.1) in the NDVI through time using repeated measures ANOVA. I used monthly (n = 12) island means for each sub-region (eastern Aleutians n = 41, western Aleutians n = 49) as the dependent variables and sub-region as the independent variable. To evaluate for regional differences in the NDVI through time I tested for a significant interaction between month and east-west sub-region.

I evaluated the effects of foxes on vegetation by testing the various seasonal NDVI parameters between fox-infested and fox-free islands using ANCOVA. I used the NDVI parameters as the response variables, island type as the independent variable, and longitude as the covariate. I also used repeated measures ANCOVA to test for differences in the NDVI between fox-infested and fox-free NDVI through time. I used monthly (n = 12) island means as the dependent variables, island type as the independent variable (fox-free = 10 islands, fox-infested = 20 islands), and longitude as the covariate. To evaluate the seasonal effect of foxes on the NDVI through time I tested for a significant interaction between month and island type.

Results

Spectrometer

The magnitude of the spectral differences between plant types is critical for the interpretation of the NDVI data. There were significant differences in the NDVI among all plant classes with forbs having the highest mean value, followed by graminoids, dwarf shrubs, and mosses ($F_{1,511} = 58.54$, $P < 0.0001$). The MODIS data appear to be an accurate measure of the vegetation communities at the peak of the growing season as I found no significant difference between NDVI values extrapolated from the composite NDVI and field estimates of percent cover vs. the Max NDVI values generated from the MODIS satellite measurements for both fox-infested islands (ANOVA, $F_{1,44} = 2.88$, $P = 0.0965$) and fox-free islands (ANOVA, $F_{1,44} = 1.60$, $P = 0.2122$, Figure 2.7).

Regional patterns

Due to the large geographic range of the Aleutian Archipelago, spatial trends in the seasonal parameters could have important impacts on the shapes of the seasonal phenology curves. Danner (Chapter 1) found that the Max NDVI was lower and occurred later in the summer from east to west across all of the islands in the archipelago. The GSL, however, increased from east to west ($r^2 = 0.39$, $P = 0.0002$). These patterns indicate that climate likely has an important effect on the shapes of the NDVI through time. This was true for the Aleutian sub-regions which were significantly different between the east and west (repeated measures ANOVA, E/W x Month, $F_{11,968} = 8.22$, $P = 0.0001$, Table 2.2, Figure 2.8a). Due to the significant effect of longitude on the vegetation dynamics, the main effect of island type (fox-infested vs. fox-free) was tested with longitude as a covariate whenever possible.

Fox effects

The effect of introduced foxes on the seabird populations was significant. The seabird density on fox-free study islands (6.63 birds/ha) was significantly greater than on fox-infested islands (-0.04 bird/ha, two sample t-test, $t = 10.03$, $P < 0.0001$ based on log-transformed data). Fox predation on seabirds indirectly led to significant differences in several metrics of plant community structure: 1) The Min NDVI was significantly lower on fox-free islands (ANCOVA with longitude, $F_{1,27} = 4.39$, $P = 0.0456$); 2) the amplitude of the seasonal NDVI curve was 10% greater on fox-free islands than fox-infested islands (5648 and 5086 respectively), although this difference is only marginally significant (ANCOVA with longitude, $F_{1,27} = 3.48$, $P = 0.0732$); 3) the vegetation greened-up more rapidly on fox-free islands where the Spring Slope was significantly steeper than on fox-infested islands (153 and 125, respectively, ANCOVA with longitude, $F_{1,27} = 4.68$, $P = 0.0395$); 4) while the duration of the growing season was a full month shorter on fox-free islands (4.3 months vs. 5.3 months), there was a significant *island type x longitude* interaction (Figure 2.9). Longitude had no effect on the season length on fox-free islands ($r^2 = 0.20$, $P = 0.1957$) but had a highly significant effect on fox-infested islands ($r^2 = 0.49$, $P = 0.0006$), indicating that the nutrient subsidies overwhelmed the longitudinal effects on the vegetation. While there was a range in the utility of the different NDVI parameters for detecting differences between fox-infested and fox-free islands, when viewed throughout an entire growing season the Fourier-smoothed phenological curves between fox-infested and fox-free islands show clear differences (Figure 2.8b). These differences were highly significant when tested over the course of a single season using repeated measures ANOVA (covariate = longitude, island type x month, $F_{11,297} = 3.85$, $P < 0.0001$, Table 2.3). NDVI peaks across a shorter time period on fox-free islands, reaches a higher peak in the summer and declines to lower levels in the winter, than the curve for fox-infested islands. These results confirm that the vegetation dynamics of the two island types have distinctively different phenological patterns.

Spatial extent

To quantify the spatial extent of the nutrient subsidy within islands for each island type, I plotted the difference in the mean NDVI values (dNDVI) between fox-free and fox-infested islands as a function of the distance from shore using a two-term exponential function (Figure 2.10). The function captured 65% the variation in the dNDVI between 0 and 1000m from shore. At the shoreline there was very little evidence of enrichment (dNDVI = 45, the function was not forced through zero), followed by rapid increase in dNDVI that peaked at 213m from shore. The dNDVI showed exponential decay with increasing distance inland. I then used this function to estimate the total area of habitat on fox-infested islands that would have been impacted by the reduction or elimination of the nutrient subsidy. I estimated that a total of 19,812 ha of habitat on fox-infested islands were enriched before the introduction of foxes (Appendix A). Other models (e.g. a linear decrease with distance from shore) would change the absolute values, but not the reported patterns or overall results.

Discussion

Large Scale Patterns Across Islands

This study shows the effects of a top level predator on vegetation communities across entire landscapes and across an entire region. Introduced foxes have indirectly altered the plant community composition and seasonal dynamics for entire islands. Using remotely sensed NDVI data I was able to show that seasonal vegetation phenology was significantly different between fox-infested and fox-free islands (repeated measures ANOVA, Table 2.3, Figure 2.8b). This result is particularly intriguing given that Maron et al. (2006) found only marginally significant differences in total vegetation biomass between fox-infested and fox-free islands. Thus remote sensing provides a considerable increase in analytical power and information through seasonal sampling that cannot be obtained by sampling a single point in time. Overall, the results presented here corroborate the findings of Croll et al. (2005) and Maron et al. (2006) and indicate that introduced foxes impact vegetation communities in a similar fashion at both small and landscape scales. My study builds on this past work by testing the same hypotheses using entirely different methodologies at substantially larger spatial scales, and confirms the importance of scale in ecological research. Important patterns that are detectable at small scales are not always significant at large scales. Likewise, patterns that are difficult if not impossible to measure at small scales can be readily apparent at large scales. My results also show that an important, previously unreported, impact of fox introductions is a significant shift in growing season. On fox-free islands, the growing season is a full month longer, the green-up is faster, and the maximum productivity is significantly higher. Thus, although there are relatively subtle changes in plant community, the cumulative impact of these changes are magnified through time.

The islands of the Aleutian Archipelago provide opportunities and challenges for using remote sensing to measure vegetation patterns. For the remote sensing techniques described here there are over 90 islands throughout the archipelago that are large enough and have low variability in intrinsic biological and physical parameters. While the physical characteristics of the archipelago are spatially homogeneous, these same characteristics can also be challenging for remote sensing. The weather of the Aleutian region can significantly hinder the effectiveness of optical remote sensing. The percentage of cloud cover is highest during the summer growing season and winter measurements are made more difficult by periodic snow cover. Sensors with low acquisition frequency but high spatial resolution such as Landsat rarely generate enough quality imagery during any single season to be useful. Previous sensors such as the Advanced Very High Resolution Radiometer (AVHRR) provide much improved temporal coverage, but coarse (1 km) spatial coverage and poor signal to noise ratios. The isolated nature of the region makes airborne remote sensing logistically difficult and expensive. Due to its high acquisition frequency, improved sensitivity, and detailed quality assurance data, MODIS NDVI is the most effective and economically viable method (the data are distributed free of charge) to measure the island landscapes through time.

Studies that make use of remotely sensed data require some form of validation to confirm the accuracy of the results. Large scale phenological data are difficult to validate on the ground (Schwartz 2003) because of logistical difficulties in simultaneously measuring vegetation parameters across time on numerous islands throughout the year. However, MODIS NDVI data have been well validated in numerous systems, for both instantaneous measures of biomass (Myneni et al. 1995) and seasonal phenology patterns (McCloy and Lucht 2004). Danner (Chapter 1) demonstrated that 250m MODIS NDVI data can be used to measure the seasonal vegetation phenology on islands in the Aleutian archipelago with a high degree of precision. When used in combination with fine scale field data, moderate scale remotely sensed data can be an effective tool (Kerr and Ostrovsky 2003). For the work presented here, the combined results of the *in situ* plant sampling and spectrometer measurements indicate that the Fourier fitted MODIS NDVI values are accurate representations of the vegetation on islands at the peak of the growing season. The composite spectrometer NDVI values for the study islands were not statistically different than the MODIS generated Max NDVI values, although the power of these tests was low (0.32 for fox-infested and 0.26 for fox-free islands) due to the small sample sizes.

It is important to note the use of longitude as a covariate in the evaluation of the fox effect. At the full spatial scale of the study there is potential for major geographic patterns to affect the vegetation dynamics in critical ways. The GSL increases significantly from east to west (Danner Chapter 1). Thus, islands in the western Aleutians appear to have phenological curves that are more similar to fox-infested islands (wider and flatter). This pattern likely obscures the fox effect on the shape of the vegetation phenology because fox-infested islands have lower, wider curves due to lower abundances of graminoids. Field studies, however, indicate that there is no difference in grass biomass or percent cover with longitude (r^2 = 0.02, $P = 0.6227$ and $r^2 = 0.03$, $P = 0.5118$ respectively, J. L. Maron, J. A. Estes, and D. A. Croll, unpublished data). The most likely explanation for the shift in seasonal phenology is a longitudinal trend in land surface temperature (Danner Chapter 1). This temperature gradient is likely causing the flattening of the phenology curve from east to west for fox-infested islands. Nevertheless, the longitudinal effect is overwhelmed by the subsidies on fox-free islands where the shape of the curve (as measured by the GSL) is not affected by longitude (Figure 2.9).

Within Island Spatial Extent of Subsidies

At the landscape level, the differences in the vegetation communities between fox-infested and fox-free islands are a function of the magnitude of net difference in nutrient subsidies between the two island types. The marine derived nutrients that constitute these subsidies must cross the land/sea interface. Compared to many other landscape boundaries, the boundary between aquatic and terrestrial environments is extreme and abrupt (Cadenasso et al. 2004). There are important ecological processes associated with boundaries, often described as “edge effects”. I define edge effects as the plant community differences between an island’s edge and the interior. The well-defined nature of the island boundaries makes it possible to precisely quantify the spatial extent of the nutrient subsidies that cross those boundaries. The spatial dynamics of the subsidy in the Aleutian Island system is likely a combination of two distinct boundary patterns: (1) a semi-permeable boundary that allows for the limited transport of wind-borne nutrients (the edge effect decays over meters, Figure 2.11) and (2) a highly permeable boundary where there is a large scale subsidy facilitated through seabirds (the edge effect decays over 100s of meters, Figure 2.11). The spatially-limited, wind driven boundary is present on all islands, while the seabird facilitated boundary has been severely restricted or eliminated on fox-infested islands. To evaluate the spatial extent of the subsidy on fox-free islands it is necessary to view these two mechanisms in combination. The difference in NDVI between fox-free and fox-infested islands, the dNDVI, is close to zero at the immediate shoreline due to the nearshore subsidy that affects all islands. This is because the island perimeter is always enriched, thus there is no differential in the NDVI between fox-infested and fox-free islands. This effect decays rapidly and is no longer detectable at 100m inland, resulting in a rapid increase in the dNDVI which peaks at 213m inland. The 200m distance bin represents the highest zone of enrichment for fox-free islands, and from this point inland the subsidy decreases (Figure 2.9).

The above model provided a novel opportunity to estimate the impacts of introduced foxes across the entire geographic range of the Aleutian archipelago. To approximate the overall extent impacts by foxes I used the dNDVI-DS function to calculate the cumulative degree of the pre-fox nutrient subsidies. This resulted in a total of 19,812 ha of habitat that would have been enriched before the introduction of foxes. The main assumption of the model is that foxes were only placed on islands with high densities of seabirds. This assumption is reasonable given that fur trappers were aware that seabirds were the primary food source for foxes and likely made the presence of seabird colonies one of their top island selection criteria. A breeding pair of foxes sold for as much as $34,000 in the early 20th century (Bailey 1993), so it was unlikely fur trappers placed foxes on islands without careful consideration for their survival. It is worth noting that the 19,812 ha cited above is a substantial underestimate of the total area potentially affected throughout the archipelago.

Twenty-six islands were excluded from the analysis because they were larger than 3400 ha, and therefore beyond the range of island sizes appropriate for making inferences from the model. These islands include an additional 177,084 ha of habitat that would be affected according to the model. However, this is likely a significant overestimate of the total area affected based on the assumption that larger islands would not support the high seabird densities, and corresponding levels of marine derived nutrients, found on smaller islands. This can be viewed in terms of the proportion of an island that is enriched as a function of the island size (Figure 2.12). The smallest islands would be enriched over 100% of their surface area, while moderate sized islands would have interior portions (>1000m from the shoreline) that did not receive nutrient subsidies. The largest fox-free islands would only have intermittent areas, directly around seabird colonies, that were enriched.

This study is unique in that it combines two rare methodologies: an ecological study of the indirect effects of predators on vegetation that encompasses entire landscapes, and a large scale remote sensing analysis of a predator mediated spatial subsidy. I have used remote sensing to measure the indirect impacts of a top-level predator on terrestrial vegetation (a) across entire landscapes, (b) spatially within the landscape, and (c) across the entire growing season. The landscape level analysis is noteworthy in that it provides the first remotely sensed evidence of indirect, predator-induced changes in vegetation. The within landscape analysis is significant because it spatially quantifies how a top-level predator was indirectly regulating a bottom-up resource. Finally, by analyzing the plant communities across the growing season, differences between island types become apparent that would not likely be detectable from a single measurement in time. These results combine to provide a more complete understanding of the role of top-level predators in food web dynamics.

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Table 2.1. Study Islands.

