AN ABSTRACT OF THE DISSERTATION OF

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Title: Spatio-Temporal Analysis and Modeling in the Marine Environment: Humpback Whale Genetic Variability and Seabird Distributions in the Northeastern Pacific Ocean.

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Dawn J. Wright

The rapid decline of marine ecosystems worldwide and the failure of traditional single species management pushed for the development of ecosystem-based conservation measures such as marine protected areas (MPA) to slow the loss of marine biodiversity. One approach to MPA creation advocates targeting marine megafauna (e.g., marine mammals, seabirds, sharks, etc.) and assumes protective measures for megafauna will extend safeguards to areas of ocean productivity and other species dependent on that productivity. The marine spatial planning (MSP) process requires spatially-explicit information resulting in the development of map products used in planning and decision making. The crux of map creation is georeferenced species occurrence data. This three-part study takes a multidisciplinary approach, combining geography, marine conservation, molecular ecology, and spatial ecology to explore species occurrence data and development of novel geoanalytical tools, spatial analyses, and predictive modeling to inform the MSP process and help design more effective MPA networks for North Pacific marine megafauna (humpback whales and seabirds). Chapter 2 includes the development of geneGIS, a customized Arc Marine data model and suite of computational GIS tools to explore, analyze, and visualize spatially-explicit, individual-based records from North Pacific humpback whale photo-identification and genetic data. Unlike most occurrence data, this presence-only dataset is enriched by the addition of genetic information enabling mangers to factor in

population structure and genetic diversity, and thus maximize species resilience, when designing MPAs. Chapters 3 and 4 focus on using presence-absence data to develop spatially-explicit ecological models to identify multispecies seabird foraging aggregations (hotspots) and assess how these locations may shift with climate change within the California Current System. Key to both components is an improved understanding of what factors influence the presence of a species and/or its genetic variability to enable present day planning and design of MPA networks to ensure adequate protection will be in place now and as climate change progresses. This information can also be used to inform policy decisions by adapting strategies to reduce non-climate stressors such as fishery pressures and coastal development in areas predicted to be important to marine species in the future.

Spatio-Temporal Analysis and Modeling in the Marine Environment: Humpback Whale
Genetic Variability and Seabird Distributions in the Northeastern Pacific Ocean

by
Dorothy Marie Dick

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APPROVED:

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Major Professor, representing Geography

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_____

Dean of the Graduate School

I understand that my dissertation will become part of the permanent collection of Oregon State University libraries. My signature below authorizes release of my dissertation to any reader upon request.

_____

Dorothy Marie Dick, Author

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Research often involves numerous collaborators and my dissertation is no exception. I would like to thank all of my co-authors who assisted with the data collection (whether it

CONTRIBUTION OF AUTHORS

Drs. C. Scott Baker and Dawn J. Wright conceived of the project in Chapter 2. Dorothy Dick, Shaun Walbridge, Tomas Follett, Erin A. Falcone, Debbie Steel, John Calambokidis, Jason Holmberg and Drs. C. Scott Baker and Dawn J. Wright contributed to the research, execution, and authorship of Chapter 2. Drs. Jaime Jahncke and Nadav Nur, and Dorothy Dick conceived of the projects in Chapters 3 and 4. Seabird survey data for Chapters 3 and 4 were collected and provided by Drs. Jaime Jahncke, Jeannette E. Zamon, David G. Ainley, Lisa T. Ballance, David Hyrenbach and Ken Morgan. Dorothy Dick and Julie Howar downloaded and processed all remotely-sensed data. Dorothy Dick and Drs. Jaime Jahncke and Nadav Nur executed data analyses for Chapters 3 and 4. Dorothy Dick, Julie Howar, Ken Morgan and Drs. Jaime Jahncke, Nadav Nur, Jeannette E. Zamon, David G. Ainley, Lisa T. Ballance, and David Hyrenbach contributed to the authorship of Chapters 3 and 4.

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1   Introduction

The widely held belief that oceans are an unlimited resource is long past. Direct and indirect anthropogenic impacts from resource extraction, waste disposal, shipping traffic, and climate change are now well-recognized causes to the current and rapid decline in marine ecosystems (Worm et al. 2006; Halpern et al. 2008; Jackson 2008; Lester et al. 2009; Foley et al. 2010). The recognition and the general failure of traditional single species management pushed for the development of more holistic alternatives such as marine ecosystem-based management (EBM). This management approach considers the entire marine ecosystem, including humans, and strives to maintain a healthy, productive, and resilient ecosystem (Laurel and Bradbury 2006; McLeod and Leslie 2009). A key component of marine EBM is marine spatial planning (MSP), a process that requires sound scientific information to identify the spatial distribution of ocean activities to maintain existing and emerging uses, reduce use conflicts, and protect and maintain ecosystem health and services for future generations (Foley et al. 2010).

One strategy of marine EBM and MSP is place-based protection through the creation of marine protected areas (MPAs), areas of ocean designated to enhance conservation of marine resources (Norse and Crowder 2005). MPAs have varying levels of protection from exploitative and extractive activities and aim to achieve one or more of the following: fisheries enhancement, biodiversity conservation, ecosystem protection, and maintenance of ecosystem integrity (Hooker and Gerber 2004). Although MPAs are considered an effective way to address threats and restore ecosystems and populations (Halpern et al. 2003; Lester et al. 2009), less than 2.5% of the worlds' oceans are protected within MPAs (Spalding et al. 2013).

A place-based approach presents many challenges including how to select, design, and monitor MPAs. One proposed method advocates for the use of marine megafauna or top predators (i.e., cetaceans, pinnipeds, seabirds, and sharks) as ecological indicators (Reeves 2000; Hooker and Gerber 2004; Lewison et al. 2012). This technique assumes that the protective measures developed for megafauna will extend to include safeguards to areas of ocean productivity and the other species dependent on that productivity. However, this assumption is confounded by the high mobility and/or migratory behavior of many marine predatory species. In such cases, where it would be virtually impossible to encompass a species entire range within a single MPA, Hooker and Gerber (2004) suggest MPA placement can still be beneficial provided threats, distribution, and life history traits are considered. For example, some baleen whales (e.g., humpback whales, *Megaptera novaeangliae*, and grey whales, *Eschrichtius robustus*) migrate annually between high-latitude feeding areas and equatorial or near-equatorial regions for breeding, while many seabirds (e.g., Cassin's auklet, *Ptychoramphus aleuticus*, and common murre, *Uria aalge*) return annually to offshore islands to breed. Protective measures in these areas should provide long-term benefits to both the targeted species and the ecosystem (Hooker and Gerber 2004).

Although MPAs designed to protect feeding and breeding grounds could reduce habitat destruction and mortality, Hyrenbach et al. (2000) argue that isolated MPAs may not provide sufficient protection to mobile marine megafauna. Conservation actions could fail completely if threats outside MPAs are not also mitigated. Instead, MPA design should contain foraging ranges and migration routes to create a network of protected areas (Hyrenbach et al. 2000) that will incorporate "the complex life history characteristics of these species, the dynamics of their ocean habitats and the vast scope of detrimental human activities" (Hooker et al. 2011, pg. 204).

Targeting regions based on important life history stages and creating networks of MPAs requires spatially explicit information on: 1. the species of interest (e.g., distribution, population structure, abundance/density, etc.); 2. the distribution of critical habitats; 3. the threats in space and time; and 4. an understanding of the physical (e.g., bathymetry, sea surface temperature, productivity, etc.) and biological processes (e.g., migration, dispersal, competition, reproduction, gene flow, etc.) at work (Hooker et al. 2011). This information, the core of any MPA design for marine megafauna, provides a quantitative approach to conservation priorities by mapping spatial data and relevant attributes using mathematical or logical algorithms, bringing repeatability and scientific creditability to the design process (Ferrier and Wintle 2009).

The crux of the above mapping process depends on spatially-explicit data for the species of interest (Hooker et al. 2011). For top predators this is traditionally observations of animals or groups of animals in space and time and is often referred to as sightings or occurrences. Such data are classified into one of two data types. Presence-only data (denoted as P) are locations where an animal(s) was found but contains no information about where an animal(s) was not found. P data originate from opportunistic sightings where there is no survey design or search effort recorded and includes data from strandings, museum collections, and incidental sightings (Elith and Leathwick 2009; Franklin 2009). Presence-absence data (denoted as P-A) lists locations where an animal(s) is both present and absent and is the result of systematic survey designs (i.e. line transects) that also records search effort (Elith and Leathwick 2009; Franklin 2009) and, when possible, has equal coverage probability across the study area (Buckland et al. 2001). P-A data provide a measure of density (relative or absolute) and information on habitat usage and selection. The type of data available will determine the types of questions, analyses, and outcomes that can be asked, conducted, and revealed. The goal of this research is to explore and analyze various types of spatially-explicit marine megafauna data to inform the marine spatial planning process and to help in the design of MPAs in the North Pacific.

The research presented here is deeply embedded within geography through the exploration of spatial ecological processes in space and time. It is also multidisciplinary, drawing upon the fields of marine conservation, molecular ecology, and spatial ecology. As oceans continue to decline, this approach provides a unique opportunity to contribute to the field of marine geography through the development of novel geospatial approaches and spatial analyses to advance marine megafauna conservation. Understanding what factors influence the presence of a species or its genetic variability enable present day planning and design of MPA networks to ensure adequate protection will be in place now and as climate change progresses. This information can also be used to adapt strategies to reduce non-climate stressors such as fishery pressures and coastal development in areas predicted to be important to humpback whales and seabirds in the future.

What follows are three separate research chapters, each focused on answering a specific question set and written for publication in peer reviewed journals. Chapter 2, entitled "*GeneGIS*: Geoanalytical tools and Arc Marine customization for individual-based genetic records" and already published in the journal *Transactions in GIS*, details the development of a suite of computational tools to facilitate visual exploration and spatial analyses of genetic data. The tools enable species genetic variability to be mapped across the seascape simultaneously with relevant environmental factors (e.g. bathymetry, sea surface temperature, productivity, etc.) and potential threats (e.g. fishery pressures, development, oil and gas exploration, etc.). Chapter 3, targeted for publication in *PLoS One*, assesses multispecies seabird foraging aggregations ("hotspots") in the California Current System, examines seasonal/annual variability of hotspot locations, and looks closer at pelagic areas. Chapter 4, aimed for publication in the journal *Global Change Biology*, investigates how climate-related changes will affect the hotspot locations identified in Chapter 3, assesses species sensitivity to these changes, and evaluates potential importance of seamounts in the future.

2   *geneGIS:* Geoanalytical Tools and Arc Marine Customization for Individual-Based Genetic Records

Dorothy M. Dick

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2.1   Abstract

To improve understanding of population structure, ecosystem relationships and predictive models of human impact in cetaceans and other marine megafauna, we developed *geneGIS*, a suite of GIS tools and a customized Arc Marine data model to facilitate visual exploration and spatial analyses of individual-based records from DNA profiles and photo-identification records. We used the open source programming language Python 2.7 and ArcGIS 10.1 software to create a user-friendly, menu-driven toolbar linked to a Python Toolbox containing customized geoprocessing scripts. For ease of sharing and installation, we compiled the *geneGIS* program into an ArcGIS Python Add-In, freely available for download from the website http://genegis.org. We used the Lord-Castillo et al. (2009) Arc Marine data model customization as the starting point for our work and retained nine key base Arc Marine classes. We demonstrate the utility of *geneGIS* using an integrated database of more than 18,000 records of humpback whales (*Megaptera novaeangliae*) in the North Pacific collected during the Structure of Populations, Levels of Abundance and Status of Humpback Whales in the North Pacific (SPLASH) program. These records represent more than 8,000 naturally marked individuals and 2,700 associated DNA profiles, including 10 biparentally inherited microsatellite loci, maternally inherited mitochondrial DNA, and genetic sex.