Island	Seabirds/ ha	Foxes stocked	Lat	Lon	Area (ha)	Adjusted r^2
Fox-free						
Aiktak	965.5	1921	54.2	-164.8	140	0.89
Ananiuliak	216.9	1916	53.0	-168.9	109	0.75
Bird	378.3		54.7	-163.3	60	0.63
Buldir	1910.5	1924	52.4	-184.1	1857	0.86
Chagulak	2131.6		52.6	-171.1	795	0.76
Egg	6012.4		53.9	-166.1	74	0.87
Kaligagan	2337.9	1921	54.1	-164.9	54	0.81
Ogangen	134.6	1929	53.4	-166.9	280	0.86
Segula	158.5	1920	52.0	-181.9	3308	0.92
Vsevidof	647.0	1920	53.0	-168.5	187	0.92
Fox-infested						
Adugak	17.6	1925	52.9	-169.2	51	0.69
Alaid	6.7	1911	52.8	-186.1	590	0.73
Aziak	10.5	1927	52.0	-176.2	118	0.78
Chugul	0.4	1922	51.9	-175.8	1685	0.80
Davidof	61.4	1924	52.0	-181.7	333	0.65
Igitkin	0.3	1922	52.0	-175.9	1774	0.86
Kanu	0.9	1916	51.9	-176.0	344	0.85
Kavalga	1.4	1920	51.6	-178.8	1403	0.72
Nizki	10.4	1911	52.7	-186.0	709	0.73
Ogliuga	1.3	1897	51.6	-178.6	949	0.86
Sagchudak	4.3	1914	52.0	-174.5	185	0.75
Salt	0.0	1916	52.2	-174.6	91	0.85
Samalga	0.0	1897	52.8	-169.2	378	0.87
Skagul	1.0	1897	51.6	-178.6	403	0.84
Tagadak	3.0	1925	52.0	-176.0	189	0.86
Tagalak	0.0	1916	52.0	-175.7	1336	0.81
Tanaklak	0.5	1918	52.0	-176.1	347	0.73
Ugamak	0.6	1922	54.2	-164.8	938	0.83
Ulak (West)	1.9	1924	51.4	-179.0	3019	0.64
Uliaga	0.1	1930	53.1	-169.8	855	0.83

Table 2.2. Repeated measures ANOVA. The main effect is eastern Aleutians vs. western Aleutians

Between Subjects

Source	SS	df	MS	*F*	*P*
E/W	506574.14	1	506574	0.28	0.6027
Error	5.12E+07	28	1.83E+06		

Within Subjects

Source	SS	df	MS	*F*	*P*	G-G	H-F
Time	1.20E+09	11	1.09E+08	436.67	<0.001	<0.001	<0.001
Time*E/W	1.16E+07	11	1.06E+06	4.24	<0.001	0.0096	0.0065
Error	7.69E+07	308	249805				

Table 2.3. Repeated measures ANCOVA. The main effects are fox status (fox-free vs. fox-infested islands) with longitude as a covariate.

Between Subjects

Source	SS	df	MS	*F*	*P*
Fox status	3.86E+06	1	3.86E+06	2.29	0.1418
Longitude	5.06E+06	1	5.06E+06	3.01	0.0944
Error	4.55E+07	27	1.68E+06		

Within Subjects

Source	SS	df	MS	*F*	*P*	G-G	H-F
Time	1.01E+07	11	913765	4.01	<0.0001	0.010	0.0057
Time*Fox statu	9.65E+06	11	877292	3.85	<0.0001	0.0122	0.0072
Time*Longitud	1.12E+07	11	1.01E+06	4.45	<0.0001	0.0058	0.0030
Error	6.76E+07	297	227666				

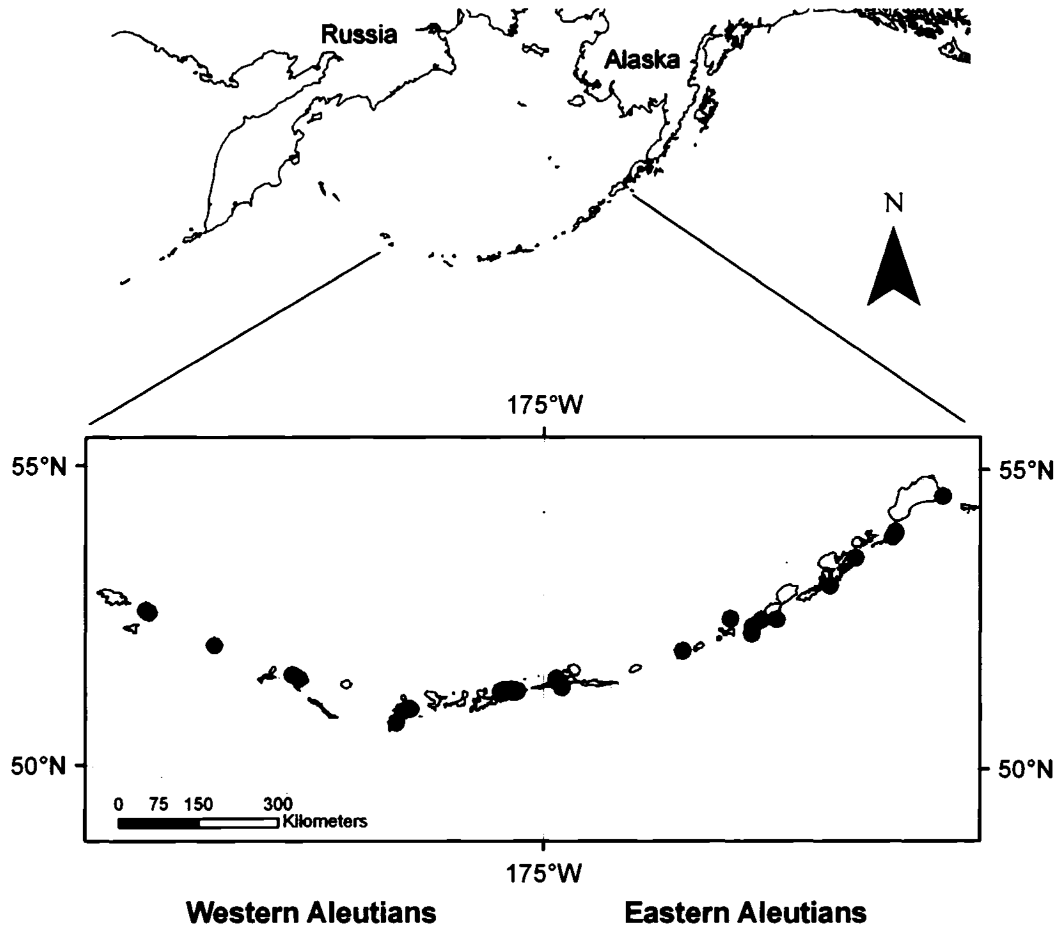


Figure 2.1. The Aleutian Islands, Alaska with study islands designated as blue (fox-free, n = 10) and red (fox-infested, n = 20). The vertical line at 175º W separates the Eastern Aleutians and the Western Aleutians. Descriptive details of each island are listed in Appendix A.

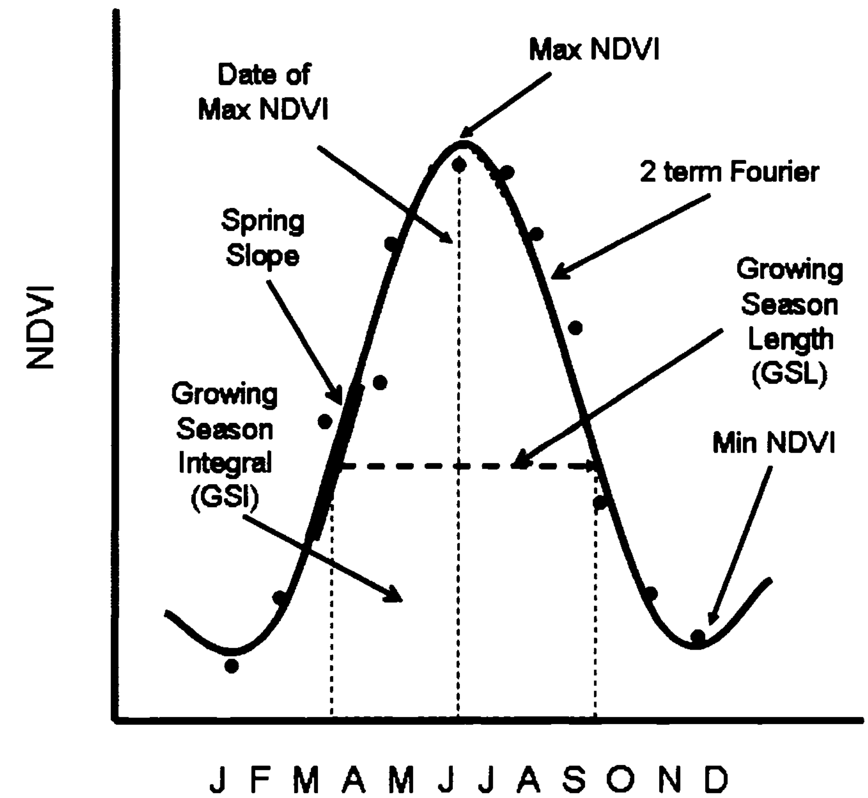


Figure 2.2. Hypothetical Fourier fitted curve representing a single growing season for a single island. Mean monthly values are indicated as blue points and the Fourier fitted curve as the red line. The six seasonal NDVI parameters are: the maxmimum and minimum values of the NDVI during the growing season (Max NDVI, Min NDVI); the time of peak of growing season (Date at Max NDVI); the growing season integral (GSI); the slope of the spring green-up (Spring Slope); and growing season length (GSL, the distance between the spring and fall inflection points).

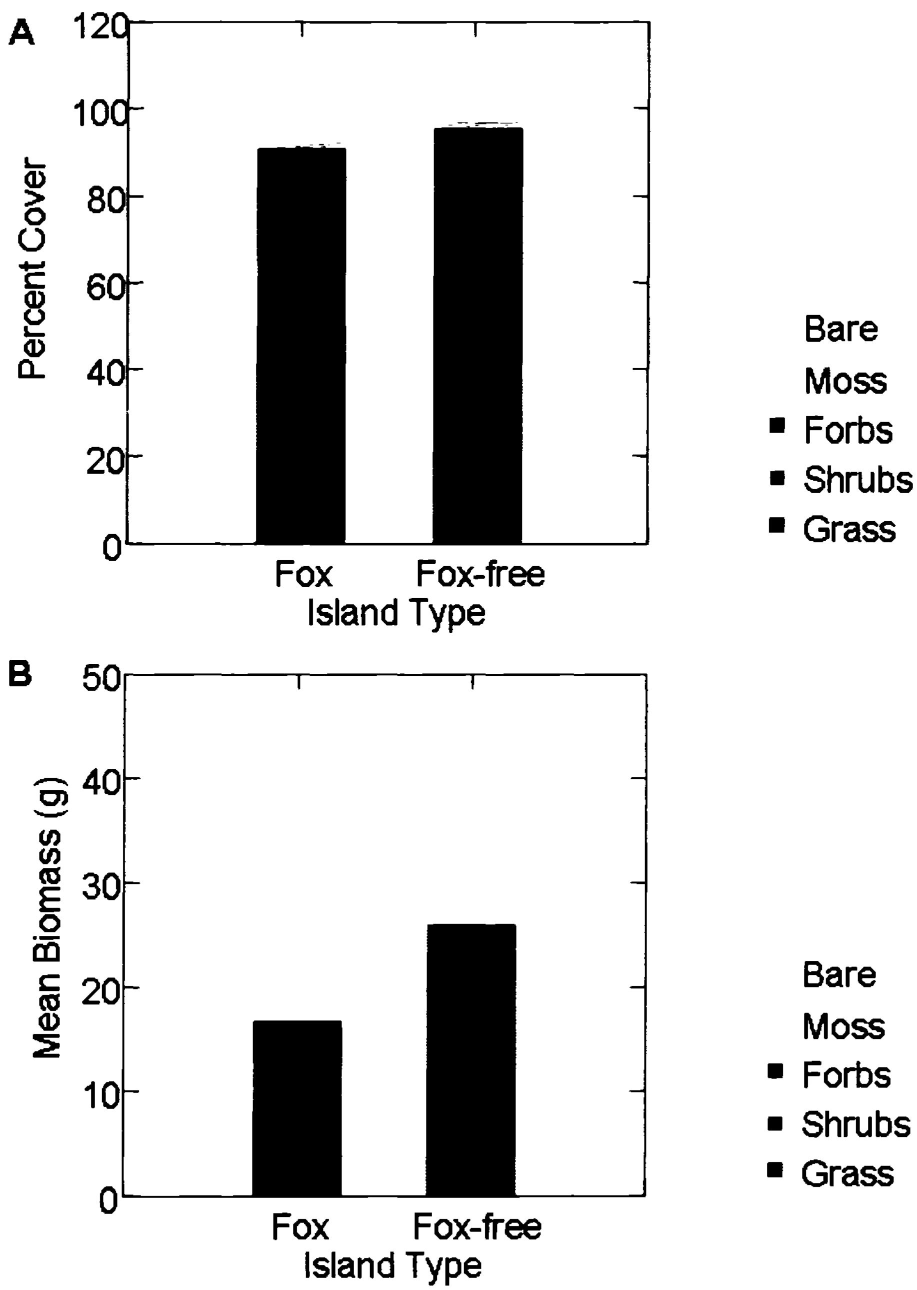


Figure 2.3. Dominant plant classes on fox-infested and fox-free island in the Aleutian Archipelago. (A) Percent cover of plant classes within 1m^2 plot. (B) Dry biomass (g/m^2). (J. L. Maron, J. A. Estes, and D. A. Croll, unpublished data).

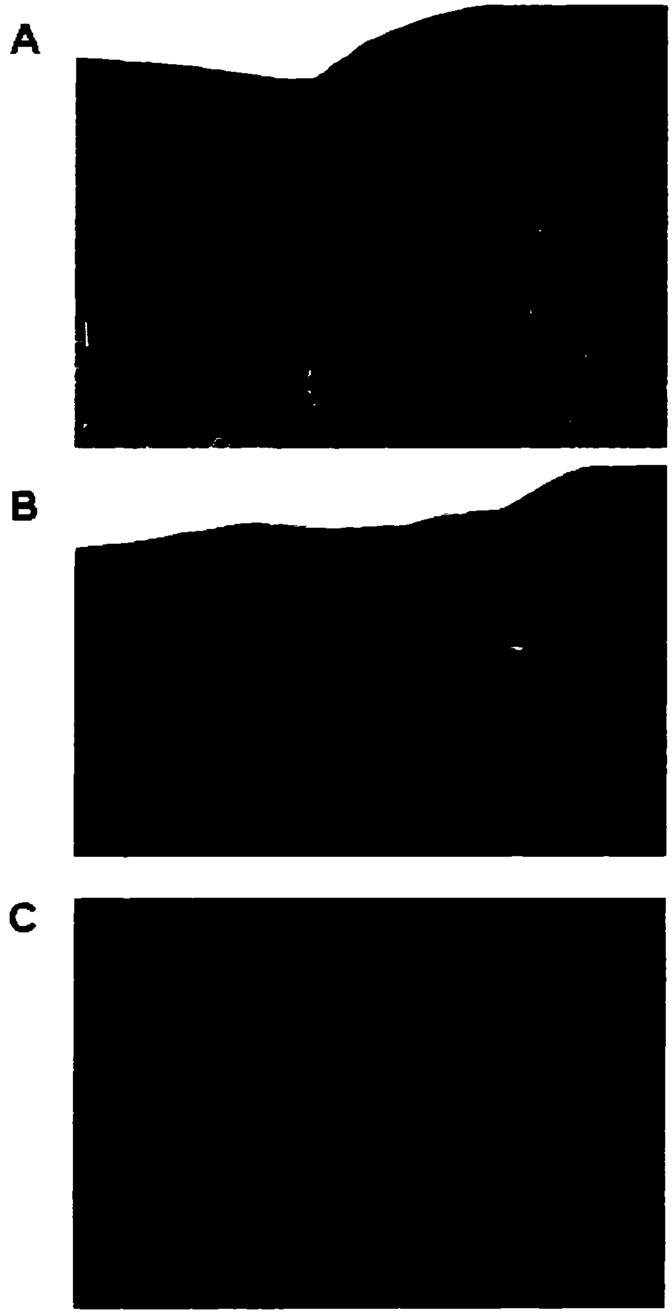


Figure 2.4. Seasonal differences in vegetation greenness. Photographs of the same general location on Adak Island during different seasons. (A) May, (B) August, and (C) January. The brown plant material in (A) is senesced grass from the previous growing season. The grasses are light brown in (C) while the shrubs are dark red-brown. Photo credits (A) Eric Danner, (B) Stacey Buckelew, University of California Santa Cruz, (C) Lisa Scharf, USFWS.

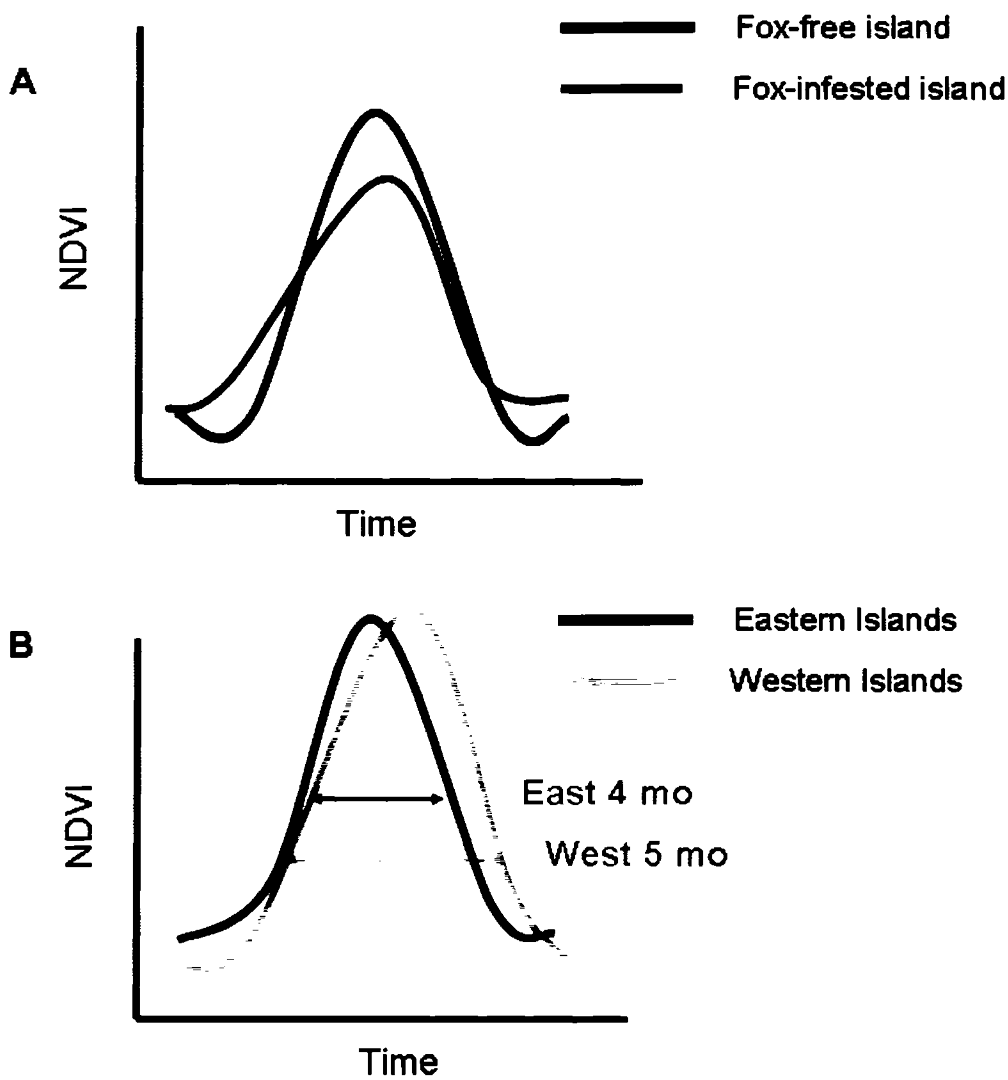


Figure 2.5. Hypothetical seasonal phenological curves. (A) Fox-free (blue) and fox-infested (red) islands. (B) Eastern Aleutian islands (dark green) and Western Aleutian islands (light green) islands. The potential differences in growing season length (GSL) is indicated by horizontal arrows and red labels.

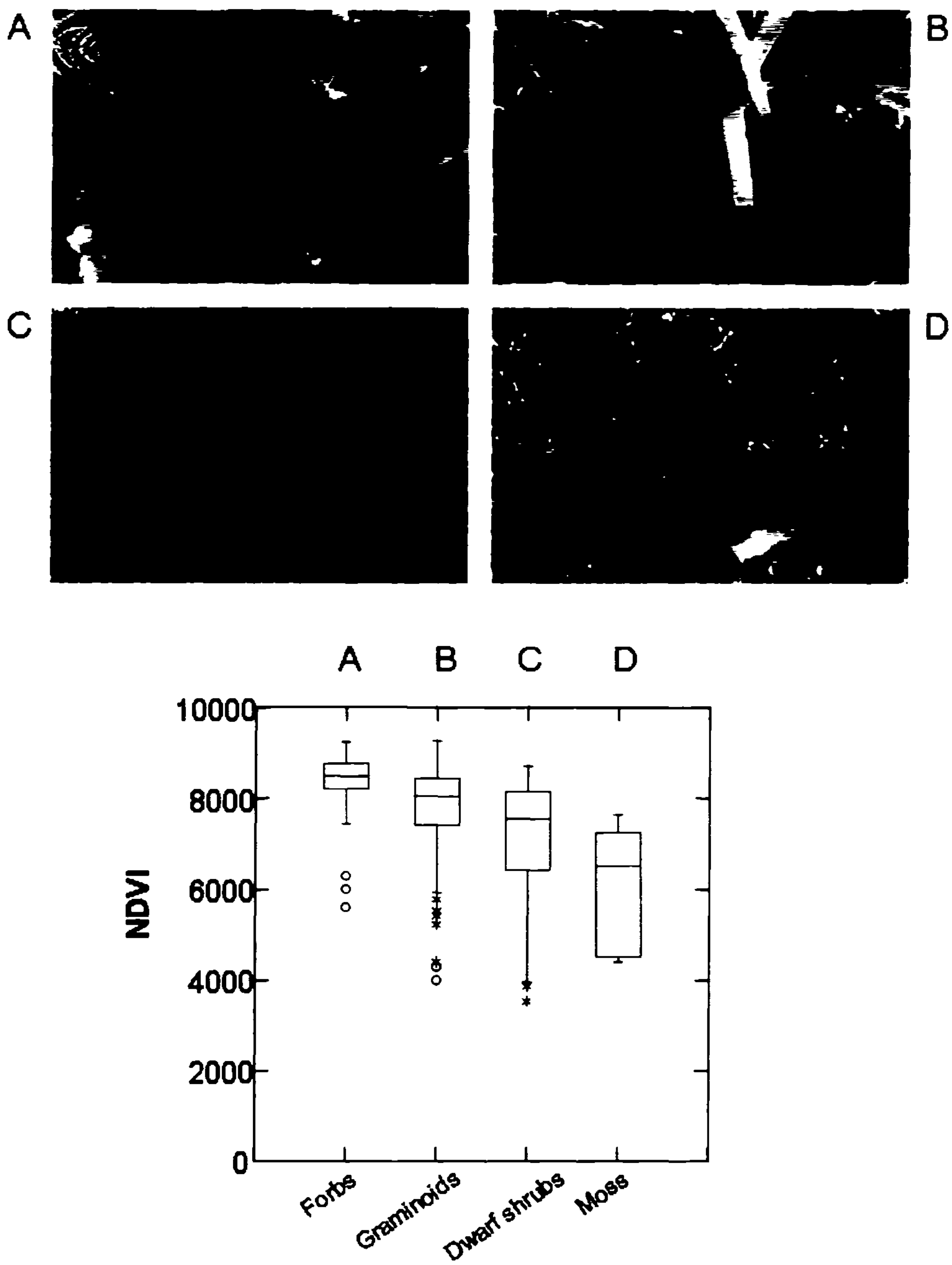


Figure 2.6. Photographs of typical plant classes and mean spectrometer generated NDVI values of (A) forbs, (B) graminoids, (C) dwarf shrubs, and (D) mosses.

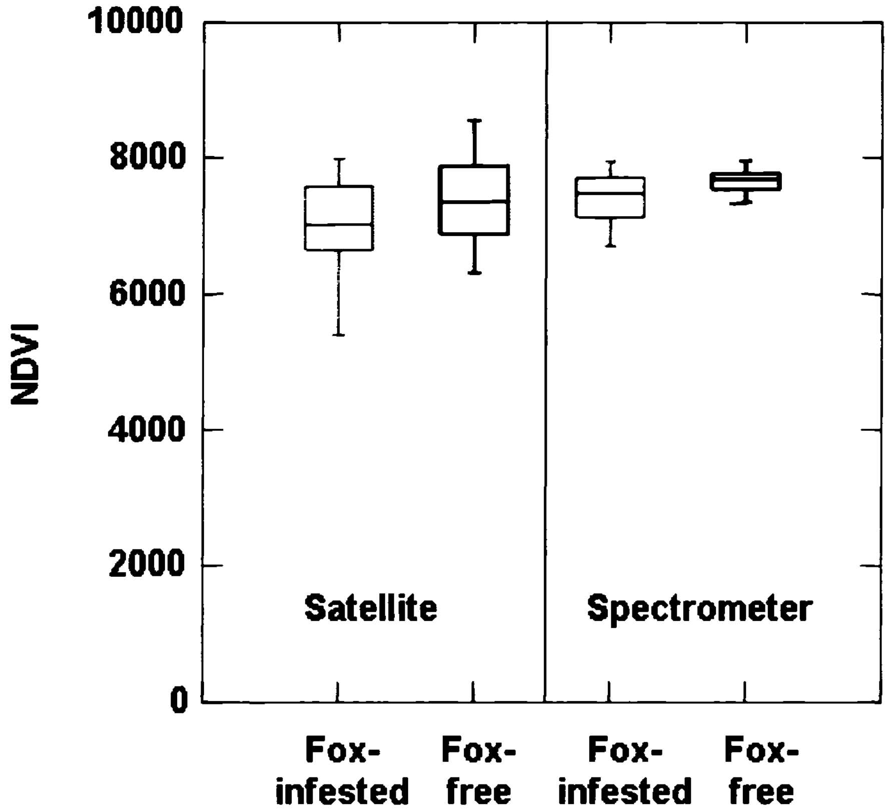


Figure 2.7. Comparison of Max NDVI values generated from MODIS satellite data and composite NDVI values based on spectrometer measurements and percent cover estimates of the dominant plant classes. Fox-infested islands are in red, fox-free islands in blue.

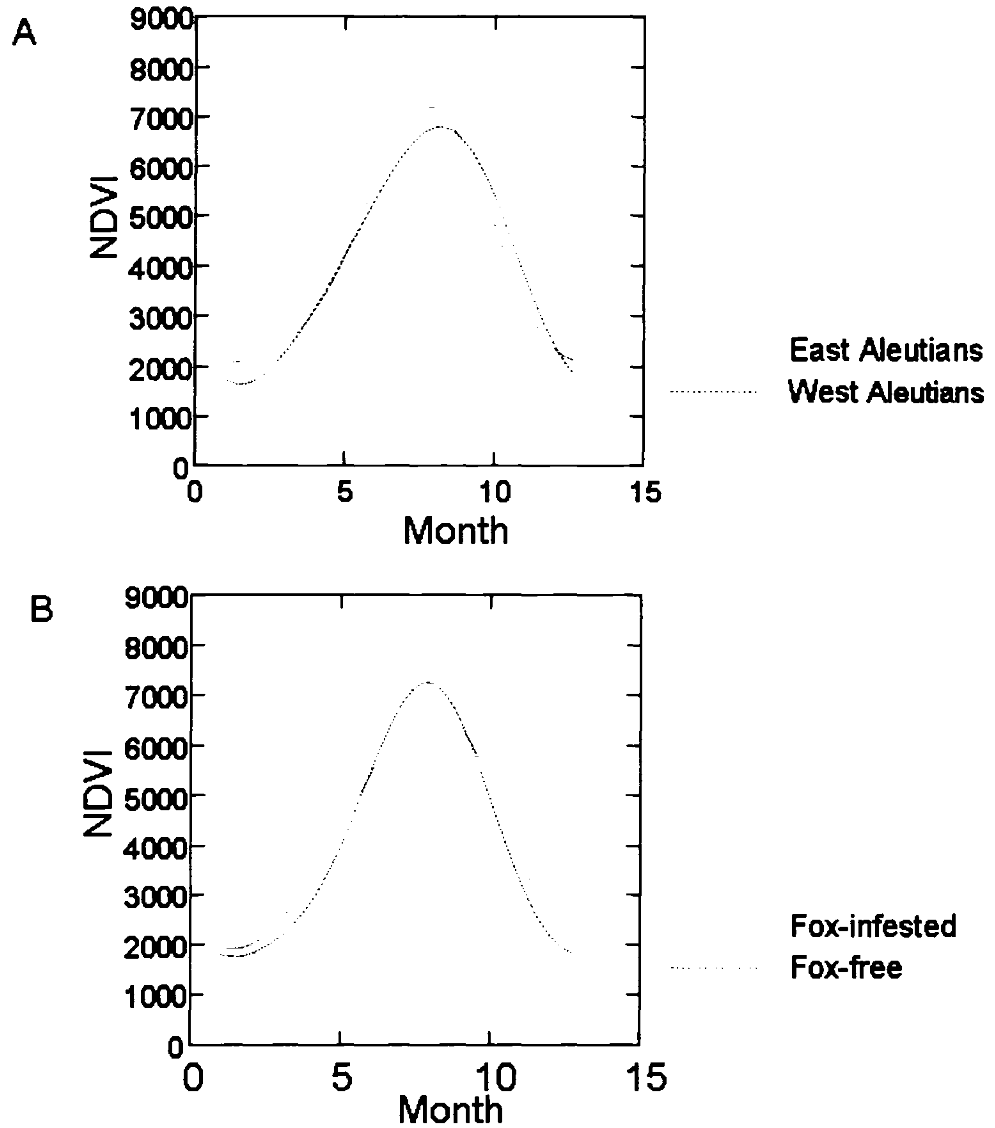


Figure 2.8. Mean Fourier transformed seasonal NDVI values. (A) Western Aleutians (blue line) and Eastern Aleutians (red line). (B) Fox-free (blue line) and fox-infested (red line) islands.