2.2 Introduction

Landscape genetics (or seascape genetics in the oceans) aims to study spatial ecological processes by combining knowledge from population genetics, landscape ecology and spatial analysis to quantify the influence of landscape features on population genetic structure (Manel et al. 2003, Storfer et al. 2007). Understanding the relationship between landscape and genetic connectivity can reveal new insights into biological processes and lead to detecting, predicting and mitigating the effects of anthropogenic landscape modification and global climate change (Wagner et al. 2012). This knowledge can aid managers in conservation measures by identifying barriers to gene flow or genetic diversity and provide alternative management scenarios to predict consequences to genetic variation and population connectivity (Storfer et al. 2007). With the advent of global positioning system (GPS) technology, growing databases of spatially explicit genetic data have opened novel analysis opportunities including the development of geographic information system (GIS) software packages such as the Landscape Genetics GIS Toolbox (Vandergast et al. 2011) and Landscape Genetics Toolbox (Etherington 2011) (Table 2.1). Additional stand-alone software such as GenGIS2 (Parks et al. 2013) and *Wildbook* (http://www.wildme.org/wildbook/) allow for the integration of genetic data with digital maps to enhance geographic and/or ecological data visualization (Table 2.1). Although these packages help to visualize various genetic metrics across geographic space, none directly calculate genetic distance measures (e.g., F-statistics) or provide estimates of kinship and relatedness while also allowing for the visualization *and* spatial analysis of multiple records from known individuals as is typical in the field of marine mammal science.

Table 2.1.Summary of spatially-based landscape genetics software packages developed to help analyze various genetic metrics in geographic space.

Landscape Genetics Software Package	Analyses Performed	GIS based?
Genetic Landscapes GIS Toolbox (Vandergast et al. 2011)	Creates raster surfaces of genetic divergence and diversity for single species (or genetic marker) and summarizes multiple genetic divergence or diversity rasters as average and variance surfaces	Yes (ArcGIS 9.3+)
Landscape Genetics Toolbox (Etherington 2011)	Creates a polyline shapefile to visualize genetic relatedness, conducts least-cost modeling to measure landscape connectivity, creates a matrix of pairwise points separated by a known barrier (either lines or landscape polygons)	Yes (ArcGIS 9.3+)
GenGIS 2 (Parks et al. 2013)	Integrates molecular biodiversity data with digital maps and habitat parameters to visualize geographic and ecological factors that influence community composition and function	No (basic mapping capabilities, supported by GDAL and R Project)
Wildbook (http://www.wildme.org/wildbook/) Developed in parallel with *geneGIS*	A web-accessible Java-based relational database management framework supporting capture-mark-recapture and molecular ecology of marine megafauna. Integrates photo-identification and genetic records, some direct calculations of F-statistics	No (basic mapping using Google Maps and export functions)

Many whale and dolphin species (cetaceans) are the focus of large-scale, long-term field studies that include numerous spatially-explicit observations of recognizable individuals. Repeated sightings of known individuals over time can reveal information on site fidelity (e.g., Baker et al. 2013), habitat use (e.g., Rasmussen et al. 2007), life history parameters (e.g., Ford et al. 2000), social organization (e.g., Baird and Whitehead 2000), distribution (e.g., Dalla Rosa et al. 2012), abundance (Barlow et al. 2011), and population structure (e.g., Baker et al. 1986, 1998, 2013). Such information is critical for protecting cetaceans and their natural ecosystems from the cumulative and synergistic effects of habitat degradation, fisheries, pollution, vessel traffic and global climate change (Reeves et al. 2003, Würsig et al. 2009).

Individual identity in cetaceans is typically determined by either photo-identification or genetic analysis. Photo-identification uses 35-mm cameras with telephoto lenses to capture distinct natural markings, color patterns, and scarring on an animal's body and/or notches and nicks along fins and fluke edges to identify individuals (Hammond et al. 1990). The photographs are reconciled to unique individuals and compiled into catalogs with associated databases for analyses and future reference. The replacement of film cameras with high-resolution digital cameras increased the accuracy, speed and efficiency of photo-identification techniques (Markowitz et al. 2003). Alternatively, genetic analysis using non-lethal collection of tissue samples (e.g., biopsy dart deployed via a crossbow or rifle, Noren and Mocklin 2012) from animals in the wild and DNA markers are used to reveal a unique genetic identity (genotype or DNA profile) for each individual. In addition to obtaining a genotype, samples can also be used to determine population structure including kinship, prey preferences through stable isotope analysis, contaminant loads, and hormonal indicators of physiological processes (Noren and Mocklin 2012).

The number of records typically generated by the two approaches differs significantly. Photo-identification, especially when using digital cameras, generates large numbers of records (1000s) because each time an individual is encountered there is an opportunity for many photographs (and associated spatio-temporal information) to be added to a database. Conversely, the number of genetic samples is typically far fewer because the genome of an individual does not change. Sampling, therefore, only needs to occur once to capture an individual's genetic identity in a database. It is critical however, that a genetic sample and an associated identification photograph are collected simultaneously and recorded accurately to insure that the two forms of individual identity are correctly associated in the database. Although linking the photographic and genetic databases via a common identity field is possible, it is often challenging. The lack of integration between the two data sources may be due to different research questions and subsequent data needs, permitting stipulations, or a lack of computational tools available to handle such data. Yet, from an analytical perspective, the extension of an individual's DNA profile to photo records where genetic data are lacking and their subsequent integration into one large database would enrich the information available that can be used for conservation and management decisions. Even when reconciled into a single database, few tools exist that enable a researcher to visualize the spatial pattern of such integrated data.

The Convention on Biological Diversity's recent call to improve biodiversity by safeguarding genetic diversity (CBD 2012) emphasizes the importance of its inclusion when planning conservation measures. A population or species with greater genetic variation should have higher resilience and be able to adapt to environmental changes and perturbations more readily (Primack 2010). The enrichment of a database by the addition of genetic information enables managers to factor in population structure and genetic diversity, and thus maximize species resilience, when developing conservation actions. But, how can we best facilitate the exploration and visualization of *spatial* patterns of genetic variability in individual-based, long-term cetacean studies? To address this question, we

develop *geneGIS*, a suite of GIS tools and a customized version of the Arc Marine data model (Wright et al. 2007) for spatially-explicit genetic and photo-identification records to enable: (1) data visualization; (2) spatial exploration, display and selection of data; (3) basic spatial analyses; (4) data extraction from relevant environmental layers; and (5) data export to specialized software packages for molecular ecology. We use data from a three-year humpback whale study in the North Pacific as our exemplar in the development and implementation of *geneGIS*. Although we focus here on the use of *geneGIS* for cetaceans, we envision *geneGIS* will be a powerful platform to enhance our understanding of population structure, ecosystem relationships and predictive models of human impact across species and ecosystems, while also contributing to the development of landscape and seascape genetics (Miller 2005, Etherington 2011, Vandergast et al. 2011, Parks et al. 2013).

2.3   Background Information

2.3.1   Humpback Whales of the North Pacific and the SPLASH Program

Humpback whales (*Megaptera novaeangliae*) occur in all major ocean basins and migrate seasonally between high latitude feeding grounds and low latitude breeding grounds (Johnson and Wolman 1984). Their coastal distribution enabled heavy exploitation by the whaling industry for several centuries (Clapham 2009) and severe depletion led to an endangered listing under the United States Endangered Species Act of 1973 and endangered/vulnerable status (1986-1990/1990-2008, respectively) by the World Conservation Union (Stevick et al. 2003, Reilly et al. 2008). In 1966 the International Whaling Commission banned commercial humpback whale hunting in the North Pacific (Best 1993). Today, most studied populations are recovering (Barlow et al. 2011), however, their presence in coastal regions remains a concern because these areas tend to be the most heavily populated and modified by humans.

To better understand the abundance, distribution and population structure of humpback whale populations in the entire North Pacific, a three-year international collaborative effort including over 50 research groups and more than 400 researchers in 10 countries was conducted from 2004-2006 (Calambokidis et al. 2008). The Structure of Populations, Levels of Abundance and Status of Humpbacks (SPLASH) program targeted all known humpback whale winter breeding and summer feeding grounds. The SPLASH program yielded 18,640 quality photo-identification images representing 7,940 unique individuals. A total of 5,669 tissue samples were also collected; 2,703 of these were genotyped resolving 2,161 individuals. Prior to beginning the *geneGIS* project, photographic and basic sample collection data (photoSPLASH) were stored in a Microsoft Access relational database, which serves as the primary data repository for the SPLASH program. In parallel development to *geneGIS*, photoSPLASH is also adapted to an online catalog and database repository (http://www.splashcatalog.org) hosted by Wildbook (http://www.wildme.org/wildbook), a Java-based software framework supporting capture-mark-recapture studies of marine megafauna. The SPLASH catalog allows users varying degrees of access to the photoSPLASH database (depending on authorization level) to search, filter, query and export records of individual-based humpback whale encounters made during the SPLASH project. Genetic analytical data from samples collected during SPLASH (geneSPLASH) including sex, maternally inherited mitochondrial DNA (mtDNA) and 10 microsatellite loci were originally stored as tabular spreadsheets in Microsoft Excel. Although separate, the databases share several common fields including Occurrence ID (a point in time and space when one or more whales were observed), Encounter ID (a point in time and space at which a photograph and/or tissue sample of an individual was collected) and Individual ID (a unique number for each distinct individual based on photograph or genotype).

During 2011-2012, photoSPLASH and geneSPLASH were merged into a single database (hereafter referred to as SPLASH). The reconciliation extended the number of encounters to include 781 new identifications from whales with no photo record and extended 1,002 different genotypes to 3,189 encounters that previously only had a photo record. This resulted in 7,335 total encounters (roughly 40% of the database) for 2,151 whales with a unique genotype. The large increase in the number of spatially-explicit encounters now extended with genetic records provides an unprecedented opportunity to explore the spatial pattern of genetic diversity of North Pacific humpback whales using GIS.

2.3.2   Conceptual Framework

The conceptual framework for *geneGIS* relies upon three key components – the location of known individuals, the measured value of environmental variables at that location, and the DNA profiles of these individuals (Figure 2.1). The configuration of these components and the data available will determine the type of research questions that can be asked. For example, data on individual location and seascape covariates can lead to questions concerning habitat preference and habitat use. Individual location data combined with DNA profiles can be used to study population structure, relatedness and kinship. Finally, DNA profiles in combination with environmental variables can be used to focus on seascape genetics to determine how the seascape may impact population structure. The point at which these pieces merge is *geneGIS*, an initiative that seeks to integrate spatially-explicit individual-based data and seascape variables to better understand the patterns and processes of genetic variability in the marine environment.
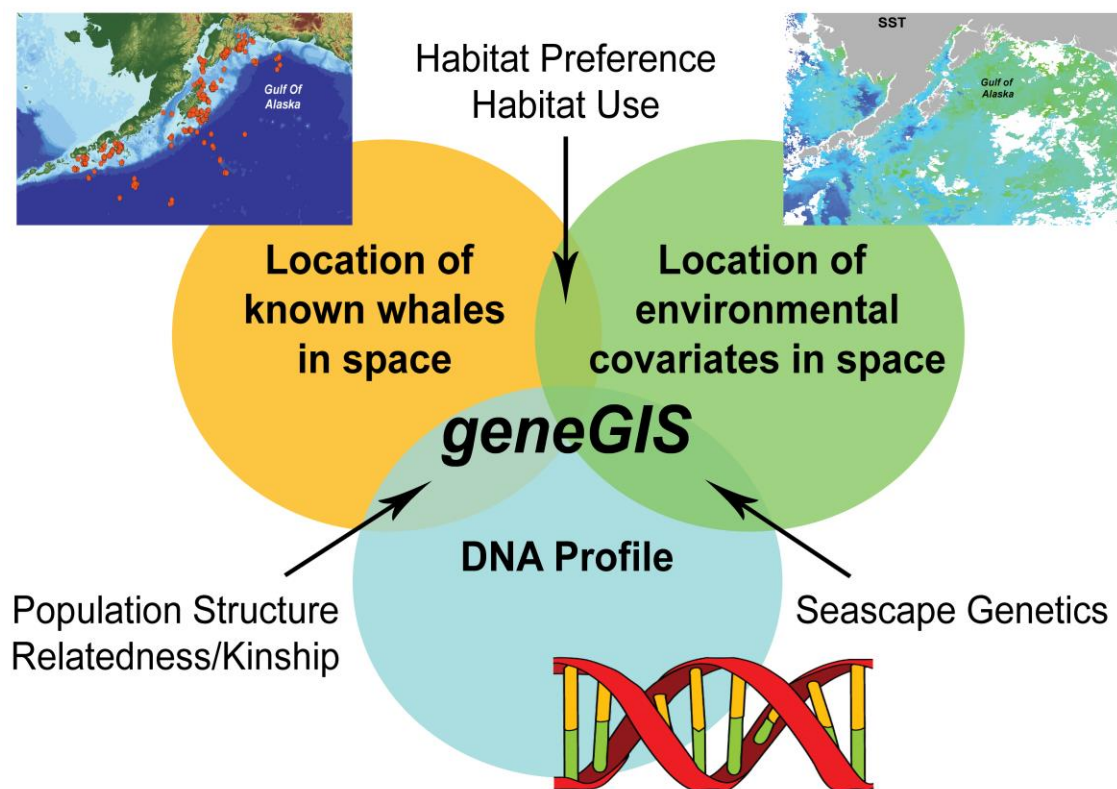
Figure 2.1.The conceptual framework used to illustrate how data for known individual locations, associated environmental variables and DNA profiles can be integrated by the *geneGIS* initiative.