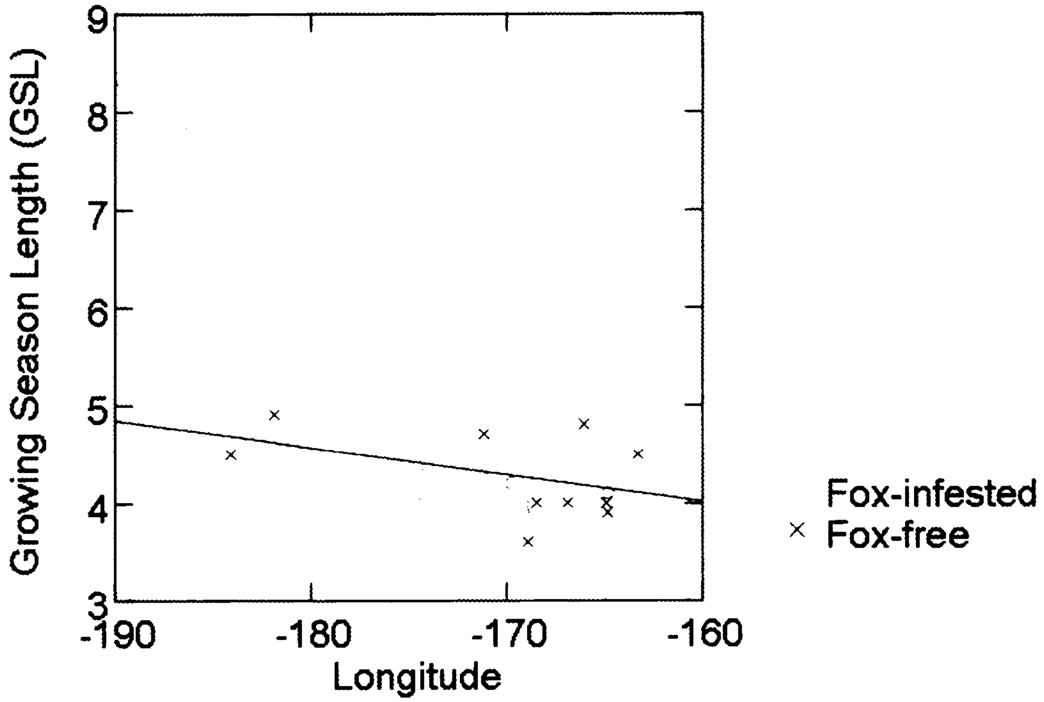
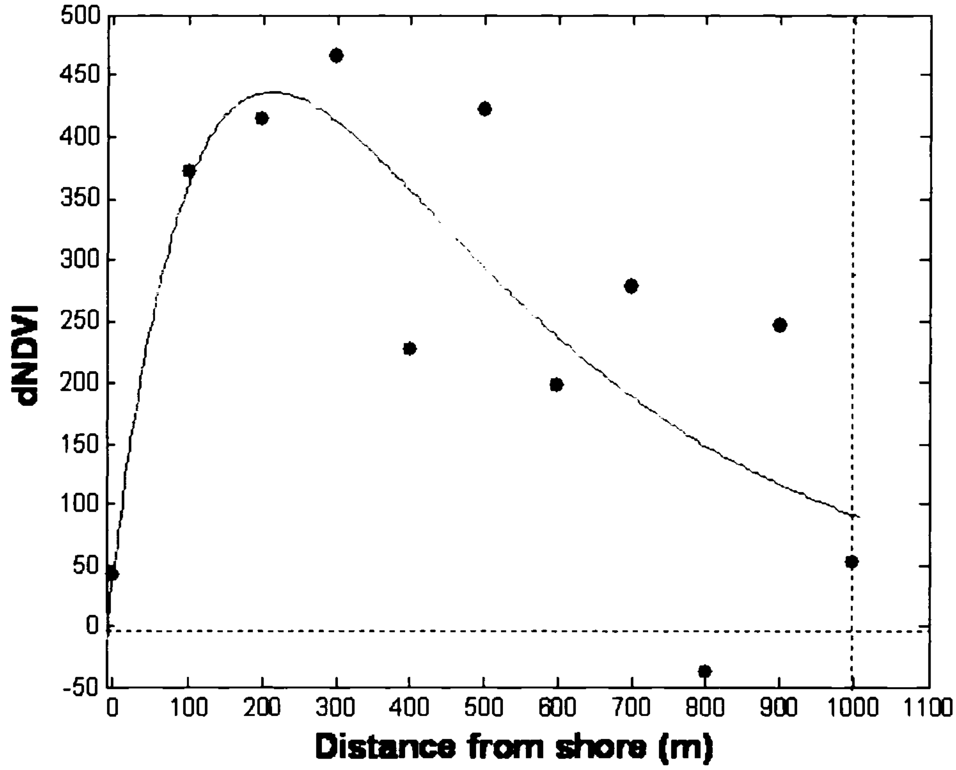


Figure 2.9. The growing season length (GSL) by longitude for fox-infested islands (red) and fox-free islands (blue).



r2 = 0.65

Figure 2.10. The relationship between the magnitude of the nutrient subsidy and the distance from the shore (100m distance bins). The dNDVI is the mean, non Fourier-smoothed NDVI on fox-free islands minus the mean NDVI on fox-infested islands for each distance bin.

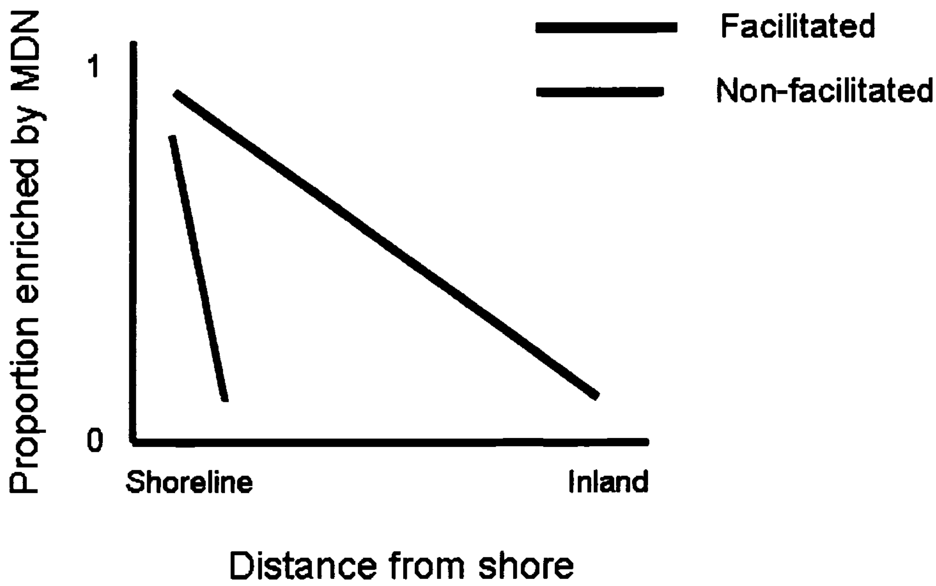


Figure 2.11. Hypothetical relationship between the proportion of the habitat enriched by marine derived nutrients (MDN) and the distance from shore for non-facilitated input (red line) and facilitated input (blue line).

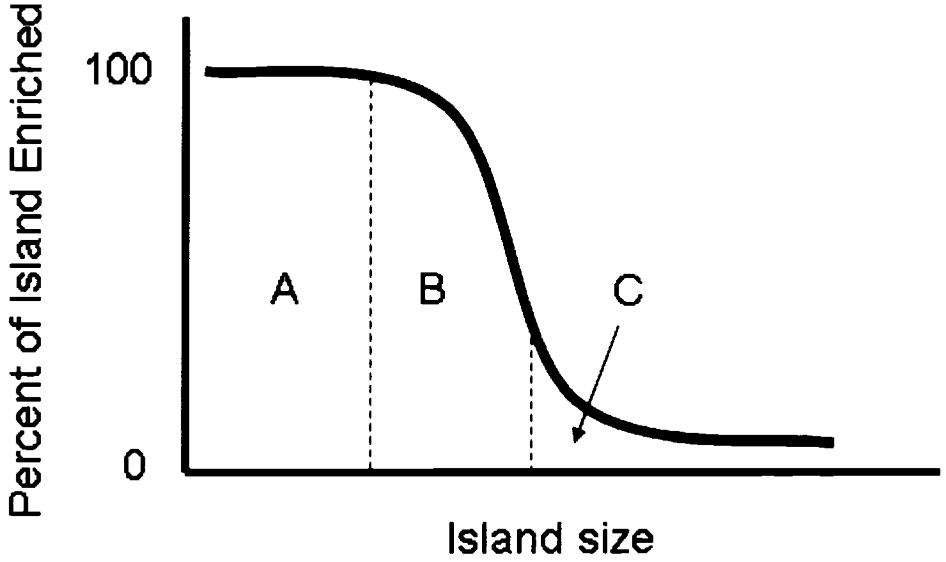


Figure 2.12. Hypothetical relationship between island size (hectares surface area) and the proportion of the habitat enriched by marine derived nutrients for fox-free islands. (A) Small islands are 100% enriched, (B) moderate sized islands are only enriched around the perimeter, and (C) large islands are only enriched in patches around seabird colonies.

Chapter 3. Subarctic island vegetation phenology: a contemporary measure of climate change

Introduction

Recent studies have demonstrated significant changes in global climate, particularly at northern mid to high latitudes (Serreze et al. 2000, Kattsov and Källén 2004). One of the best means to predict the biological response to these changes is through the examination of the response of primary producers to climate variability across space and time. For example, a number of investigators have shown significant responses of ecosystems to climate differences over small scales and short time scales using experimental approaches (Chapin and Shaver 1985, Zavaleta et al. 2003). While field studies are necessary to measure small scale responses in a controlled manner, remote sensing can complement these studies by providing information over large spatial scales that can be used to interpret the results of smaller scale studies (Potter and Brooks 1998). In this study I use remotely-sensed data to examine the effects of climate differences on the seasonal phenology of plant communities in a broadly replicated study across the Aleutian archipelago of Alaska.

There have been numerous studies on both the effects and the predictions of warming on the arctic (Chapin et al. 1995) and subarctic (Rupp et al. 2000). Many of these studies cover substantial geographic ranges, but in these cases the study systems are often confounded by spatial heterogeneity in the biotic and abiotic conditions of the target habitats. For example, gradients in climate are often correlated with biological gradients in species composition and with physical gradients in soil or elevation. At larger scales, remote sensing studies have documented significant warming and associated changes in plant production in the high northern latitudes (Myneni et al. 1997, Behrenfeld et al. 2001, Nemani et al. 2003), however these studies are likewise confounded by spatial heterogeneity across the target habitats. In order to make accurate predictions about the effects of future climate change it is important to have contemporary measurements of vegetation dynamics across large scales in a system in which temperature effects are not spatially confounded.

The islands of the Aleutian Archipelago provide a unique opportunity to examine biological responses to climate change across broadly replicated island ecosystems. The archipelago spans 1900km of longitude and 500km of latitude (Figure 3.1) with islands that are similar in shape and size, geological composition, soil, and geological age (Gard 1977). They contain similar plant communities, and have limited animal populations that comprise relatively simple food webs (Maron et al. 2006). Yet while these factors are constant there is a significant cooling gradient from east to west across the archipelago (Chapter 1).

The Normalized Difference Vegetation Index (NDVI), a remotely-sensed index based upon the ratio of red and near infrared optical bands [(NIR-RED) / (NIR+RED)], is a widely accepted standard metric for terrestrial vegetation (Pettorelli et al. 2005, Maron et al. 2006). The NDVI is an optical measurement of "greenness" that correlates strongly with standing plant biomass (Myneni et al. 1995) and, when integrated across time, with above ground net primary productivity (Tucker and Sellers 1986). When acquired at frequent intervals, NDVI data can be used to generate precise phenological measurements of seasonal vegetation dynamics. Phenology curves (Figure 3.2) can serve as baselines from which informative quantitative parameters can be extracted regarding the timing and magnitude of seasonal production events (Jonsson and Eklundh 2002, Schwartz 2003, Zhang et al. 2003).

The NDVI has been used in a number of studies to measure the effects of climate change across large spatial scales (Schwartz 2003). For example, using a global analysis, Potter and Brooks (1998) found that three climate indices (degree days, annual precipitation, and annual moisture index) accounted for 70-80% of the geographic variation in maximum and minimum NDVI values in 1984. In northwest Mexico, NDVI has been found to be highly responsive to levels of precipitation (Salinas-Zavala et al. 2002). Unlike northwest Mexico, plant growth in the Aleutian archipelago is not precipitation-limited (Amundsen 1977) and thus there is little inter-annual variation in NDVI patterns (Chapter 1). In these systems, temperature is the most important factor in regulating NDVI dynamics (Kawabata et al. 2001, Ichii et al. 2002), and this has been confirmed in studies of arctic ecosystems (Dormann and Woodin 2002, Jia et al. 2002, Stow et al. 2004), and the Aleutian Islands (Chapter 1).

Specifically, in this study I use NDVI to examine the response of primary producers to differences in land surface temperature, percent cloud cover, and percent snow and ice cover across multiple growing seasons across the Aleutian archipelago by contrasting NDVI among islands located with clearly different regional climates. Ultimately, this approach provides a model for generating rigorous predictions of ecosystem responses to climate forcing.

Methods

The general goal of this chapter is to measure the ecosystem level response of vegetation to a range of climates. My overall approach includes the measurement of vegetation dynamics across the entire landscape of multiple islands over time under a longitudinal range of climates. I describe a suite of NDVI based vegetation parameters for each island and base the analysis on the annual integrated value of the NDVI (iNDVI). I then make estimates about the longitudinal range of primary production based on correlations of iNDVI with a satellite based measure of net primary production (Npp). I use this study system to determine which climate variables (i.e., temperature, snow/ice or cloud cover) affect plant production on islands and what the quantitative relationship is between those variables and kg C/m^2 produced. I present the data in two forms: as monthly means through a single season by three longitudinal sub-regions (eastern, central, and western Figure 3.1); and as annual summary values for each island by longitude. All statistical analyses were done using the annual summaries by longitude. Using these results, I then make general predictions about the impacts of future climate change on plant production in the Aleutian archipelago.

Study Islands

I defined the Aleutian archipelago as ranging from Attu Island (172°56' E, 52°00' N) in the west to Caton Island (162°25' W, 54°23'N) in the east, an area spanning ~1900km of longitude and ~500km of latitude (Figure 3.1). The Aleutian archipelago contains >450 islands and offshore rocks ranging in size from <1ha to >400,000ha. The vegetation is maritime tundra, dominated by grasses, dwarf shrubs, lichens, and forbs (Amundsen 1977). There are no trees or large shrubs and the maximum vegetation height rarely exceeds 1m (Danner, personal observations). Even though the archipelago spans a large geographic range, the islands are relatively homogeneous in rock types, soil, and geological age (Gard 1977). The islands are also homogeneous in species composition and for many of the physical factors associated with plant growth (Maron et al. 2006). I compiled a suite of biotic and abiotic factors useful in tracking vegetation dynamics and regressed each factor against latitude and longitude for each island to test the assumption of archipelago-wide homogeneity as well as to determine the magnitude and direction of any spatial gradients that may be present. These factors included: (1) dimensional descriptors of each island, including planar surface area (log transformed), the perimeter to area (P/A) ratio (log transformed), and mean elevation (log transformed); (2) data on soil and plant characteristics; (3) and monthly rainfall data. I used polygon shapefiles and Digital Elevation Models (DEMs) in ArcGIS to generate the physical descriptors of each island. For some analyses I used plant and soil data that were collected from 19 islands as part of a separate study (Croll et al. 2005, Maron et al. 2006). Ten of these islands have high densities of seabirds (>0.1 bird / m^2) which have significantly altered the soil and plant chemistry (Croll et al. 2005, Maron et al. 2006), and were therefore excluded from the analyses.