2.3.3 Key Requirements

The success of the *geneGIS* initiative depends on several key requirements. To maximize the number of potential users, we target molecular ecologists and marine mammal scientists with little to no GIS background. Thus, tools must be easy to install and operate within ArcGIS. *geneGIS* must also be able to work with the various data types and data storage formats of our users. Most databases of genetic records are small (~ 100s to 1000 of records) and are stored in flat tabular formats such as Microsoft Excel spreadsheets. Data may consist of letters (e.g, genetic sex - M: male, F: female, U: unknown or nucleotide sequence - ATTGCAATGGCCTTA), numbers (e.g., microsatellite allele sizes - 122, 124), or alphanumeric sequences (e.g., mtDNA haplotype codes - F2, A+, E2). Photo-identification

databases typically contain 1000s of records and may or may not be stored in a relational database structure. Therefore, *geneGIS* must be able to function with the unique data types of genetic data stored in simple data tables and relational databases. For these reasons we chose a two pronged approach, a suite of GIS tools designed to function with flat tables and relational databases, plus an option to import data into a customized Arc Marine relational data model. The latter provides an additional opportunity to store and manage data in a relational database framework created specifically for marine data and can increase interoperability with other relational databases such as *Wildbook*.

2.4   *geneGIS* Tools

2.4.1   Software Platform and Tool Architecture

We developed *geneGIS* tools using the open source programming language Python (version 2.7) and ArcGIS software (version 10.1). Although a commercial product, ArcGIS is well known, widely used, and considered the dominant platform used by GIS professionals (Roberts et al. 2010). As part of its built-in capabilities, Python scripts can be written to create customized geoprocessing tools that are run using simple dialog windows. This makes tools accessible to non-GIS experts and allows them to be combined with other standard ArcGIS tools for more complex spatial analyses. Moreover, because Python is an open source language, it allows GIS specialists to share and further customize scripts, a tradition that *geneGIS* builds upon by also being open source.

We used two new ArcGIS features released with ArcGIS version 10.1 – the Python toolbox and the Python add-in. A Python toolbox is a geoprocessing toolbox created entirely in Python and can be edited in any editor. Unlike script tools in custom ArcToolboxes which are composed of three separate parts, a Python toolbox holds the parameter definitions, code validation and the source code in a single location using Python classes. From a developer's perspective, the Python toolbox provides a more streamlined environment for

tool creation. Yet, from a user's perspective, a Python toolbox and tools look and function like any other.

A Python add-in is a customization that interfaces with ArcGIS for Desktop (e.g., ArcMap) to enable additional functionality for custom tasks. The add-in is created using a freely available Python Add-In Wizard and is comprised of a single zipped package (with .esriaddin extension) containing a configuration XML file, the geoprocessing Python scripts, and any additional resource files necessary for the add-in. Add-ins are easily installed by downloading the add-in file to a user designated folder and double-clicking on the .ersiaddin icon.

For our purposes, these two new features enabled an interactive environment for the user by developing a user-friendly menu driven toolbar that links to the Python toolbox containing the geoprocessing scripts (Figure 2.2). By containing the entire *geneGIS* program within a Python add-in, a non-GIS expert can easily download, install and use *geneGIS* with a few mouse clicks.
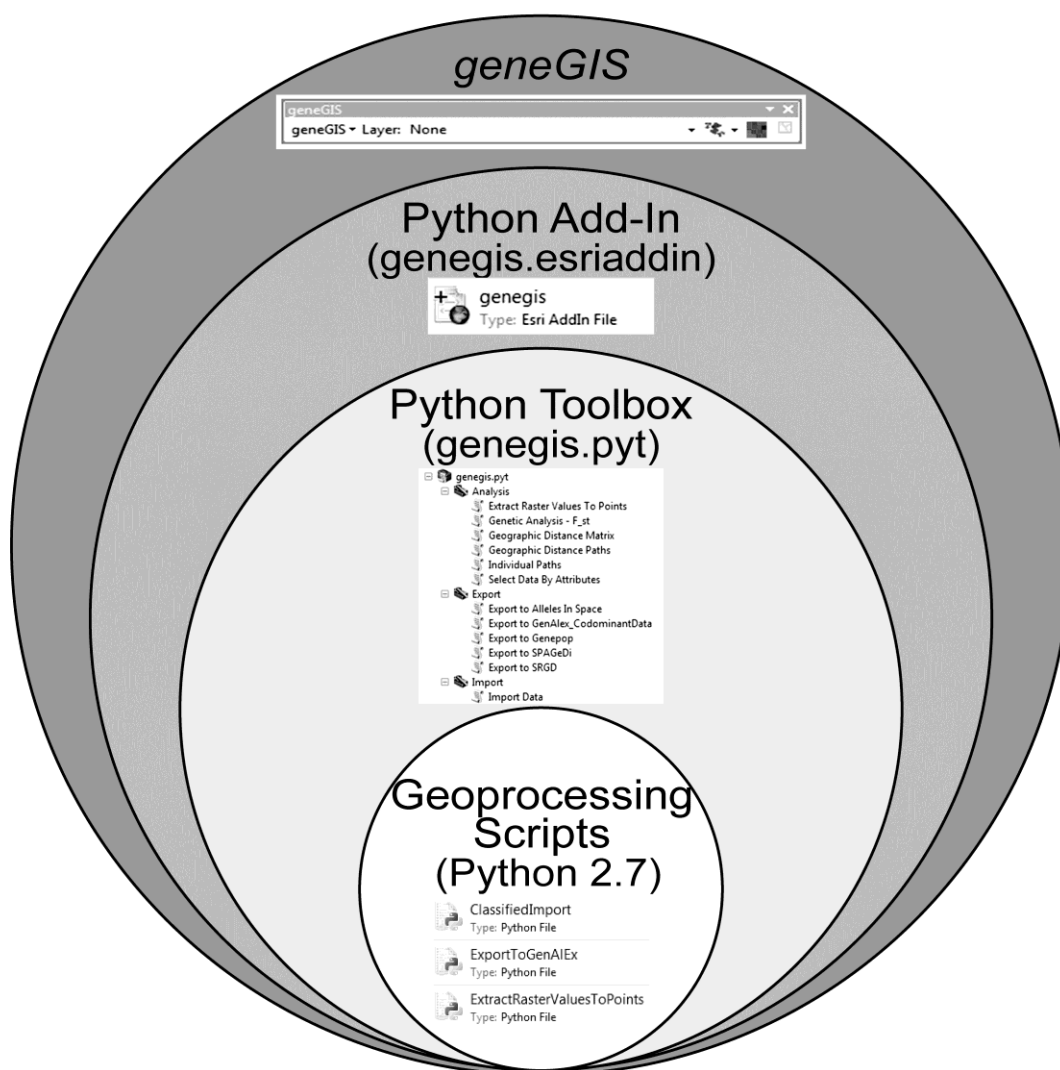
Figure 2.2. A diagram detailing the tool architecture of *geneGIS*. At its core are the customized geoprocessing scripts written in Python that are stored within a Python toolbox. The Python toolbox is then plugged into ArcGIS via a Python add-in to create a user-friendly, menu driven toolbar.

2.4.2   Standard Input File

To aid non-GIS users in importing data into *geneGIS*, we developed a standardized input file format, the Spatially Reference Genetic Data file or SRGD (Figure 2.3). The SRGD is a comma separated value file (CSV) and specifies the minimum data requirements necessary to use

geneGIS. Based on expert opinion, we selected the most common data fields and formats used by molecular ecologists for inclusion in the SRGD file. Any additional data deemed necessary by the researcher (e.g., group size, behavior etc.) may also be included. A complete description of the SRGD input file format, a sample dataset (courtesy of Cascadia Research Collective, http://www.cascadiaresearch.org) and tutorial are freely available for download from the *geneGIS* website, http://genegis.org.

	A	B	C	D	E	F	G	H	I	J	K	L	M	N	O
1	Sample_ID	Individual_ID	Source_ID	Latitude	Longitude	Date_Time	Region	Sex	Haplotype	L_GATA417	L_GATA417	L_Ev37	L_Ev37	L_Ev96	L_Ev96
2	1	1001	Photo	13.9038	-90.7658	2004/03/09T11:39:00	Central America								
3	2	1001	Photo	20.6	-105.6	2006/02/16T07:40:00	Mainland Mexico								
4	3	1002	Photo	13.7991	-90.9955	2004/02/07T14:56:00	Central America	M		206	222	208	220	157	163
5	4	1002	Photo	10.9808	-85.8615	2004/02/16T16:25:00	Central America	M		206	222	208	220	157	163
6	5	1002	Photo/Genetic	11.0253	-85.9176	2005/01/25T07:41:00	Central America	M		206	222	208	220	157	163
7	6	1003	Photo	8.7206	-83.8183	2004/02/11T10:33:00	Central America	M	F2	206	226	196	208	147	163
8	7	1003	Photo	8.7396	-83.7873	2004/02/27T15:46:00	Central America	M	F2	206	226	196	208	147	163
9	8	1003	Photo	8.7122	-83.82	2004/03/13T00:00:00	Central America	M	F2	206	226	196	208	147	163
10	9	1003	Photo	10.96	-85.91	2004/03/18T11:35:00	Central America	M	F2	206	226	196	208	147	163
11	10	1003	Photo/Genetic	13.7851	-90.2733	2005/02/22T15:02:00	Central America	M	F2	206	226	196	208	147	163
12	11	1004	Photo/Genetic	8.708	-83.7341	2004/04/02T08:09:00	Central America	F		207	222	192	198	161	163
13	12	1004	Photo	13.769	-90.2985	2005/02/20T08:49:00	Central America	F		207	222	192	198	161	163
14	13	1004	Photo	13.8271	-90.4306	2005/02/20T09:15:00	Central America	F		207	222	192	198	161	163
15	14	1005	Photo	12.8006	-87.653	2005/01/16T15:23:00	Central America								
16	15	1006	Genetic	8.8413	-83.6498	2004/03/10T09:15:00	Central America	F	A+	214	214	192	210	161	163

Figure 2.3. An example of the SRGD.csv input file format for *geneGIS*. The individual-based photo and genetic databases were merged and the genetic information extended to the photo encounters. Columns A, B, and C represent fields considered to be identifiers and have the suffix _ID. Columns J-O represent three biallelic microsatellite loci, 2 columns per locus, each with a L_ prefix. Individuals 1001 and 1005 have photo-only encounters; individual 1006 had a genetic-only encounter; and individuals 1002-1004 have had their genetic information extended to their photo-only encounters.

2.4.3   *geneGIS* Tools

At the time of this writing, *geneGIS* consists of 12 tools grouped into four categories (Import, Export, Genetic Analysis and Geographic Analysis), plus a Help category that links to *geneGIS* website resources (Table 2.2). A key goal of *geneGIS* is to allow novel ways of data exploration through visualization, spatial selection, data extraction and basic analyses of genetic data in relation to the marine environment. This information is critical during hypothesis development for spatially explicit analyses. We do not intend to duplicate the

efforts of other specialized software packages for molecular ecology such as GenAlEx (Peakall and Smouse 2006, 2012), Genepop (Raymond and Rousset 1995, Rousset 2008), Alleles in Space (Miller 2005), and SPAGeDi (Hardy and Vekemans 2002), but instead enable exploratory analyses and data export in an appropriate format to those programs for further analyses. We also offer data export as a Keyhole Markup Language (KML) file for use with software such as Google Earth and a SRGD file format compatible for data upload into the *Wildbook* relational database management framework. In addition, we provide two tools (Summarize Encounters, Compare Encounters) invoked with buttons from the toolbar that allow the user to interactively spatially select up to two different groups of points and provide some basic statistics about that selection including the number of samples, the number of unique individuals and the number of unique individuals common to both selections.