MODIS Satellite Data

To measure the spatiotemporal patterns in plant production and climate, I used five datasets from the MODIS Terra satellite platform, including two vegetation datasets: NDVI and Npp; and three climate datasets: snow/Ice cover, cloud cover, and land surface temperature (LST). The NDVI, snow/ice, and cloud data were all from the 250m 16-Day Vegetation Indices (MOD13Q1) product. The LST was from the 1km 8-Day Land Surface Temperature/Emissivity (MOD17A3) product. The Npp data was from the 1km Yearly Net Primary Production (MOD17A3) product. These products are all components of the MODIS Terra satellite and are integrated and designed to be used together. The processing and analysis of each dataset are discussed below.

NDVI

I evaluated the effectiveness of MODIS 250m NDVI data for precisely measuring the seasonal phenology of relatively small landscapes in Chapter 1. MODIS NDVI is most often applied to regional and global vegetation studies, but has been shown to be effective for islands as small as 50ha (Chapter 1). I used MODIS Terra 250m NDVI 16-day composites from 2001 through 2004 (MOD13Q1). The quality of the NDVI data in the Aleutian region can be highly variable due to the atmospheric effects (primarily cloud cover), snow and ice, shadows, and satellite viewing angles. To reduce the amount of variability in the data, I restricted per-pixel VI quality (MODLAND) values to 0 or 1 ["VI produced, good quality" and "VI produced, check QA quality", (Huete et al. 1999)] and removed pixels with snow or ice. For each island I calculated the mean value of all pixels (that passed the above criteria) for each 16-day sample period, and then averaged these two values for each month to obtain a single monthly mean. For each island I fit the mean monthly values from four consecutive years, 2001-2004, to a two-term Fourier function (MATLAB Curve Fitting Tool, version 1.1.3) using the following equation:

$$y = a_0 + a_1 \cos(xp) + b_1 \sin(xp) + a_2 \cos(2xp) + b_2 \sin(2xp)$$

where x = time (month) and $p = 2\pi / (\max(x)) - (\min(x))$, or 0.53 for each island. This is a nonlinear least squares fit with the assumption of normally distributed errors. I checked plots of the residuals for normal distribution of errors. I used the adjusted r^2 value from each island as the measure of the goodness of fit of the data to the Fourier equation. I generated NDVI values at 3-day increments from the Fourier function and then averaged the values within each of the three Aleutian sub-regions to generate mean seasonal phenology curves for western, central, and eastern sub-regions. For each island I then extracted five seasonal parameters from the NDVI fitted line (Figure 3.2): the maximum and minimum values of the NDVI during the growing season (Max NDVI, Min NDVI); the date of peak of growing season (Date at Max NDVI); the growing season integral (GSI); and the amplitude of the growing season (Amp NDVI). These variables are commonly used in climate change literature as measures of the effects of warming on season length (Menzel and Fabian 1999, Behrenfeld et al. 2001), onset of spring (Schwartz et al. 2002), and total production (Paruelo et al. 1997).

Annual Net Primary Production

I used annual estimates of net primary productivity from the MODIS Net Primary Production dataset for 2001, the only year for which these data are available. These data are correlated with iNDVI, in part because the NDVI from MOD13Q1 are used in the Npp algorithm (Running et al. 1999). The MODIS Npp data consist of 1km pixels that are the summary of series of different MODIS 16-day MODIS products. The resulting Npp values are measured in kilograms of carbon per square meter over the course of a calendar year. Therefore these data do not have any seasonal dimension, and are just an annual summary. The MODIS Npp data are used in this study to predict an approximate total production value (kg C/m^2) from the results of the iNDVI analysis.

Snow/Ice and Cloud Cover

I used the MODIS NDVI quality data to estimate the monthly percent cloud cover and the percent snow/ice cover for each island. MODIS NDVI datasets include associated quality data that separately identify the presence of clouds and snow/ice on an individual pixel basis (presence = yes or no). I calculated the percent cloud cover for each island as the proportion of pixels that were positive for clouds for each time period. From these data I then calculated an annual mean percent cloud cover. I used the same process in the calculation of the percentage of snow/ice cover.

Land Surface Temperature

I generated the mean monthly land surface temperatures (LST) for each island from MODIS MOD11A2 1km Land Surface Temperature/Emissivity data. I averaged the 8-day values into monthly means and then fit these means to a two-term Fourier function following a similar protocol as the NDVI analysis described above. I restricted the analysis to daytime temperatures and per-pixel quality values equal to 0 ["LST produced, good quality" (Wan 1999)]. I generated LST values at 3-day increments from the Fourier function and then averaged the values within each of the three Aleutian sub-regions to generate mean seasonal LST profiles for western, central, and eastern sub-regions. For each island I then extracted three seasonal parameters from the LST curves: the annual integrated temperature (iLST), the date of peak temperature (Date of Max LST), and the growing degree days (GDDs, days where the LST was above 5°C).

Statistical Analyses

I used 59 islands throughout the Aleutian archipelago for the analysis (Appendix C). I excluded islands with high densities of seabirds (>1000 birds / ha, n=12) from the analysis. This was done for two reasons: 1) seabirds have been shown to have significant impacts on plant species composition and production by vectoring nutrients from the sea to land (Croll et al. 2005, Maron et al. 2006, Danner Chapter 1), and 2) nutrient availability plays a critical role in vegetation response to climate change in arctic ecosystems (Dormann and Woodin 2002, Callaghan 2004), and therefore the elevated nutrient level on seabird islands could alter the results. For the remaining islands, the dataset consisted of monthly estimates of the mean NDVI, which I used to generate five seasonal parameters that describe the relevant annual phenological events.

I approached the analysis of the relationship between longitude and the iNDVI in a series of steps: 1) I used linear regression to test for east-west trends in the vegetation dynamics vs. longitude. While all the NDVI parameters were included to inform the reader of the general spatial patterns, I only used the integrated seasonal value, the iNDVI, in subsequent analyses. 2) I then used linear regression to test for longitudinal trends in extracted seasonal temperature parameters, snow/ice cover, and cloud cover. 3) I used step-wise multiple regressions to determine which climate factors had the greatest contribution to the iNDVI. 4) I then calculated the direct and indirect relationships between longitude, the significant climate factors, and iNDVI using path analysis (Wootton 1994). Finally, I tested the relationship between the iNDVI and Npp, and Npp and longitude using linear regressions.

Results

Characteristics of the Aleutian Islands

Despite spanning 1900km in longitude, the Aleutian Islands are spatially homogeneous for most of the non-NDVI or climate factors tested. There were no significant differences in island area, P/A ratio, or mean elevation with latitude or longitude (Table 3.1). There were no significant spatial or island dimensional trends in the biotic and abiotic vegetation parameters (Table 3.2).

Regional NDVI

There were, however, distinct differences in the Fourier smoothed seasonal NDVI phenological curves, Fourier smoothed LST, and monthly climate variables by sub-region across the Aleutian archipelago (Figures 3.3 and 3.4). To further evaluate longitudinal patterns, these qualitative relationships were tested statistically using linear regression of the NDVI summary variables for each island against longitude. Overall, most of the seasonal NDVI parameters linked to production declined from east to west. I found significant relationships between the climate variables and the NDVI parameters. The analysis for each of these sections follows. The Max NDVI decreased significantly ($r^2 = 0.08$, $P = 0.0330$, Figure 3.5a) and occurred later in the season ($r^2 = 0.08$, $P = 0.0330$, Figure 3.5c) from east to west. While the Max NDVI was lower in the western Aleutians, the Minimum NDVI was also lower ($r^2 = 0.32$, $P < 0.0001$, Figure 3.5b), contributing to a significant increase in the seasonal amplitude from east to west ($r^2 = 0.08$, $P = 0.0330$, Figure 3.5d). Even though the amplitude of the NDVI increased from east to west, there was also a significant decrease in iNDVI ($r^2 = 0.20$, $P = 0.0005$, Figure 3.5e). This pattern is likely due to the later onset of warming and colder winter temperatures in the western Aleutians, as discussed below.

Regional climate

The were also significant longitudinal trends representing a cooling from east to west in most of the climate variables tested. The percent cloud cover and percent snow/ice cover increased significantly from east to west ($r^2 = 0.07$, $P = 0.0397$, Figure 3.6a, and $r^2 = 0.09$, P

= 0.0244, Figure 3.6b, respectively), and the date of the Peak LST occurred later in the growing season ($r^2 = 0.28$, $P < 0.0001$, Figure 3.6c). However, there were no east-west trends in the number of Growing Degree Days ($r^2 < 0.01$, $P < 0.7611$, Figure 3.6d).

Climate/NDVI

While longitudinal trends in the climate variables were not always significant, the relationships between these climate variables on the iNDVI were consistent. The iNDVI was negatively related to cloud cover ($r^2 = 0.18$, $P = 0.0007$, Figure 3.7a), snow/ice cover ($r^2 = 0.17$, $P = 0.0011$, Figure 3.7b), Date of Max LST ($r^2 = 0.16$, $P = 0.0016$, Figure 3.7c), and GDDs ($r^2 = 0.09$, $P = 0.0227$, Figure 3.7d). I next evaluated the relationship between longitude, the proximal climate factors just discussed and iNDVI using path analysis (Figure 3.8). GDDs were excluded from the analysis because of low contribution to the model. As noted above, when measured in the absence of other variables the iNDVI was positively correlated with longitude (path coefficient r = 0.44, Figure 3.8a). I calculated the relationship between longitude and the three most likely causal climate variables: longitude was strongly negatively correlated with Date of Max LST (r = -0.52) and moderately negatively correlated with percent cloud cover (r = -0.27, Figure 3.8b), and cover of snow/ice (r = -0.29). Yet the percent cover of clouds, the percent cover of snow/ice, and Date Max LST all had similar direct effects on the iNDVI (-0.24, -0.24, and -0.23 respectively, Figure 3.8b). The overall positive indirect effects of Date of Max LST (0.12), percent cover of snow/ice (0.07), and percent cover of clouds (0.06), combine to explain 0.25 of the effect of longitude on iNDVI. In summary, these three climate variables, which were each negatively correlated with longitude, accounted for more than 50% (0.25) of the total positive effect of longitude on the iNDVI (0.44). There were no significant interactions between the climate variables (Date of

Max LST x snow/ice cover, Date of Max LST x cloud cover, snow/ice cover x cloud cover), and thus they were not included in the model.

Net Primary Production

While there is a significant longitudinal gradient in iNDVI, it would be more useful to have a biologically meaningful metric. Thus, I also examined the relationships between the iNDVI, Npp, and longitude using MODIS Net Primary Production data. The mean annual Npp from each island was moderately correlated with iNDVI ($r = 0.44$, Figure 3.9b). The Npp declined from a mean of 5.3 kg C/m^2 at the eastern end of the archipelago to 4.3 kg C/m^2 at the western end of the archipelago (Figure 3.9a). For every degree of longitude from east to west there was about a 50g C/m^2 decrease in productivity.

Discussion

Our ability to make predictions about ecosystem response to climate change is in part dependent on our understanding of the relationship between climate and plant production. Large scale remote sensing studies have demonstrated the effects of climate on vegetation at the global (Myneni et al. 1997, Potter and Brooks 1998, Nemani et al. 2003) and regional (Paruelo and Lauenroth 1998, Cook et al. 2005) scales. Most similar to the work presented here, Suzuki et al. (1997) found climate-related longitudinal trends in the plant phenology across Siberia using the NDVI. While the large geographic scale of these studies is informative, it also presents problems of interpretation. In almost all cases regional comparisons incorporate multiple animal and plant species ranges, biomes, rock and soil types, and climate regimes. These different factors, alone or interacting with one another, can confound any analysis, making it difficult to rigorously disentangle the effects of climate from other physical or biological inputs. Shaver and Kummerow (1992), noted that predictions about the effect of climate on plant growth based on climate gradients can be faulty because of the unknown nature of climate correlated variables. For example, gradients in nutrient levels, which are limiting factors in arctic plant growth, may be correlated with climate (Chapin et al. 1995). Even when examining the same species across large spatial scales, the ecotypic differences in plant growth rates may be more important than climate factors (Shaver et al. 1979).

This study largely avoids these issues. First, with the exception of temperature related climate variables, there are no significant gradients in plant species composition or growth related factors across the Aleutian archipelago (Table 3.2). Second, I used entire ecosystems (islands) as replicates for this study, an approach that is not possible in most regional studies. The landscape level analysis used in this study substantially reduces the probability that species level variation might confound the results. It is unlikely that ecotypic differences across space would covary identically for all plant species in the community resulting in a significant longitudinal pattern. In the absence of longitudinal gradients in species composition, nutrient levels, or island shape and size, the spatial differences in the seasonal vegetation dynamics of the Aleutian archipelago can most likely be attributed solely to spatial differences in climate.

Overall, plant production was lower as climate became cooler across the large longitudinal range of the Aleutian archipelago. While the individual coefficients of determination were relatively low, nearly every seasonal NDVI related parameter indicated a decline in plant production from east to west. The iNDVI was used as the primary response variable because it is the most concise summary of the other NDVI based parameters and has been shown to be highly correlated with net primary production, particularly in areas that are not limited by precipitation (Schloss et al. 1999) such as the Aleutian archipelago. Of the four climate variables tested, the percentage of snow/ice cover had the strongest effect on the iNDVI (Table 3.3). In high northern latitude systems the spatial and temporal distribution of snow and ice determines the period over which plants can intercept solar radiation and grow. In Arctic systems the start and duration of the snow-free period is determined by the interaction between snow amount and temperature (Callaghan 2004). In addition, the timing of the snowmelt is a major factor in the onset of growth (Shaver and Kummerow 1992).

Two other climate variables did have strong longitudinal trends, Date of Max LST and percent cloud cover, but each had marginal direct contributions to the iNDVI (Figure 3.8b). There is a 29 day delay in time of peak NDVI between the eastern and western ends of the archipelago (Figure 3.7c). This delay in warming likely inhibits plant production in the western part of the archipelago during the critical spring and early summer growth window. In addition, cloud cover was 20% higher in the western end of the archipelago, lowering the total amount of solar radiation available, a critical resource for Aleutian vegetation (Amundsen 1977). These factors appear to work synergistically to drive a significant east-west decline in iNDVI across the archipelago (Figure 3.8). The biological significance of this trend can be inferred from the results of the MODIS Npp longitudinal analysis; there was a 1 kg C/m^2 differential in production (amounting to a 19% production differential) between the eastern and western ends of the archipelago (~20° longitude). The combined effects of snow/ice cover, cloud cover, and delay of seasonal warming cause a 50g C/m^2 reduction in primary production with every degree of longitude from east to west. There is still a substantial portion of variation in iNDVI with longitude that is not accounted for by the three climate variables (r = 0.19). The vegetation of the Aleutian archipelago is highly influenced by the marine environment (Amundsen 1977), and the influence of oceanographic patterns may have a significant contribution to the seasonal plant dynamics. Recent studies have documented significant oceanic temperature difference between the eastern and western Aleutians (Hunt and Stabeno 2005, Rodionov et al. 2005). The interaction of oceanographic and terrestrial dynamics is beyond the scope of this study, but deserves further attention.

A potentially confounding issue associated with using satellite based phenological patterns as metrics of climate related change involves shifts in species composition that are likely to accompany those changes. Warming related increases in shrub abundance are widely predicted in the arctic (Callaghan 2004), and have been documented using remote sensing (Sturm et al. 2001). Using the methods presented here plant community types can have significantly different phenological signatures (Chapter 2). Shrub dominated communities generally have significantly lower seasonal shifts in biomass than grass dominated communities. These differences can be detected in the magnitude of the width and peak of the phenological curves. However, future changes in climate and species composition would require careful evaluation and ground validation of how the relative abundances of different plant species may change as a function of climate change.

The majority of the available literature on northern high latitude climate change involves arctic species and predicted changes above the Arctic Circle, 66°N. In many cases these predictions involve melting of permafrost, and other frozen soil and small water body related changes. The northern most range of the Aleutian archipelago (62°N) is south of the Arctic Circle. The soil rarely freezes in the Aleutians because the archipelago is heavily influenced by the marine environment (Amundsen 1977). Thus, while there has been significant warming in the arctic that may be positively feeding back on itself (Chapin et al. 2005), the climate changes associated with the Aleutian archipelago are likely to be more associated with oceanographic conditions (Rodionov et al. 2005). The scenarios for ocean climate change are uncertain as most models are atmosphere oriented (Loeng 2004). While the relationship between oceanographic conditions and insular vegetation is beyond the scope of this paper, it represents a critical area for future study. Yet in terms of the effects of climate on terrestrial vegetation, the results presented here are applicable regardless of the mechanism.

This study shows that there are contemporary differences in seasonal vegetation patterns that are strongly related to gradients in climate. The biological, physical, and geographic structures of the Aleutian archipelago make it a unique and critical system for studying the effects of climate on terrestrial vegetation. This dataset can serve as an important baseline for the measurement and modeling of future climate change. While it is not possible to isolate a single factor from this study that is driving the decline in primary production with longitude, the important factors are all temperature related. Thus, these results clearly outline the effect of a climate gradient on plant production; warmer climates result in significantly more carbon production. This study is unique in that it demonstrates this pattern over a large geographic range in a rigorously replicated manner.

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Table 3.1 Multiple linear regressions results for the geographic distribution of island physical parameters: island area (log ha), thickness, and mean elevation (log meters) against latitude and longitude.

Variable	N	Latitude	Longitude
Area (log hectares)	90	0.161	0.127
P/A ratio (log meters)	90	0.111	0.093
Mean elevation (log meters)	90	0.912	0.790

Table 3.2. Multiple linear regressions results for the geographic distribution of island vegetation parameters: variables by island area (log ha), thickness (a measure of shape), latitude and longitude. Plant values are the means of grass and forb values

Variable	N	Area	P/A ratio	Latitude	Longitude
Soil total N	9	0.551	0.823	0.160	0.165
Soil total C	9	0.562	0.656	0.101	0.067
Soil total P	9	0.356	0.988	0.094	0.554
Plant %C	9	0.249	0.177	0.473	0.078
Plant %N	9	0.654	0.944	0.192	0.381
Forb Cover	9	0.184	0.468	0.596	0.159
Grass Cover	9	0.122	0.143	0.874	0.125
Moss Cover	9	0.191	0.410	0.657	0.327
Shrub Cover	9	0.762	0.976	0.176	0.667

Table 3.3. Multiple regression of climate variables against iNDVI.

Dep Var: iNDVI N: 59 Multiple R: 0.6117 Squared multiple R: 0.3741
Adjusted squared multiple R: 0.3278 Standard error of estimate: 18924.6

Effect	Coefficient	Std Error	Std Coef	Tolerance	t	P(2Tail)
CONSTANT	493021	74835.6	0.0000	.	6.5881	0.0000
Cloud cover	-59993	30032.5	-0.2391	0.8089	-1.9976	0.0508
Snow cover	-93198	47548.6	-0.2362	0.7983	-1.9601	0.0552
Date Max LST	-15604	8730.2	-0.2280	0.7124	-1.7874	0.0795
Longitude	708	502.4	0.1871	0.6572	1.4088	0.1646

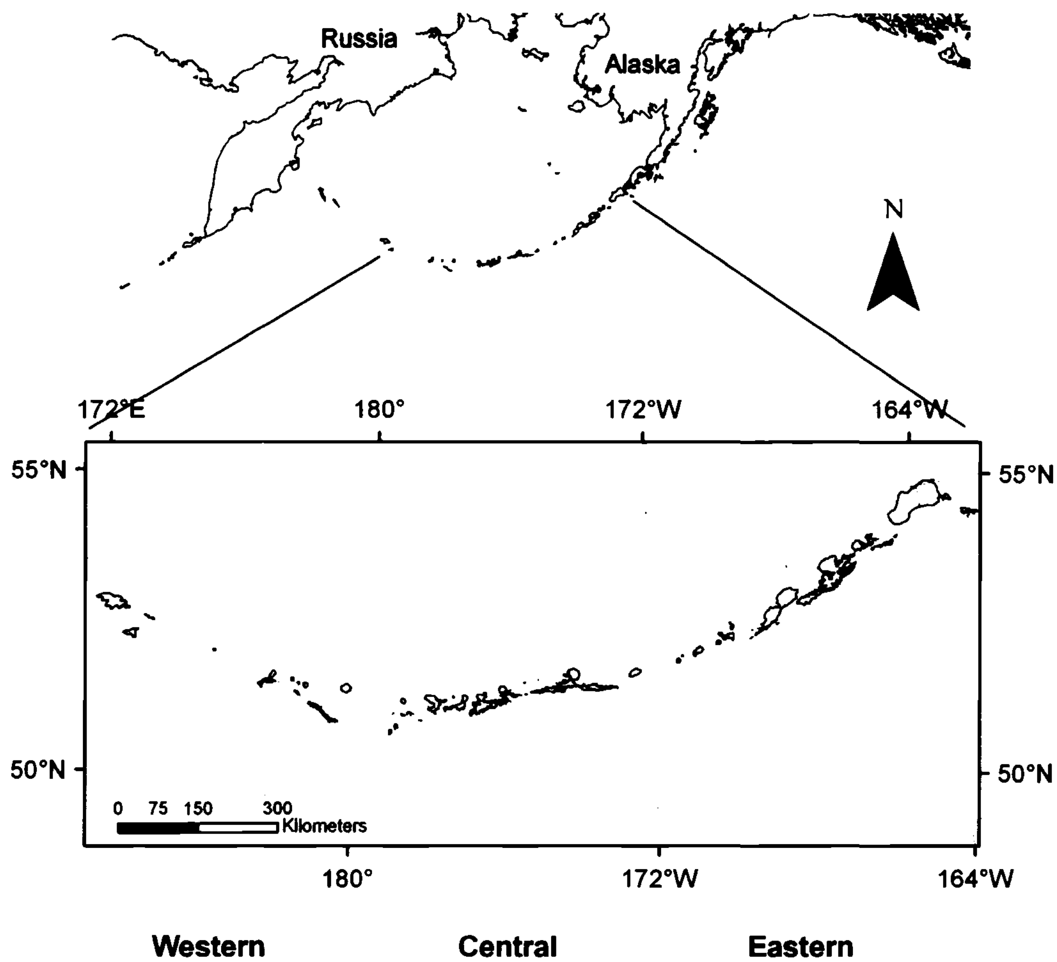

Figure 3.1. The Aleutian Islands, Alaska. The three climate sub-regions are denoted by longitudinal lines: Western (-172°E to -180°W), Central (-180°W to -172°W), and Eastern (-172°W to -164°W).

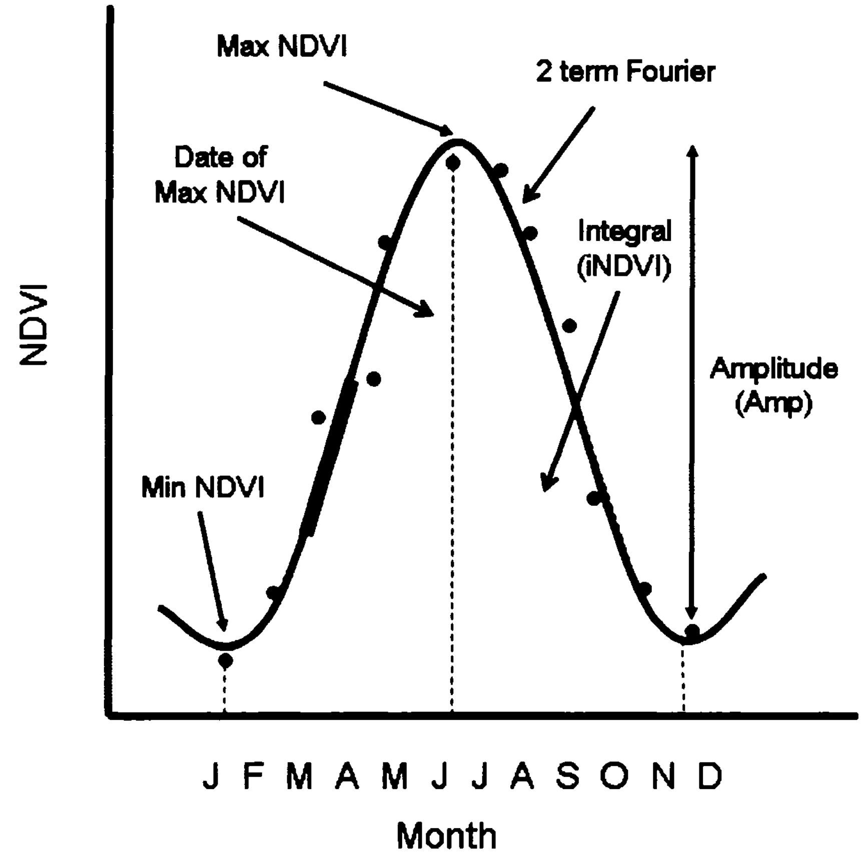

Figure 3.2. Hypothetical Fourier fitted curve representing a single growing season for a single island. Mean monthly values are indicated as blue points and the Fourier fitted curve as the red line. The five seasonal NDVI parameters are: the maximum and minimum values of the NDVI during the growing season (Max NDVI, Min NDVI); the date of the peak of growing season (Date at Max NDVI); the growing season integral (GSI); and the amplitude of the growing season (Amp).

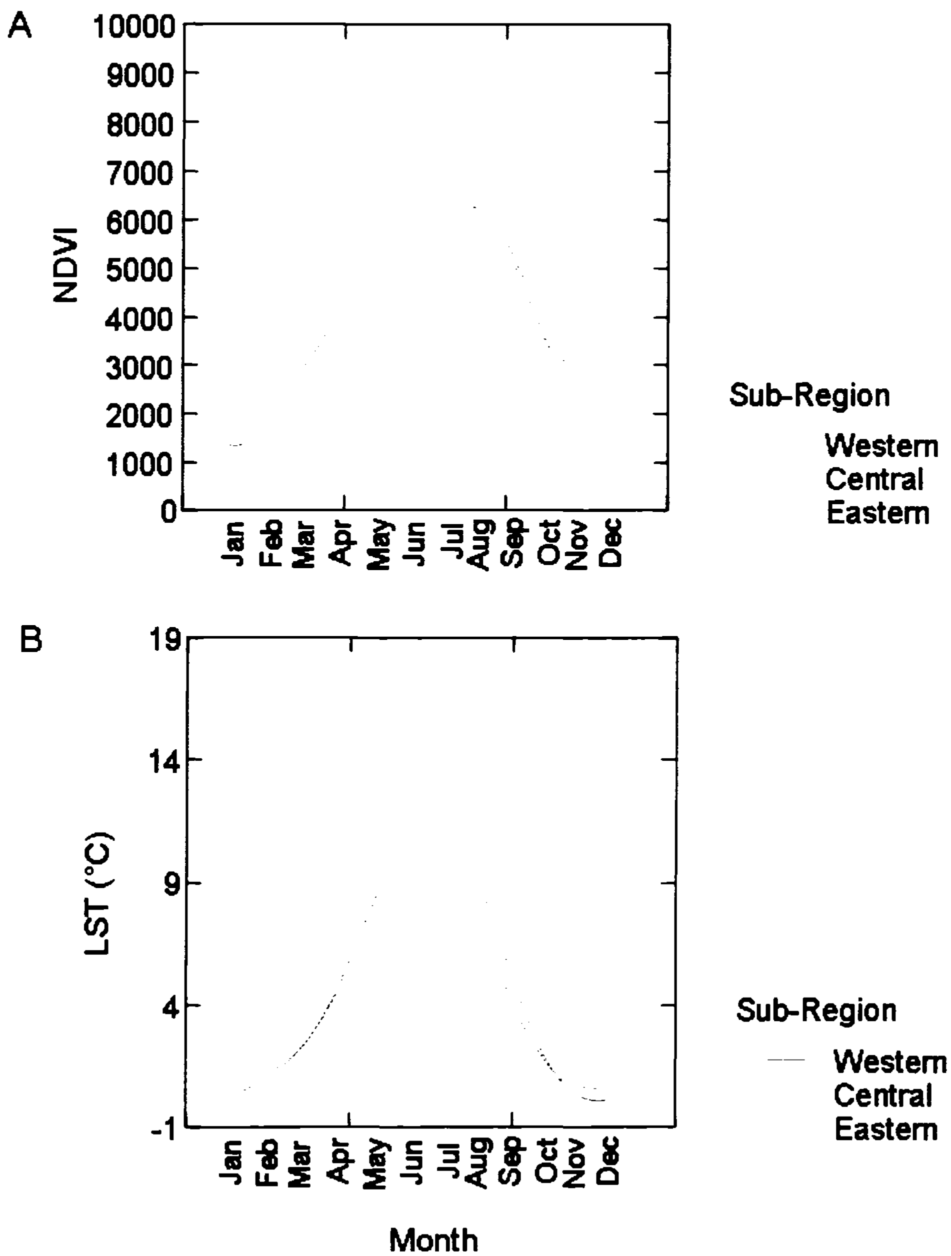

Figure 3.3. Mean seasonal Fourier-smoothed NDVI and land surface temperature (LST) values for each of the Aleutian sub-regions: western (red), central (dashed blue), and eastern (dashed red). (A) Mean NDVI. (B) Mean land surface temperature (LST).