Table 2.2. Suite of tools available in *geneGIS* release 0.2 for ArcGIS 10.1.

Tool	Function	Reference Information
Import – Imports spatially reference data into ArcGIS		
Import	Creates a new file geodatabase (if one does not exist) and imports individual-based genetic and photographic data from the SRGD.csv input file into a file geodatabase point feature class. A copy of the table is also placed in the geodatabase.	
Export – Exports data from ArcGIS feature class		
Export to Alleles in Space	Creates a file for use with Alleles in Space (AIS), software for the joint analysis of inter-individual spatial and genetic information.	Miller 2005 http://www.marksgeneticsoftware.net
Export to GenAlEx	Creates a text file formatted for use with GenAlEx, an MS Excel Add-in for population genetic analyses.	Peakall and Smouse 2006, 2012 http://biology. anu.edu.au/GenAlEx
Export to Genepop	Creates a text file formatted for use with Genepop, a web based program for population genetic analyses.	Raymond and Rousset 1995 Rousset 2008 http://genepop.curtin.edu.au
Export to KML	Creates a KML file, viewable in ArcGIS Explorer, ArcGlobe, and Google Earth.	
Export to SPAGeDi	Creates a file formatted for SPAGeDi, software for the spatial pattern analysis of genetic diversity.	Hardy and Vekemans 2002 http://ebe.ulb.ac.be/ebe/SPAGeDi.html
Export to SRGD	Creates a SRGD formatted table (CSV) for data uploading to *Wildbook*, a software framework for mark-recapture studies.	http://www.wildme.org/wildbook
Genetic Analysis		
Calculate F-statistics	Uses SPAGeDi software to calculate a variety of F-statistics and outputs them to a text file. Text file opens upon completion.	Hardy and Vekemans 2002 http://ebe.ulb.ac.be/ebe/SPAGeDi.html

Tool	Function	Reference Information
Geographic Analysis		
Compute Geographic Distance Matrix	Computes a full pairwise geodesic distance matrix between all input locations, such as encounters with individual whales. Calculations performed using Vincenty's formulae, accurate to within 0.5mm. Output is a comma separated value (CSV) file.	
Compute Geographic Distance Paths	Computes pairwise geodesic arcs connecting all input points. The arcs represent the shortest distance (great circle distance) between locations. An attribute of the distance is also included as an output column, "Distance_in_km".	
Individual Paths	Creates individual paths, linking a selected set of individuals across all locations they have been encountered. Assumes linear movement between locations. Output is a new feature class.	
Extract Raster Values	Extracts values from one or more raster layers based on encounter (point) locations. Extracted values are added to the attribute table of the designated feature class. A new column is added for each input raster and based upon the raster name, prefixed with 'R_'.	
Help		
geneGIS Homepage	Takes the user to the project website homepage	http://genegis.org/
geneGIS Documentation	Takes the user to the project documentation webpage	http://genegis.org/documentation.html

2.4.4   *geneGIS* Application Examples

We use the reconciled and extended SPLASH data to illustrate a series of applications using the tools in *geneGIS* and ArcGIS to explore, develop and begin to answer spatially-explicit research questions. Examples are broken down into the five current key functions of *geneGIS*: (1) data visualization; (2) spatially explore, display and select data; (3) export data; (4) data extraction from environmental layers; and (5) conduct basic spatial analyses.

2.4.4.1   *Data Import and Data Visualization*

The first step in any *geneGIS* application requires the import of georeferenced genetic data into ArcGIS. SPLASH data are formatted to meet the SRGD file specifications (Figure 2.3) and imported into a file geodatabase point feature class using the Import Tool (Figure 2.4A). To provide geographical context, a base map layer can be added (Figure 2.4B). Initial data visualization provides the added benefit of quickly identifying and enabling the correction of questionable coordinates such as whales sighted on land.
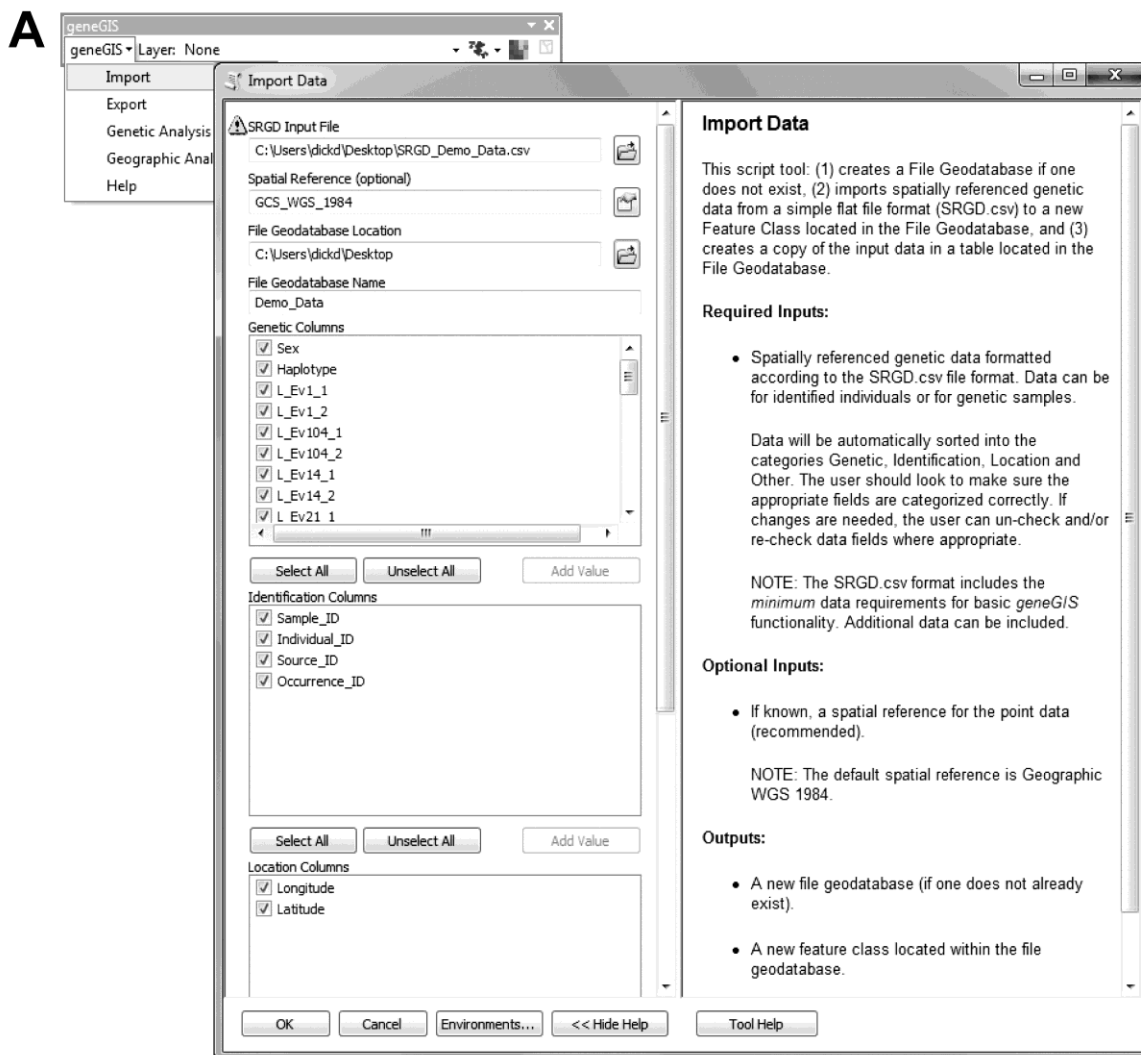
Figure 2.4A. An example workflow using *geneGIS* – invoking the Import tool from the *geneGIS* toolbar and the dialog box filled according to the descriptive help text to the right. The warning icon next to the SRGD Input File provides a reminder that the microsatellite loci will be suffixed with an '_1' or '_2' when this tool is run.
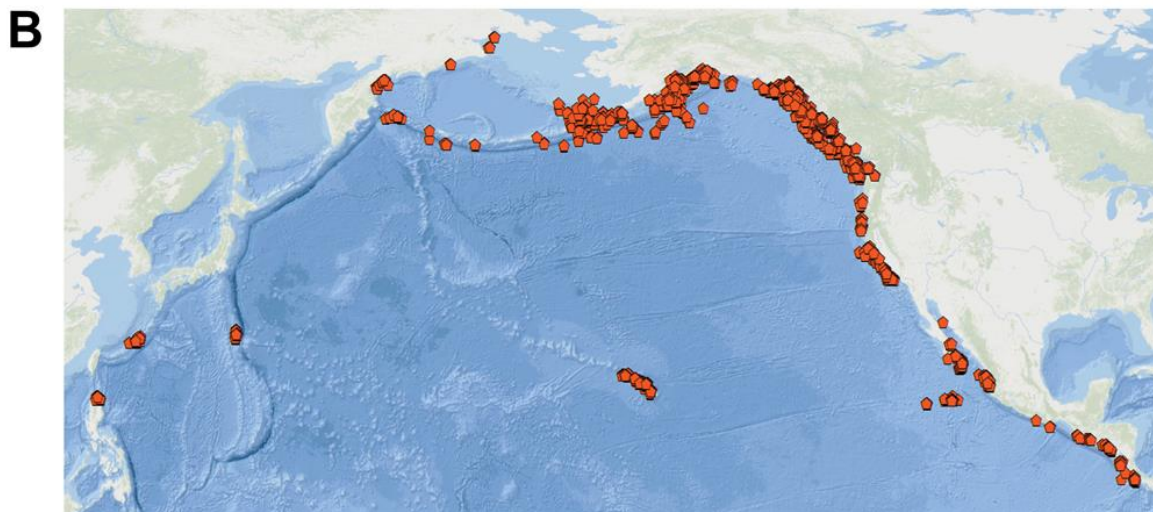
Figure 2.4B. An example workflow for *geneGIS* – visualizing an output point feature class created from all individuals encountered during the SPLASH program from 2004-2006. For geographic context, the Esri Ocean Basemap (http://esriurl.com/obm, courtesy of Esri and its partners), is also added.

2.4.4.2 Spatial Exploration, Data Selection, and Data Export

These functions can assist with answering research questions such as: "Are humpback whale populations in the Western Gulf of Alaska and Southeast Alaska genetically differentiated?" Genetic differentiation between populations is a common question in molecular ecology; however, it is often limited to researcher-defined populations based on *a priori* knowledge and less often uses the specific spatial location of collected samples. To enhance the potential for using spatial exploration rather than *a priori* divisions, *geneGIS* enables the user to interactively spatially select points. Using the Summarize and Compare Encounter tools from the *geneGIS* toolbar, one group of points ("populations") is spatially selected and briefly summarized for each area of interest (Figure 2.5A). Note, the text box reports on the total number of encounters and total individuals, as well as individuals found in both spatial strata (i.e., photo-ID resightings or genotypes recaptures). The Export to