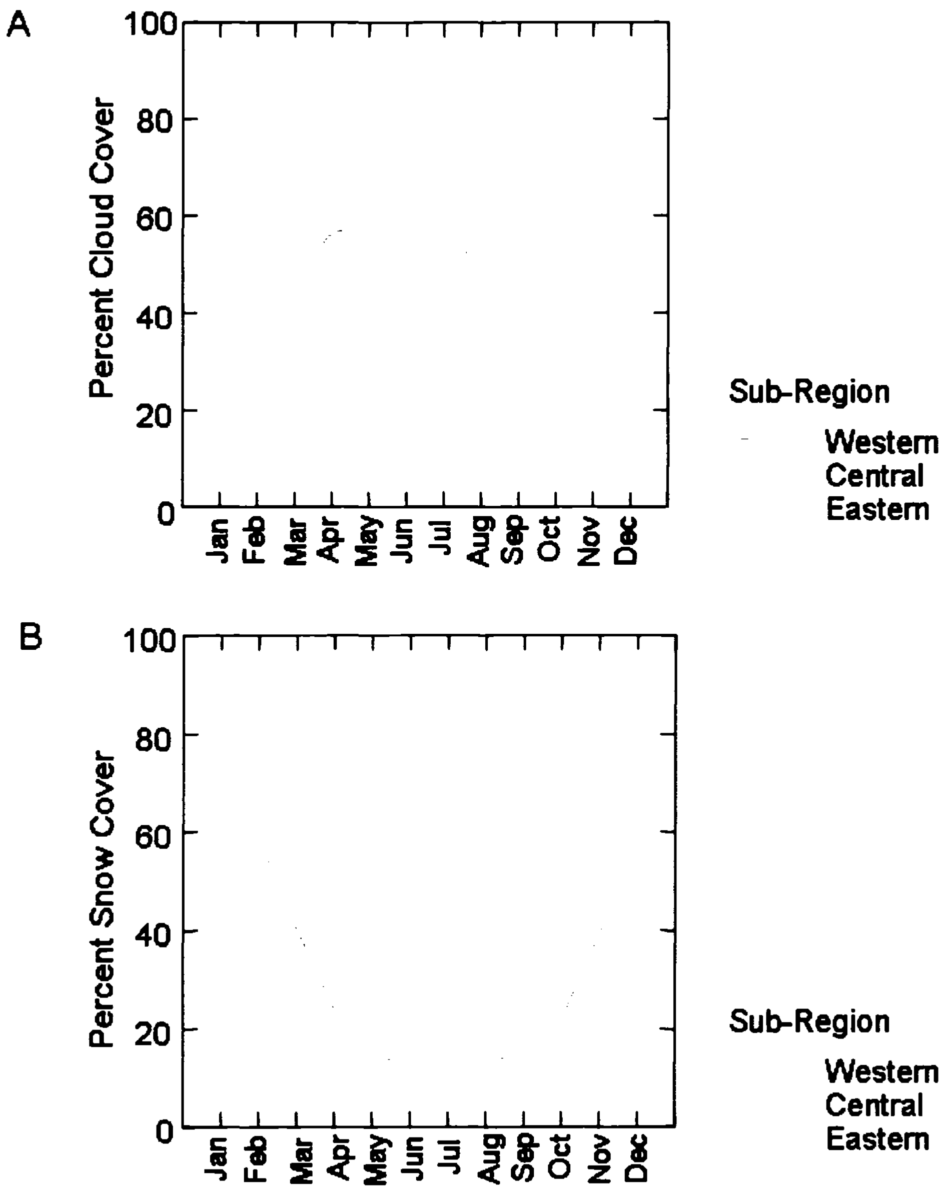

Figure 3.4. Seasonal climate variables for each of the Aleutian sub-regions: western (red), central (dashed blue), and eastern (dashed red). (A) Mean monthly percent cloud cover. (B) Mean monthly percent snow/ice cover.

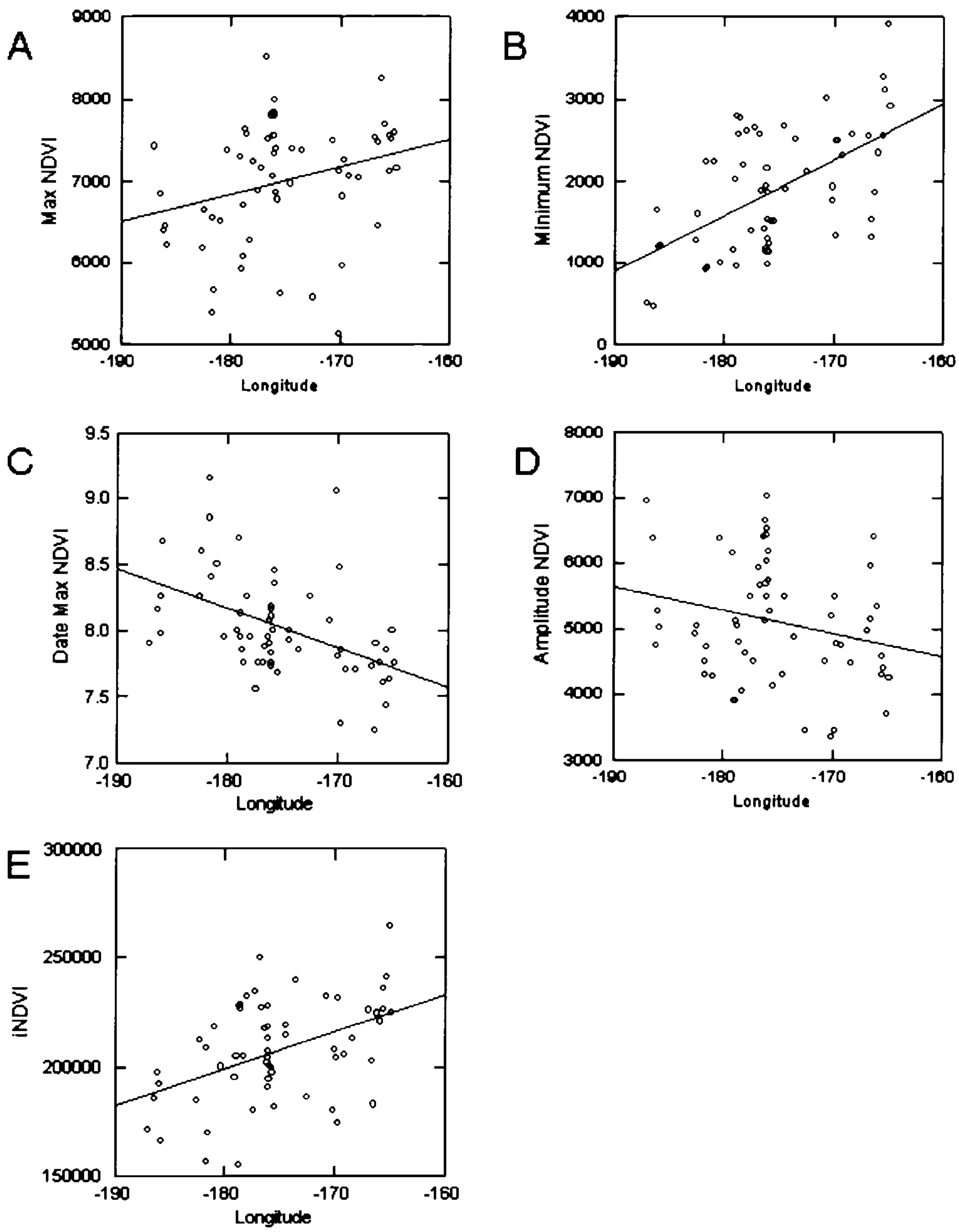

Figure 3.5. Relationships between longitude and NDVI seasonal parameters. (A) Max annual NDVI, (B) Minimum annual NDVI, (C) Date of Max NDVI, (D) Seasonal amplitude, and (E) iNDVI.

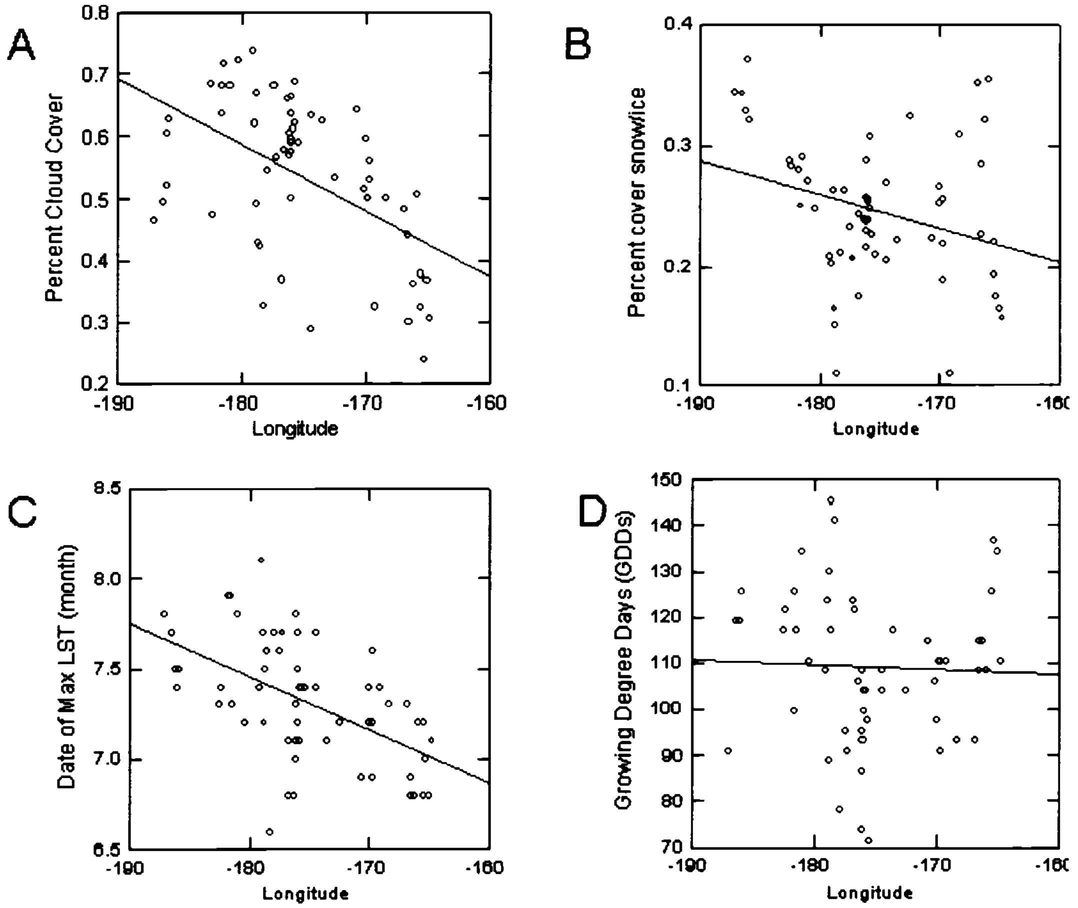

Figure 3.6. The relationships between longitude and climate parameters. (A) Percent snow/ice; (B) Cloud cover; (C) Date of Max LST; and (D) Growing Degree Days (GDDs).

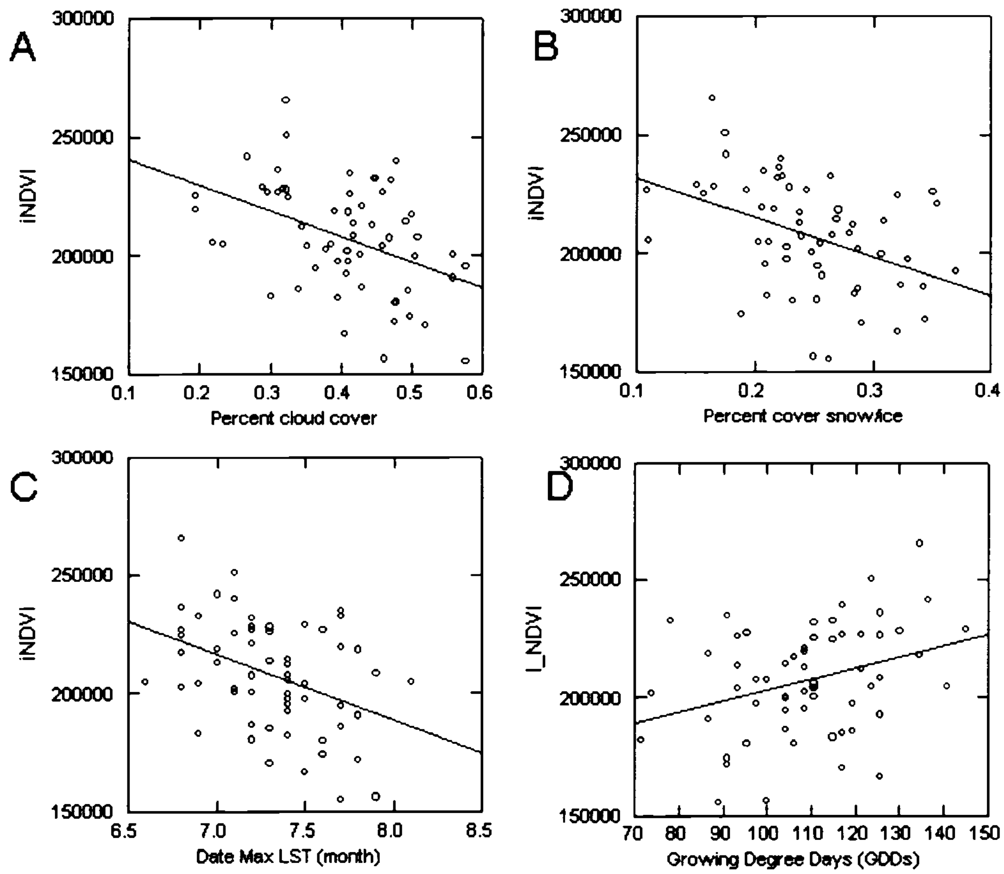

Figure 3.7. The relationships between the iNDVI and climate parameters. (A) Percent cloud cover; (B) percent snow/ice; (C) Date of Max LST; and (D) Growing Degree Days (GDDs).

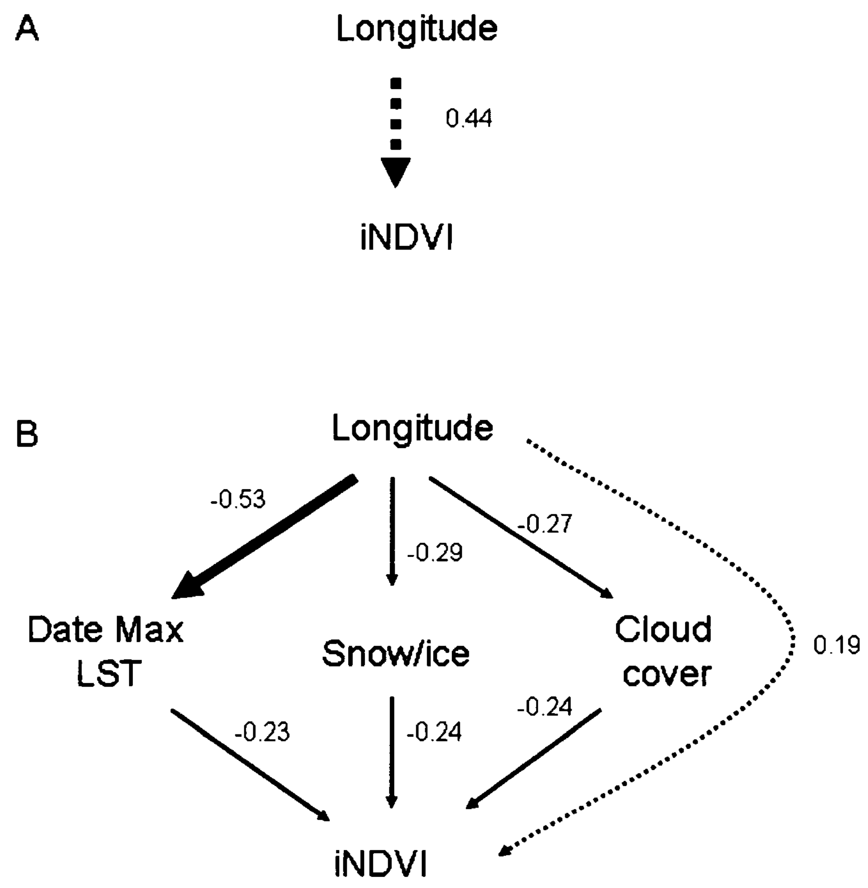

Figure 3.8. Path diagram estimating the relative importance of indirect effects (longitude) and indirect effets (seasonal date of the maximum land surface temperature [Date of Max LST], percent cover of snow and ice, and percent cover of clouds) on the iNDVI. Arrows designate the direction of correlation; the numbers adjacent to the arrows represent the size of the abundance effect (path coefficients).

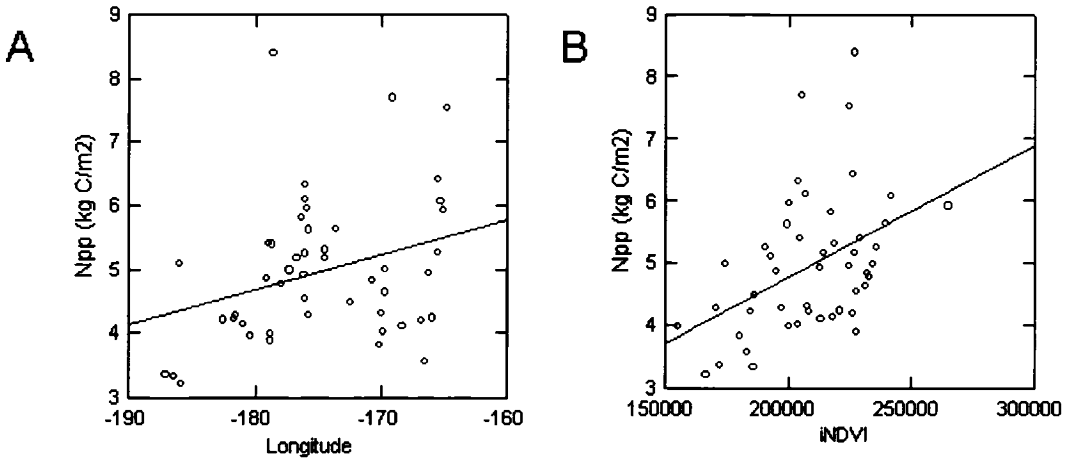

Figure 3.9. Relationship between Net Primary Production (Npp kg C/m2) to (A) longitude, and (B) the integrated NDVI (iNDVI).

Appendix A. Islands used in the analysis of chapter 1

Island	Lat	Lon	Area(ha)	P/A ratio (x1000)	Mean Elevation (m)	No. 250m Pixels
Adak	51.8	-176.7	71,299	0.56	178	13,277
Adugak	52.9	-169.2	51	10.06	12	10
Agattu	52.4	-186.4	21,826	0.51	128	4,072
Akun	54.2	-165.6	15,587	0.77	146	2,907
Akutan	54.1	-165.9	32,776	0.39	284	6,096
Alaid	52.8	-186.1	590	2.54	41	110
Amaknak	53.9	-166.5	1,073	2.32	96	203
Amatignak	51.3	-179.1	3,324	1.04	216	623
Amchitka	51.5	-181.0	30,051	0.71	83	5,600
Amlia	52.1	-173.6	43,660	0.68	152	8,133
Amukta	52.5	-171.3	4,832	0.66	227	901
Anagaksik	51.9	-175.9	84	5.32	61	15
Asuksak	51.9	-176.1	104	5.06	134	17
Atka	52.2	-174.4	102,632	0.57	238	19,130
Attu	52.9	-187.1	88,068	0.31	295	16,412
Avatanak	54.1	-165.3	3,367	1.44	137	628
Aziak	52.0	-176.2	118	4.73	53	21
Bobrof	51.9	-177.4	773	1.72	230	144
Carlisle	52.9	-170.1	4,066	0.70	389	758
Chuginadak	52.8	-169.8	16,418	0.54	330	3,063
Chugul	51.9	-175.8	1,685	1.60	150	312
Crone	51.7	-176.6	98	8.66	38	16
Davidof	52.0	-181.7	333	4.36	114	61
Dora	51.8	-176.8	123	6.85	25	23
Fenimore	52.0	-175.6	57	7.71	42	10
Gareloi	51.8	-178.8	6,617	0.51	445	1,226
Great Sitkin	52.0	-176.1	15,167	0.47	387	2,819
Herbert	52.8	-170.1	5,256	0.66	380	982
Hog	53.9	-166.6	103	4.60	16	19
Igitkin	52.0	-175.9	1,774	1.78	164	337
Ilak	51.5	-178.3	138	3.94	23	26
Kagalaska	51.8	-176.3	11,613	0.84	174	2,164
Kagamil	53.0	-169.7	4,007	0.78	213	743
Kanaga	51.8	-177.3	35,999	0.54	124	6,736
Kanu	51.9	-176.0	344	3.07	113	66
Kasatochi	52.2	-175.5	475	1.89	121	89
Kavalga	51.6	-178.8	1,403	1.94	38	264

Appendix A. (continued)

Island	Lat	Lon	Area(ha)	P/A ratio (x1000)	Mean Elevation (m)	No. 250m Pixels
Khvostof	52.0	-181.7	233	3.55	77	44
Kiska	52.0	-182.5	27,437	0.68	177	5,115
Little Kiska	52.0	-182.3	708	2.80	61	130
Little Sitkin	51.9	-181.5	6,261	0.61	272	1,178
Little Tanaga	51.8	-176.1	6,998	1.28	133	1,306
Nizki	52.7	-186.0	709	2.60	19	134
North	51.8	-176.8	57	7.78	31	12
Ogliuga	51.6	-178.6	949	2.06	10	177
Oglodak	52.0	-175.4	153	4.40	86	29
Peter	53.7	-166.8	55	6.10	31	10
Rat	51.8	-181.7	2,647	1.59	85	496
Ringgold	51.8	-176.8	143	4.67	29	26
Rootok	54.0	-165.5	1,198	1.45	156	225
Sadatnak	52.0	-174.4	102	6.16	13	17
Sagchudak	52.0	-174.5	185	3.81	27	31
Salt	52.2	-174.6	91	6.40	38	16
Samalga	52.8	-169.2	378	4.03	7	73
Sedanka	53.8	-166.2	10,059	0.85	183	1,876
Seguam	52.3	-172.5	20,406	0.35	330	3,805
Semisopochnoi	51.9	-180.4	22,021	0.33	256	4,099
Shemya	52.7	-185.9	1,402	1.44	32	266
Skagul	51.6	-178.6	403	3.09	7	75
Staten	51.8	-176.8	100	5.68	30	18
Tagadak	52.0	-176.0	189	3.62	74	35
Tagalak	52.0	-175.7	1,336	1.60	139	251
Tanaga	51.8	-178.0	50,708	0.42	281	9,503
Tanaklak	52.0	-176.1	347	2.78	76	65
Tigalda	54.1	-165.1	8,999	0.76	123	1,679
Ugamak	54.2	-164.8	938	2.55	103	175
Ulak (East)	52.0	-175.9	54	6.69	38	13
Ulak (West)	51.4	-179.0	3,019	1.24	71	569
Uliaga	53.1	-169.8	855	1.74	293	157
Umak	51.9	-176.0	3,607	1.26	175	668
Umnak	53.3	-168.4	176,354	0.21	285	32,898
Unalaska	53.7	-166.9	269,901	0.36	311	50,367
Yunaska	52.6	-170.7	16,763	0.42	202	3,123

Appendix B. Fox-infested islands with associated estimated area formerly enriched by seabirds

Island	Year foxes introduced	Latitude	Longitude	Area (ha)	% enriched	Hectares enriched
Adugak	1925	52.9	-169.2	51	50%	25
Alaid	1911	52.8	-186.1	590	77%	454
Amatignak	1923	51.3	-179.1	3324	45%	1497
Asuksak	Unk	51.9	-176.1	104	83%	87
Avatanak	1920	54.1	-165.3	3367	60%	2031
Aziak	1927	52.0	-176.2	118	78%	92
Bobrof	1930	51.9	-177.4	773	65%	505
Caton	Unk	54.4	-162.4	1819	63%	1141
Chugul	1922	51.9	-175.8	1685	65%	1094
Clifford	Unk	54.4	-162.8	160	74%	118
Crone	Unk	51.7	-176.6	98	68%	66
Davidof	1924	52.0	-181.7	333	78%	260
Dora	Unk	51.8	-176.8	123	62%	77
Elma	Unk	54.4	-162.5	281	72%	202
Hog	1914	53.9	-166.6	103	76%	78
Igitkin	1922	52.0	-175.9	1774	71%	1254
Kanu	1916	51.9	-176.0	344	79%	272
Kasatochi	1927	52.2	-175.5	475	70%	331
Kavalga	1920	51.6	-178.8	1403	70%	978
Khvostof	1924	52.0	-181.7	233	79%	185
Nizki	1911	52.7	-186.0	709	74%	525
North	Unk	51.8	-176.8	57	59%	34
Ogliuga	1897	51.6	-178.6	949	70%	663
Rat	1922	51.8	-181.7	2647	60%	1592
Ringgold	Unk	51.8	-176.8	143	79%	113
Sagchudak	1914	52.0	-174.5	185	84%	157
Salt	1916	52.2	-174.6	91	76%	69
Samalga	1897	52.8	-169.2	378	75%	285
Shemya	1911	52.7	-185.9	1402	62%	872
Skagul	1897	51.6	-178.6	403	77%	309
Staten	Unk	51.8	-176.8	100	71%	71
Tagadak	1925	52.0	-176.0	189	80%	152
Tagalak	1916	52.0	-175.7	1336	68%	903
Tanaklak	1918	52.0	-176.1	347	83%	288
Ugamak	1922	54.2	-164.8	938	81%	758
Ulak (West)	1924	51.4	-179.0	3019	56%	1686
Uliaga	1930	53.1	-169.8	855	65%	554
				Mean	70%	535
				Total		19,778

Appendix C. Study islands in the Aleutian archipelago used in the analysis for chapter 3.

Island	Adj r2	Area (ha)	Lat	Lon	Date Max LST	Percent Cloud	Percent Snow/Ice
Adak	0.86	71299	51.8	-176.7	6.8	58%	18%
Agattu	0.91	21826	52.4	-186.4	7.7	49%	29%
Akun	0.76	15587	54.2	-165.6	6.8	38%	14%
Akutan	0.89	32776	54.1	-165.9	7.2	51%	40%
Alaid	0.74	590	52.8	-186.1	7.5	52%	32%
Amaknak	0.77	1073	53.9	-166.5	6.9	30%	25%
Amatignak	0.89	3324	51.3	-179.1	7.4	74%	28%
Amchitka	0.72	30051	51.5	-181.0	7.8	68%	22%
Amlia	0.82	43660	52.1	-173.6	7.1	63%	11%
Asuksak	0.81	104	51.9	-176.1	7	59%	27%
Atka	0.89	102632	52.2	-174.4	7.4	63%	27%
Attu	0.95	88068	52.9	-187.1	7.8	47%	57%
Avatanak	0.80	3367	54.1	-165.3	7	24%	8%
Aziak	0.78	118	52.0	-176.2	7.1	57%	38%
Bobrof	0.78	773	51.9	-177.4	7.6	68%	22%
Carlisle	0.90	4066	52.9	-170.1	7.4	60%	34%
Chuginadak	0.75	16418	52.8	-169.8	6.9	50%	30%
Chugul	0.80	1685	51.9	-175.8	7.4	69%	38%
Davidof	0.61	333	52.0	-181.7	7.9	68%	32%
Gareloi	0.77	6617	51.8	-178.8	7.7	67%	40%
Great Sitkin	0.90	15167	52.0	-176.1	7.8	66%	37%
Herbert	0.72	5256	52.8	-170.1	7.2	52%	32%
Hog	0.70	103	53.9	-166.6	6.8	44%	36%
Igitkin	0.86	1774	52.0	-175.9	7.1	61%	28%
Ilak	0.71	138	51.5	-178.3	6.6	33%	29%
Kagalaska	0.83	11613	51.8	-176.3	6.8	66%	10%
Kagamil	0.85	4007	53.0	-169.7	7.2	56%	18%
Kanaga	0.81	35999	51.8	-177.3	7.7	57%	15%
Kanu	0.85	344	51.9	-176.0	7.5	59%	18%
Kavalga	0.72	1403	51.6	-178.8	7.2	49%	14%
Kiska	0.86	27437	52.0	-182.5	7.3	68%	28%
Little Kiska	0.69	708	52.0	-182.3	7.4	48%	21%
Little Sitki	0.85	6261	51.9	-181.5	7.3	72%	32%
Little Tanaga	0.87	6998	51.8	-176.1	7	60%	19%
Nizki	0.71	709	52.7	-186.0	7.4	60%	41%
North	0.66	57	51.8	-176.8	7.1	37%	9%

Appendix C. (continued)

Island	Adj r2	Area (ha)	Lat	Lon	Date Max LST	Percent Cloud	Percent Snow/Ice
Ogliuga	0.86	949	51.6	-178.6	7.5	43%	11%
Oglodak	0.62	153	52.0	-175.4	7.4	59%	42%
Rat	0.67	2647	51.8	-181.7	7.9	64%	28%
Rootok	0.78	1198	54.0	-165.5	7.2	33%	15%
Sagchudak	0.75	185	52.0	-174.5	7.7	29%	19%
Samalga	0.87	378	52.8	-169.2	7.4	33%	27%
Sedanka	0.91	10059	53.8	-166.2	6.8	36%	28%
Seguam	0.82	20406	52.3	-172.5	7.2	53%	39%
Semisopochnoi	0.86	22021	51.9	-180.4	7.2	72%	27%
Shemya	0.70	1402	52.7	-185.9	7.5	63%	29%
Skagul	0.84	403	51.6	-178.6	7.6	42%	10%
Tagadak	0.86	189	52.0	-176.0	7.7	57%	25%
Tagalak	0.81	1336	52.0	-175.7	7.4	62%	21%
Tanaga	0.79	50708	51.8	-178.0	7.7	55%	37%
Tanaklak	0.73	347	52.0	-176.1	7.3	50%	2%
Tigalda	0.77	8999	54.1	-165.1	6.8	37%	9%
Ugamak	0.83	938	54.2	-164.8	7.1	31%	12%
Ulak (West)	0.64	3019	51.4	-179.0	8.1	62%	13%
Uliaga	0.83	855	53.1	-169.8	7.6	53%	28%
Umak	0.90	3607	51.9	-176.0	7.2	64%	21%
Umnak	0.93	176354	53.3	-168.4	7.3	50%	37%
Unalaska	0.89	269901	53.7	-166.9	7.3	48%	43%
Yunaska	0.81	16763	52.6	-170.7	6.9	64%	14%