GenAlEx tool from the Export menu is used to export the selected data as a single file composed of the two selected populations to the text file input format required by GenAlEx v6.5 (Peakall and Smouse 2006, 2012) (Figure 2.5B). Additional analysis in GenAlEx, using mtDNA known to reflect maternal migration traditions, indicates the two populations are significantly differentiated (F_{ST} = 0.197, p < 0.01). To better illustrate this genetic differentiation, haplotype frequency pie charts were created within Excel (Figure 2.5C). Data can also be exported using the Export to Genepop tool and the output file meets the format requirements for Genepop (Raymond and Rousset 1995, Rousset 2008). In both cases, exports to GenAlEx and Genepop allow for microsatellite or mtDNA analyses of genetic differentiation.
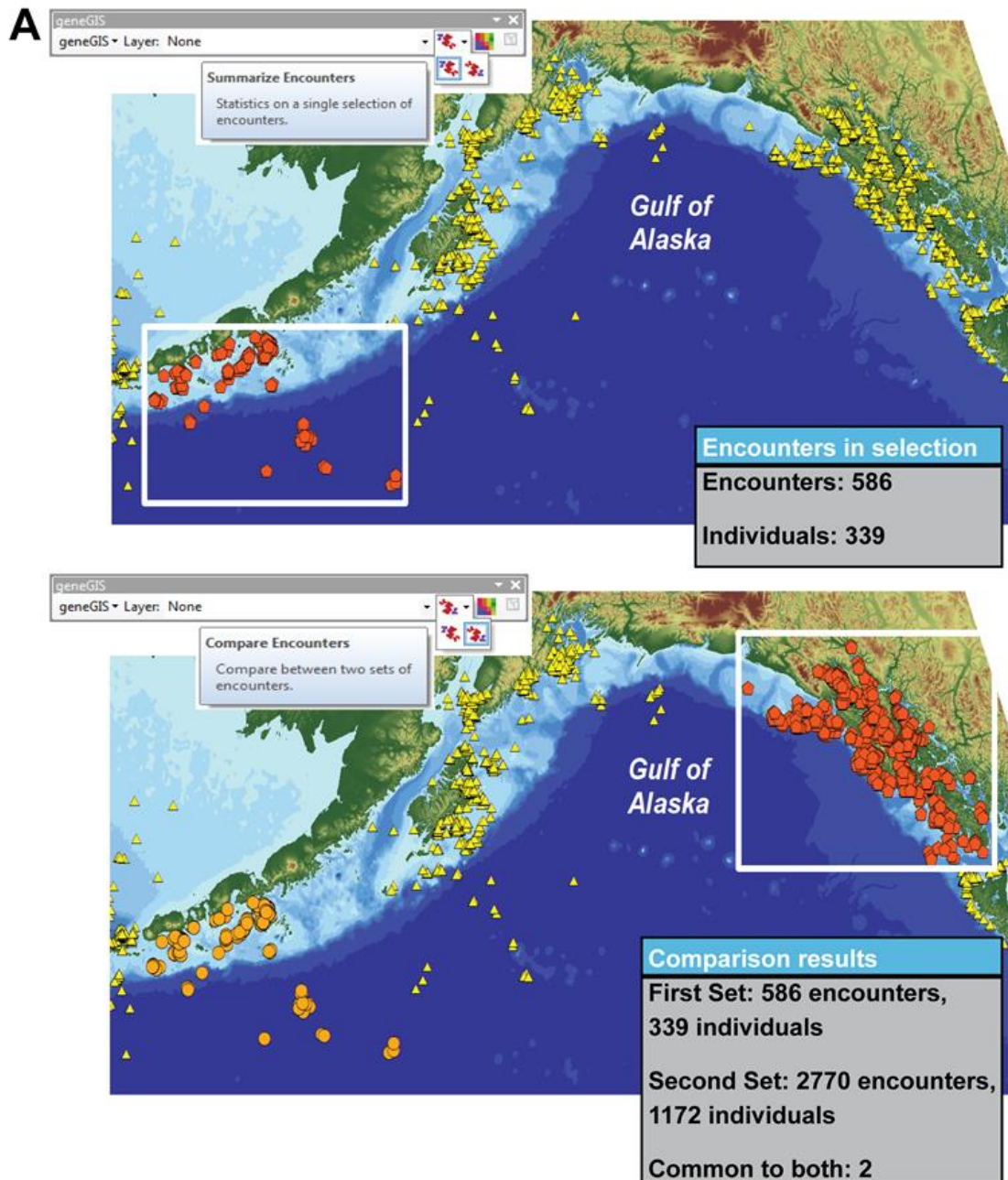
Figure 2.5A. An example workflow using *geneGIS* – spatial selection using SPLASH data. Data are spatially selected using the Summarize Encounter (top) and Compare Encounter (bottom) tools on the *geneGIS* toolbar.
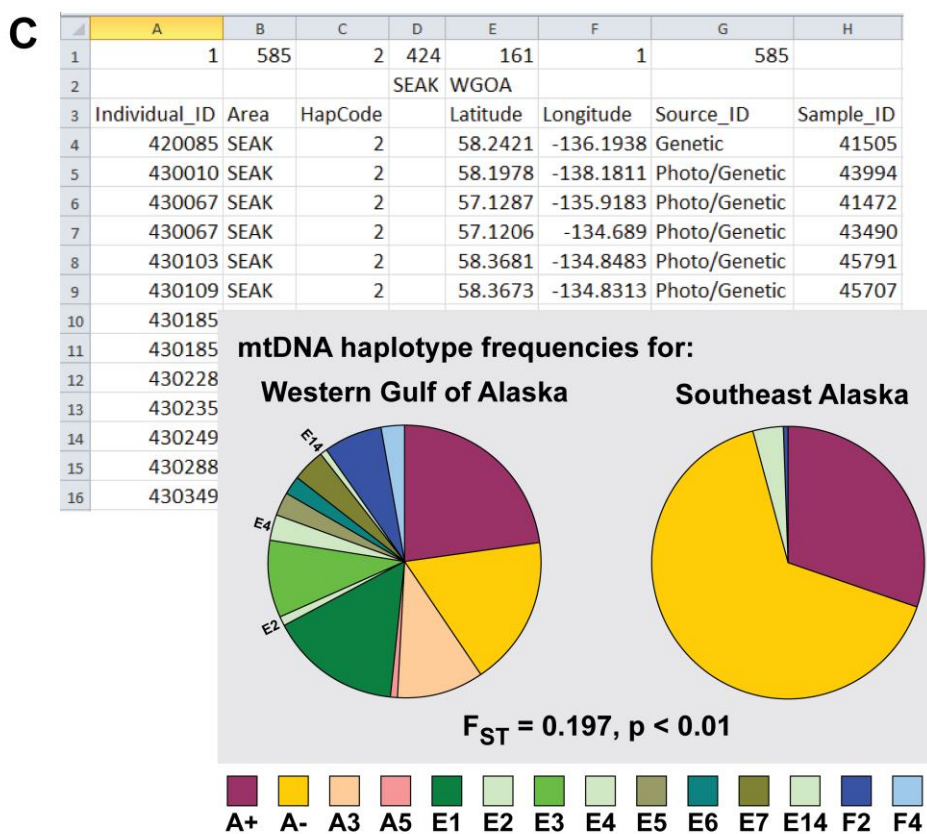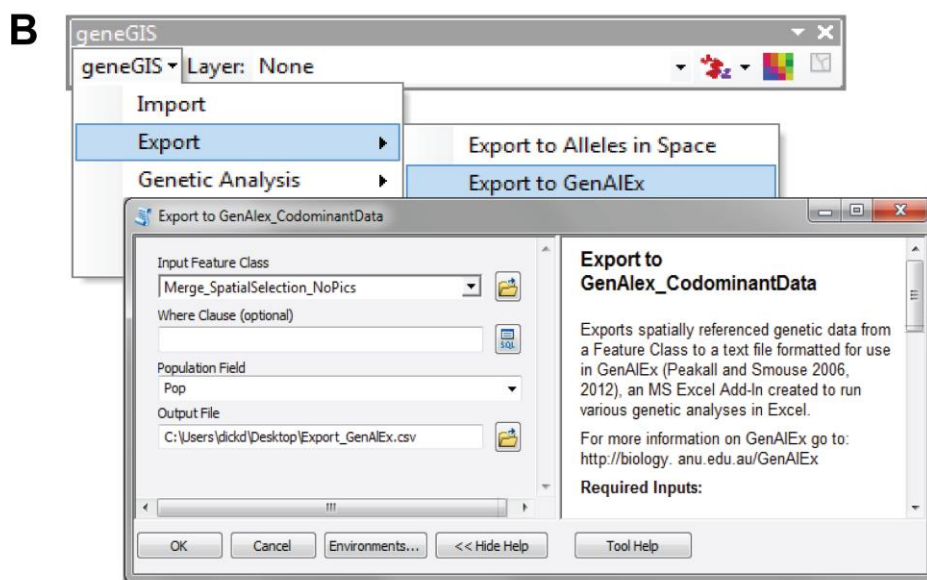
Figure 2.5B,C. An example workflow in *geneGIS* – data export using SPLASH data. The Export to GenAlEx tool can be used for additional genetic analyses(B); a test for genetic differentiation in GenAlEx confirms the two "populations" are significantly differentiated based on mtDNA (C).

An alternate analysis of genetic differentiation can be done directly within ArcGIS using the program SPAGeDi (Hardy and Vekemans 2002), although currently limited to microsatellite data. In this instance, once the two spatial selections are completed, the standard ArcGIS Merge tool is used to merge the selected data into one feature class. The Calculate F-statistics tool from the Genetic Analysis menu invokes SPAGeDi to calculate F-statistics and create an output tab delimited text file that is opened directly within ArcGIS (Figure 2.5D).
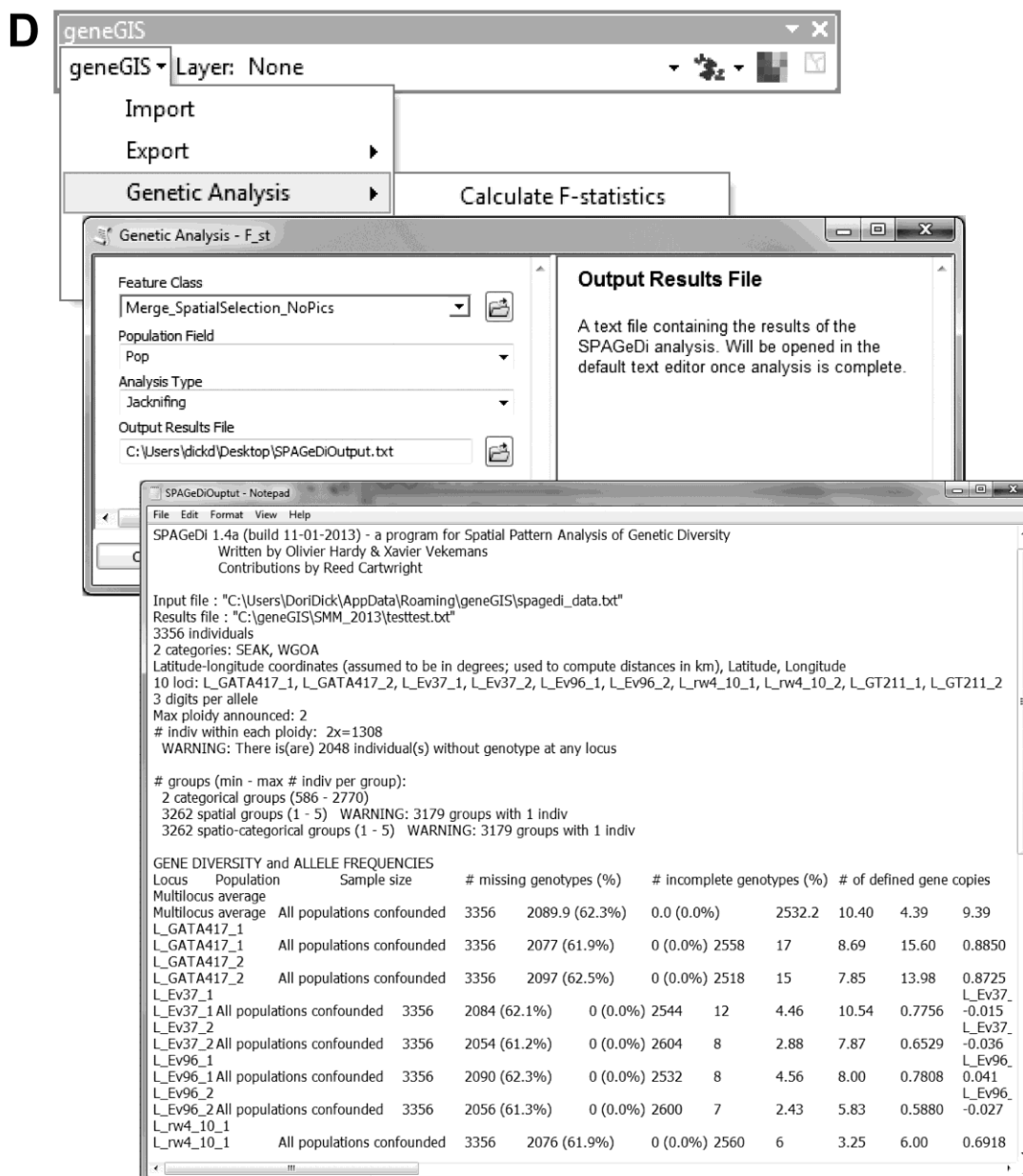
Figure 2.5D. An example workflow in *geneGIS* – calculating F-statistics within ArcGIS using SPLASH data. The alternate method involves merging the two selected "populations" using the standard ArcGIS Merge tool followed by the Calculate F-statistics tool from the *geneGIS* toolbar to invoke SPAGeDi to test for genetic differentiation based on microsatellite DNA.

2.4.4.3   Data Extraction from Environmental Layers

Data extraction can assist with exploring the relationship between environmental variables and individual presence/absence to assist with answering research questions such as: "Within a set of whales of known mtDNA haplotype is there any evidence of preference for particular depths?" In this instance, data from known individuals or mtDNA lineages can be mapped with one or more environmental raster layers such as bathymetry (e.g., the GEBCO_08 Grid, version 20100927, http://www.gebco.net) (Figure 2.6A). The Extract Raster Values tool from the Geographic Analysis menu (or toolbar button) is used to extract cell values of the bathymetry layer for each sample point location of the input feature class (Figure 2.6B). Extracted values are recorded to a new field in the attribute table of the feature class. New fields are named according to the raster layer used and prefixed with 'R_' (e.g., R_GEBCO). Using the standard ArcGIS table export option, the extracted values can be further analyzed in Excel or other graphing software package to create a frequency histogram (Figure 2.6C). In this example, the results from the data extraction suggest that the A- and E3 mtDNA haplotypes occur more frequently at different modal depths, 110m and 150m respectively.
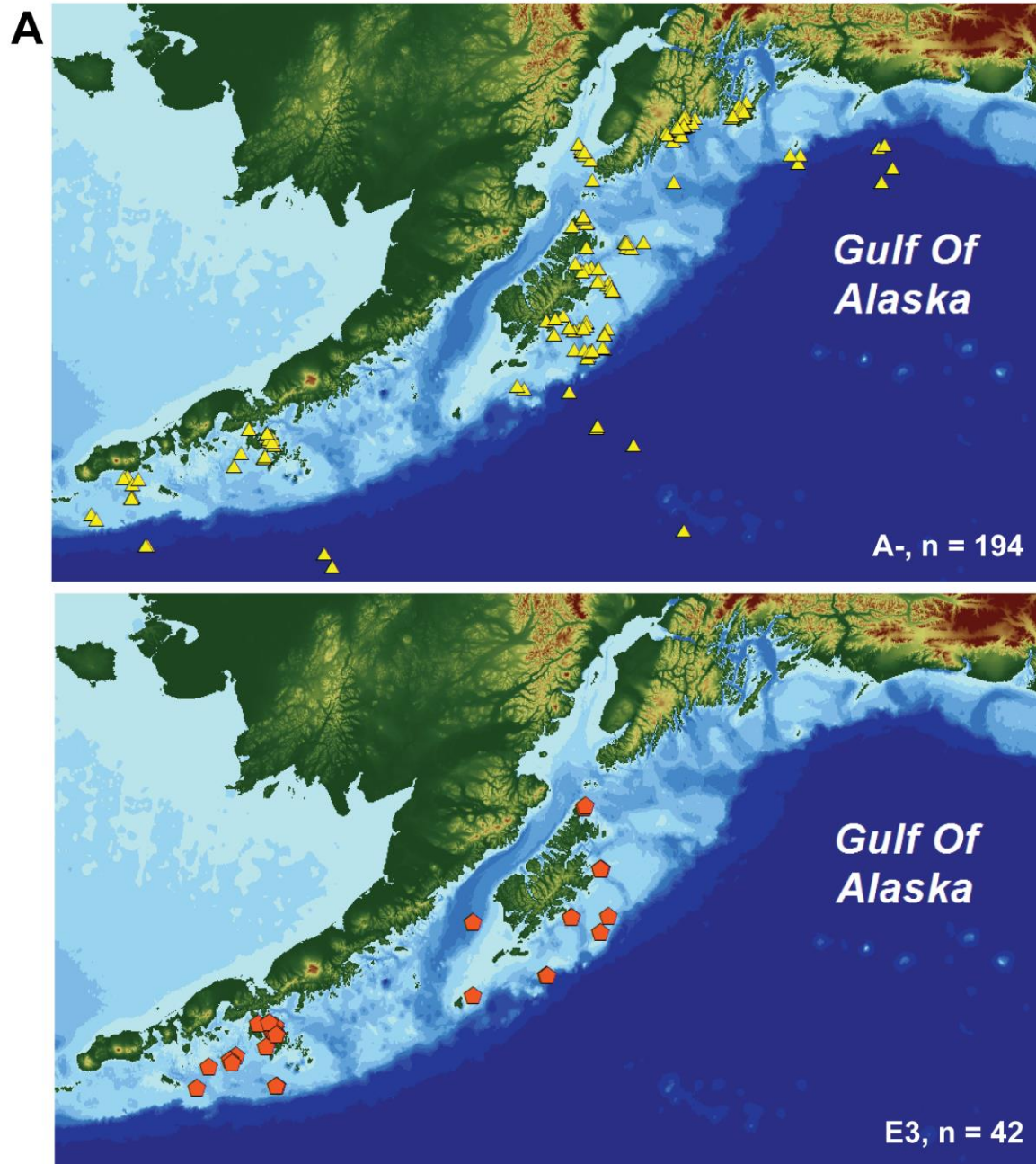
Figure 2.6A. An example workflow in *geneGIS* - Extract Raster Values from bathymetry using SPLASH data. Individuals with known mtDNA haplotypes (A- top, E3 bottom) from the SPLASH data are mapped over a bathymetric raster layer.
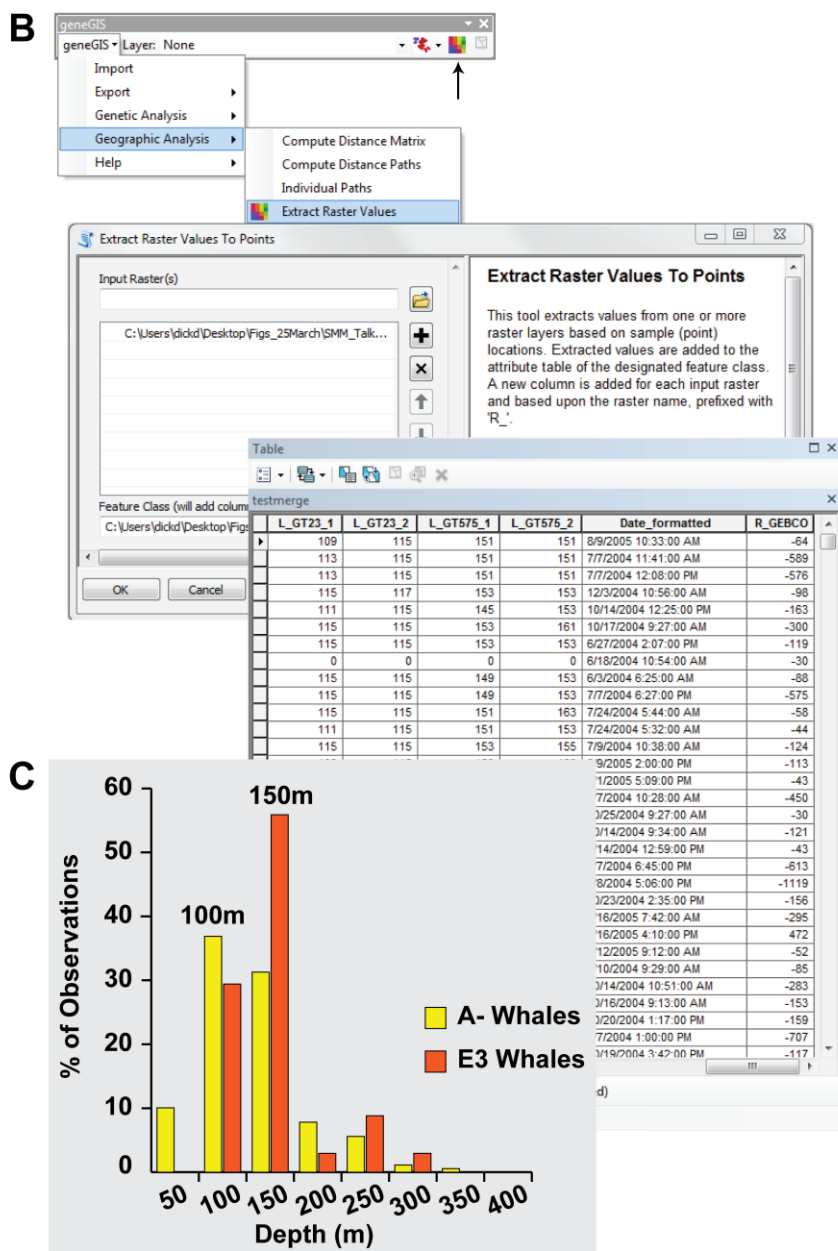
Figure 2.6B,C. An example workflow in *geneGIS* using the Extract Raster Values tool with the SPLASH data. (B)The Extract Raster Values tool is used to extract cell values from the raster (top and middle) and record them into a new field named after the raster, R_GEBCO (bottom). (C) The data are exported using ArcGIS's table export option to enable further analysis in Excel or other graphing software package to create a frequency histogram. In this example, the results from the data extraction suggest that the A- and E3 mtDNA haplotypes occur more frequently at different modal depths, 110m and 150m respectively.

2.4.4.4 Basic Spatial Analysis

Basic spatial analysis can assist with answering research questions such as: "How do the spatial distributions of humpback whales with different mtDNA haplotypes vary within a region?" The loading of genetic data into ArcGIS via *geneGIS* now provides the user with additional opportunities to conduct further spatial analyses using the standard default tools within ArcGIS Toolbox. For example, the Directional Distribution tool within the Spatial Statistics Toolbox summarizes the central tendency, dispersion and directional trends in both the X and Y direction to visualize differences in the spatial distributions of the variable of choice (Mitchell 2005). Using one standard deviation and the same mtDNA haplotypes from above (A- and E3), the output polygons represent the location where 68% of whale encounters occurred (Figure 2.7) and quickly enables the visualization of different haplotype distributions.
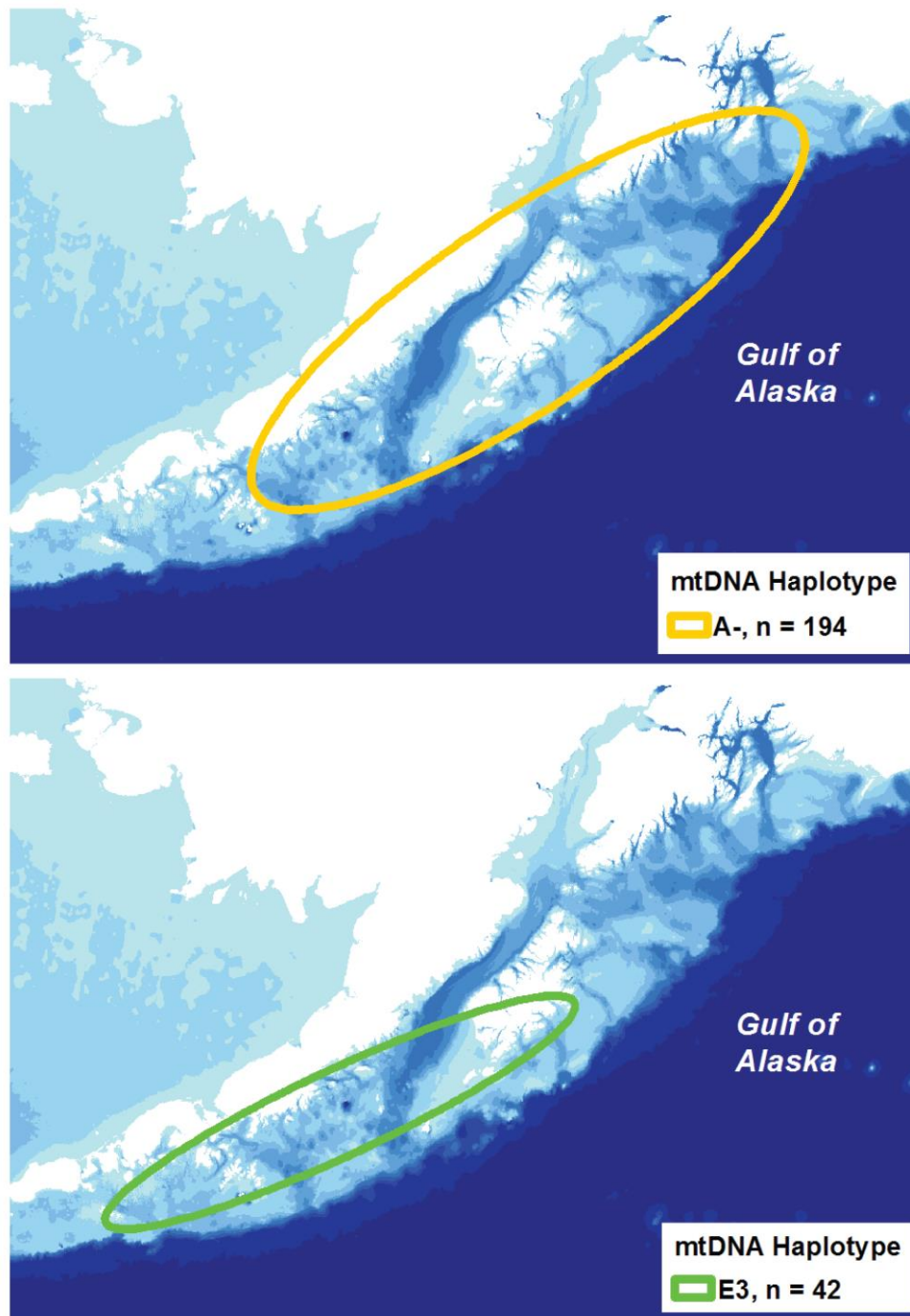
Figure 2.7. An example of a basic spatial analysis available as a result of loading genetic data into ArcGIS via *geneGIS*. Output from the Directional Distribution tool, a standard default tool from ArcGIS within the Spatial Statistics toolbox, displays the spatial distribution trends for the A- (top) and E3 (bottom) mtDNA haplotypes using one standard deviation ellipse.

2.5   Arc Marine Customization

2.5.1   Brief Background

Wright and Goodchild (1997) challenged the predominantly terrestrial-based GIS community to expand the capabilities of GIS to include the marine environment and the unique properties of ocean data. Released a decade later, the Arc Marine data model provided a GIS framework developed specifically for managing and mapping typical marine data types and conducting complex spatial analyses in the oceans (Wright et al. 2007). The data model produces a geodatabase resulting from the ability of the user to build validation rules, apply real-world behavior to features, and combine or link them to tables using relationship classes (Wright et al. 2007). Arc Marine is used worldwide by hundreds of researchers in marine ecology, marine geology, and marine physics (Isenor and Spears 2013). In addition, because marine research is so widely varied in the types of research conducted and the data required for that research, Arc Marine provides a common structural template that researchers can customize for their needs.

Lord-Castillo et al. (2009) provided one of the earliest Arc Marine customizations developed to map the movement and distribution of endangered whale species from satellite telemetry data. Keeping the core of the data model, this customization relies on three Arc Marine base classes: (1) the Vehicle object class to model a moving instrument carrying platform represented by the tagged animal; (2) the InstantaneousPoint feature class, subtype Location Series to hold the spatial and temporal sequence of the Argos satellite locations; and (3) the MarineEvent object class to enable dynamic sequencing of the time stamped animal movement paths to create spatial locations (Lord-Castillo et al 2009).

We use the Lord-Castillo et al. (2009) customization as the starting point for our customization for two reasons. First, the Lord-Castillo et al. (2009) structure already

considers the concept of an "individual". Although the identity of the whale might be unknown relative to the population, it can be used as a means to recognize the one-to-one relationship between a whale and a satellite tag. Second, it provides the flexibility of merging the two customizations together at some point in the future if satellite telemetry data are added to the reconciled photo-identification and genetic databases.

2.5.2   Customization Specifics

To include individual-based genetic and photographic data within the Arc Marine framework, we retain nine key Arc Marine classes and populate them as illustrated in Figure 2.8. The Cruise and SurveyInfo classes are preserved, containing information related to the specific cruise and survey, while the MarineEvent class is used to record the Occurrence, a point in time and space when one or more whales are observed (Figure 2.8A). Similar to Lord-Castillo et al. (2009), the Vehicle class represents the animal, but is further specified as a known individual with an assigned identity. The InstanteousPoint feature class subtype LocationSeries represents the Encounter, a discrete point in time and space at which an individual is sampled, while the MarineObjects class is used to define two Encounter Subtypes - PhotoID and SampleCollected (Figure 2.8B). Depending on the Encounter subtype, the Measurement class is used to define the type of SampleAnalysis conducted, while the MeasuredData and Parameter classes hold the information related to the analyses outputs (e.g., sex, mtDNA haplotype, microsatellite alleles) (Figure 2.8C).
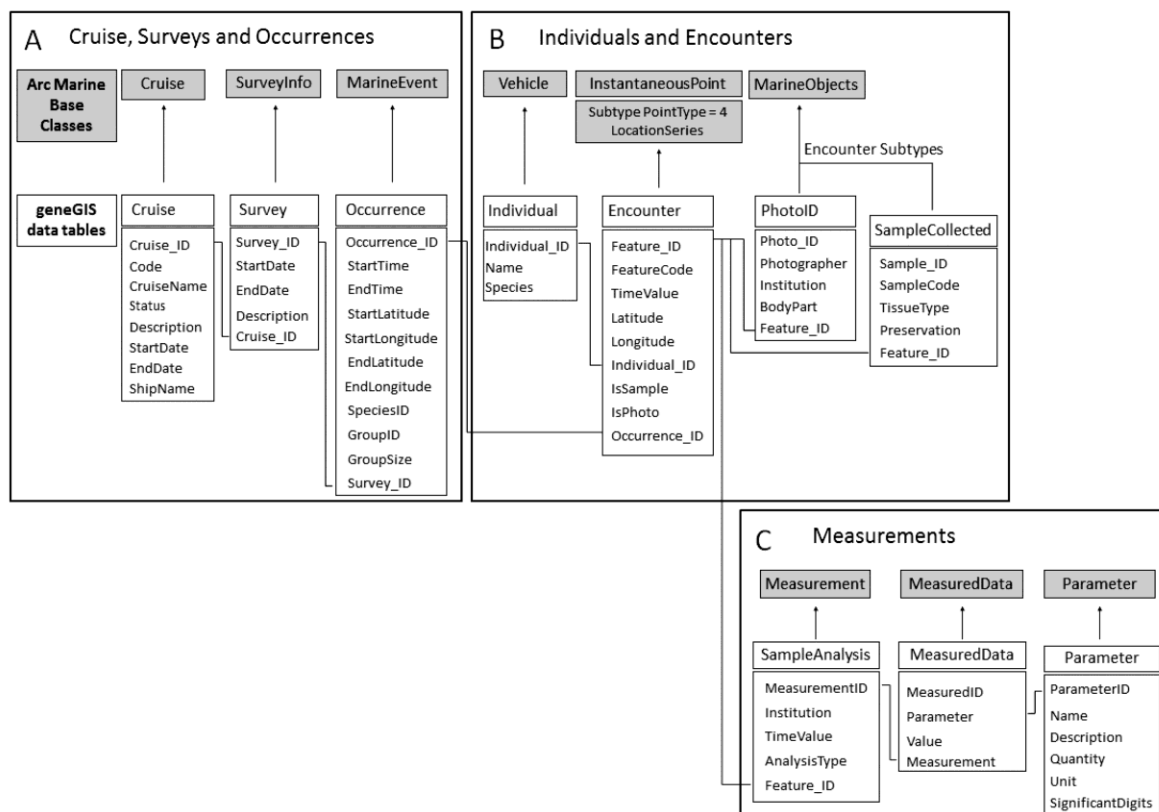
Figure 2.8. Generalized diagram of an Arc Marine customization for individual-based genetic and photo-identification data from cetaceans. Illustrations of how *geneGIS* data tables fit into Arc Marine base classes for: A) Cruise, Surveys and Occurrences, B) Individuals and Encounters (PhotoID or Samples) and C) Measurements (SampleAnalysis, MeasuredData and Parameter). This customization developed as part of the *geneGIS* initiative.

2.5.3   SPLASH Implementation

The application of the Arc Marine customization for reconciled genetic and photo-identification SPLASH data is shown in Figure 2.9 and described here. During the three-year SPLASH program, there were multiple research cruises. Each Cruise is given a unique identifier and the table is populated with all relevant cruise information. During a single cruise, there are multiple daily Surveys, each with its own identifier, and within each survey, whenever a group of whales is sighted, there is an Occurrence and information about the

group is recorded (Figure 2.9A). An Occurrence may lead to a related Encounter when either of the two Encounter Subtypes, PhotoID or SampleCollected, take place (Figure 2.9B). The type of analyses (SampleAnalysis) and the subsequent results (MeasuredData and Parameter) of the data collected from the Encounter Subtypes (Figure 2.9C) provides the information necessary to assign a unique Individual identity (Figure 2.9B). Figure 2.10A shows the data loaded into the ArcMarine customization using the classes outline above. Note that there is a single feature class (f_Encounter) while there are nine tables (denoted with a t_). Figure 2.10B shows the point locations of humpback whales off southeast Alaska and Northern British Columbia mapped by spatial location (top), by sex (middle) and by mitochondrial haplotype (bottom) from the geodatabase.

A

Cruise

Cruise_ID	Code	CruiseName	StartDate	EndDate
36	200406_SEAK	SPLASH Summer 2004	6/12/2004	9/16/2004
37	200506_SEAK	SPLASH Summer 2005	6/01/2005	10/02/2004
38	200512_HI	SPLASH Winter 2005	12/10/205	03/15/2006

Survey

Survey_ID	StartDate	EndDate	Cruise_ID
1216	6/01/2005	6/01/2005	37
1217	6/02/2005	6/02/2005	37
1218	6/04/2005	6/04/2005	37

Occurrence

Occurrence_ID	StartTime	EndTime	StartLat	StartLong	EndLat	EndLong	SpeciesID	GroupID	GroupSize	Survey_ID
1	08:32	08:56	56.5225	-131.2021	56.3160	-131.4256	hump	1	7	1216
2	09:10	10:26	56.2254	-131.5125	56.1874	-131.6698	hump	1	3	1216
3	11:48	12:17	56.0687	-131.7945	55.9273	-131.8408	hump	2	5	1216

Cruise, Surveys and Occurrences

B

Individual

Individual_ID	Name	Species
0177	Dutchy	hump
0518		
1434		
1538		

Encounter

Feature_ID	FeatureCode	TimeValue	Individual_ID	Latitude	Longitude	IsSample	IsPhoto	Occurrence_ID
756	UAFB-0604-0001	06/01/2004 09:18	3413	56.2257	-131.5223	F	T	2
757	UAFB-0604-0002	06/01/2004 09:22	1538	56.2190	-131.5486	T	T	2
758	UAFB-0604-0003	06/01/2004 09:27	3554	56.1932	-131.6143	F	T	2

PhotoID

Photo_ID	Photographer	Institution	BodyPart	Feature_ID
232	Straley	UAS	fluke	757
412	Pierszalowski	OSU	fluke	684

SampleCollected

Sample_ID	SampleCode	TissueType	Preservation	Feature_ID
116	SEAK010034	skin & blubber	Ethanol 10%	757

Individuals and Encounters

C

SampleAnalysis

MeasurementID	Institution	TimeValue	AnalysisType	Feature_ID
54	OSU	09/02/2006	sex	757
55	OSU	09/02/2006	dlpHap	757
56	OSU	09/03/2006	MicSat	757

MeasuredData

MeasuredID	Parameter	Value	Measurement
134	Male		54
135	E1		55
136	Ev37	208	56
137	Ev37	220	56

Parameter

ParameterID	Description
Male	Y chromosome
E1	Humpback haplotype
Ev37	Humpback microsatellite loci

Measurements

Figure 2.9. A diagram of how individual-based genetic and photo-identification SPLASH data fit in the customized *geneGIS* Arc Marine data model for (A) Cruise, Surveys and Occurrences, (B) Indiviudals and Encounters and (C) Measurements. Tables are related according to similar grey scale colored data fields.
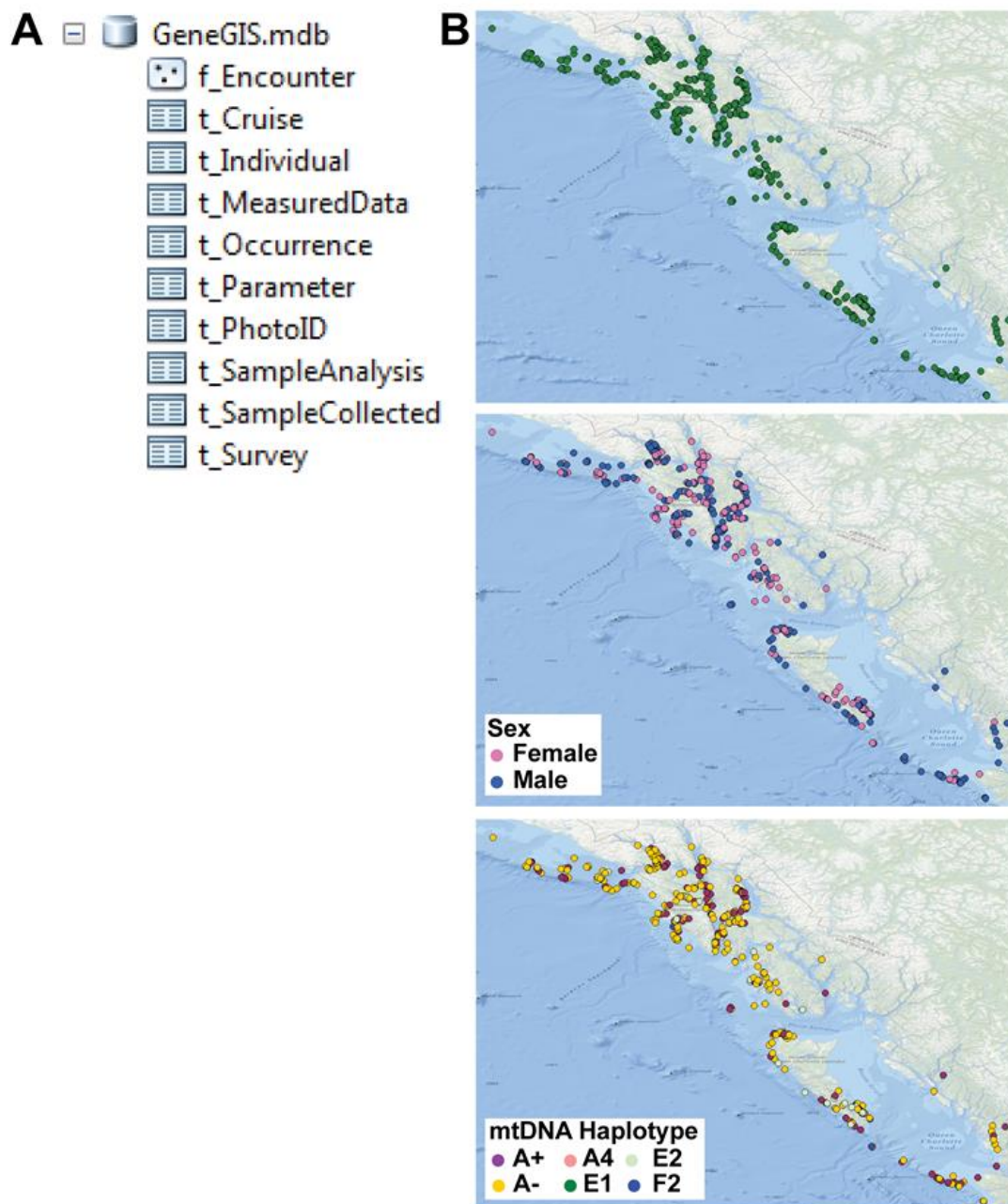
Figure 2.10. (A) SPLASH data loaded into the customized Arc Marine data model, showing one point feature class (f_Encounter) and 10 tables tailored to handle reconciled photo-identification and genetic data associated with long-term cetacean studies. (B) ArcMap screen shots of humpback whale encounters from SE Alaska and Northern British Columbia loaded into the geodatabase by spatial location (top), by sex (middle) and by mtDNA haplotype (bottom). Basemap courtesy of Esri, http://esriurl.com/obm, and its partners.

2.6   Visualizing the Spatial Distribution of Humpback Whale mtDNA Haplotypes

Genetic analyses using both mtDNA haplotypes and microsatellite loci reveal North Pacific humpback whales have a complex population structure (Baker et al. 1998, 2013). Significant genetic differentiation occurs among breeding grounds and among feeding grounds. Further, although humpback whales show strong site fidelity to both breeding and feeding grounds, there is greater mtDNA haplotype diversity on some feeding grounds suggesting a much different population structure occurs while whales are feeding compared to breeding (Baker et al. 2013). Such findings have a number of important conservation implications, including the recognition that protective measures based solely on the breeding grounds will not successfully capture the species' genetic diversity.

In the Gulf of Alaska, for example, mtDNA diversity is high and population boundaries are not obvious, confounding conventional molecular ecology methods that require researchers to define spatial strata *a priori* (Baker et al. 2013, Beebee and Rowe 2008). Consideration of the spatial component, such as the distribution of individual animals across space using explicit geographic coordinates is relatively rare. By incorporating spatially-explicit genetic data using *geneGIS*, the missing spatial component can be included. In addition, it allows for further analyses that incorporate environmental data (e.g., sea surface temperature, bathymetry, etc.) to explore the relationship between population divisions and the seascape.

Using *geneGIS* we build upon Section 3.4.3 to present one possible method using spatially-explicit encounters of known individuals to explore the spatial distribution of mtDNA haplotypes. SPLASH data following the SRGD.csv format are imported into ArcGIS using the Import tool from the *geneGIS* toolbar. Although this data format includes the field 'Region' as a means to provide some locational information, this represents researcher-defined strata and we purposely choose not to use it. Instead, we use the Summarize

Encounter button to spatially select the points located in the region of interest - Northern and Western Gulf of Alaska. Whale encounters are mapped by haplotype to visually demonstrate the high diversity of mtDNA haplotypes (Figure 2.11A). The Directional Distribution tool within the Spatial Statistics toolbox is used to measure the orientation and direction of the haplotype distributions. Of the 18 haplotypes recorded in this area, ellipses using one standard deviation for nine (n ≥ 10) haplotypes are calculated (Figure 2.11B). Although the visual interpretation of plotting the encounters by haplotype (Figure 2.11A) may provide a sense of orientation, the standard deviation ellipse analysis makes the trend in haplotype distribution clear while also using a statistical calculation (Figure 2.11B) (Mitchell 2005). As a next step this information can be combined with various environmental variables deemed important to humpback whales on their foraging grounds to begin to answer spatially explicit ecological questions related to pattern and process.
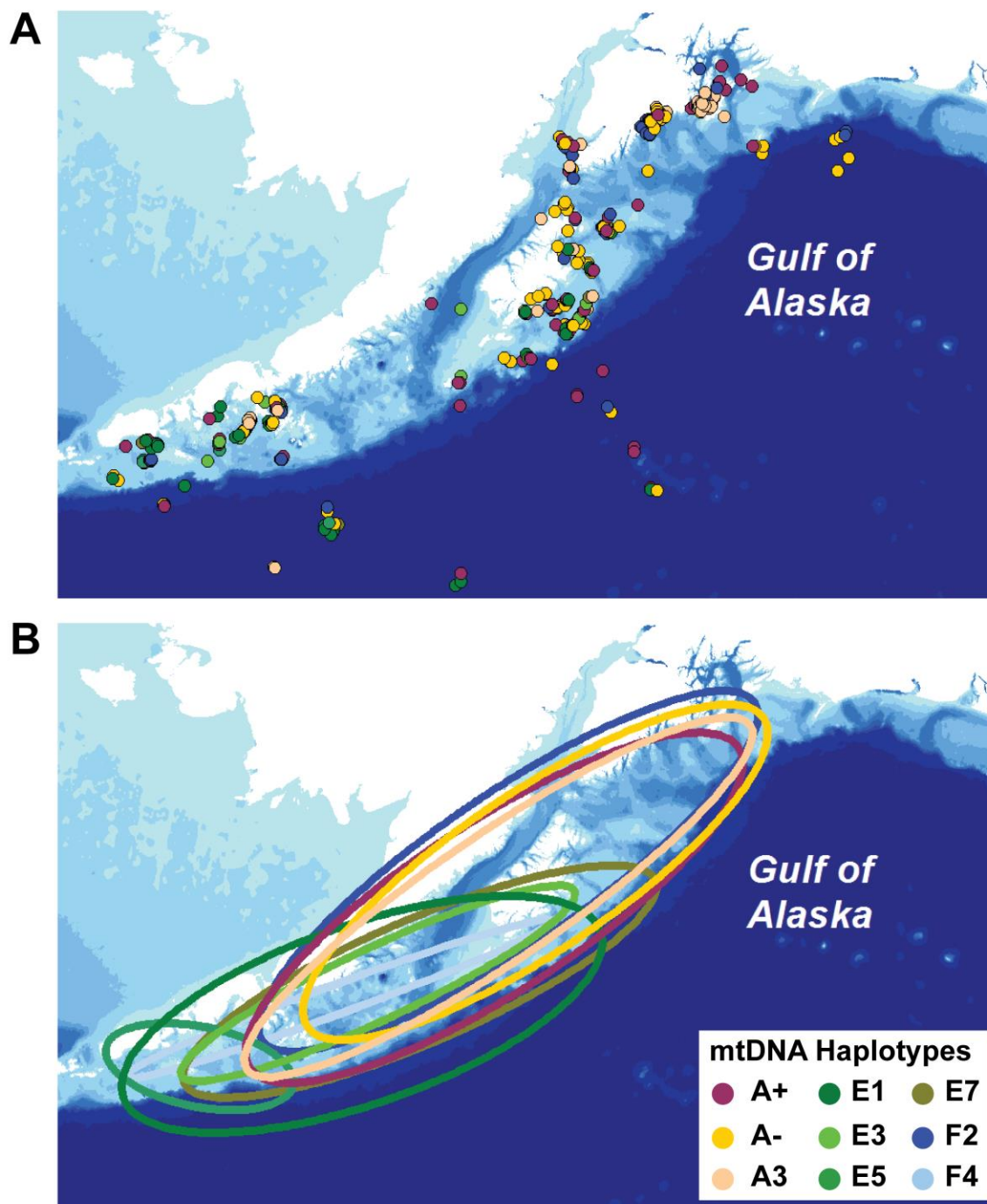
Figure 2.11. Screenshots of spatially selected humpback whale encounters, mapped by (A) mtDNA haplotype and (B) calculated ellipses with one standard deviation showing the spatial distribution of humpback whale haplotypes in the Northern and Western Gulf of Alaska.

2.7   Conclusion

geneGIS is the first suite of ArcGIS tools and the first customized Arc Marine data model to incorporate and analyze individual-based genetic data in a seascape context. The suite of tools in *geneGIS* provide novel methods of data visualization, spatial selection, data extraction and spatial analyses to the field of molecular ecology, while the customization of the data model to include these data types will provide the opportunity to link with other data sets and tools created by the broader marine GIS community. The inclusion of the spatial component moves the visualization and analyses of population structure data beyond traditional descriptive text and pie charts of haplotype/allele frequencies based on researcher-defined boundaries. In this way, researchers are now better equipped to pose and answer questions using environmental information relevant to the study species in geographic space, which will be increasingly important as the marine environment continues to change due to anthropogenic modifications and global climate change.

This process revealed three primary directions to help guide future development of GIS tools for molecular ecology research. First, although we did not want to duplicate the efforts of already existing analytical packages (e.g., GenAlEx, Genepop), providing the option to calculate some of the more common genetic analyses (e.g., F-statistics for both microsatellite and mitochondrial DNA, Mantel tests) directly within *geneGIS* reduces the need to move back and forth between software packages and the need to learn additional applications. Second, there is a need to build upon the strengths of GIS and improve the accessibility of data visualization methods and spatial analyses available to non-GIS users. This could include developing methods to calculate a continuous raster surface of relatedness/kinship (e.g., heat maps or kernel distributions) across a landscape. Finally, although the user base we target is likely to know what environmental variables to include, they may be unaware of how to acquire them. Thus, it would be useful to include a method for improved access to relevant environmental layers. One possibility would be to develop a

button on the *geneGIS* toolbar that links the user to some of the common websites where such data is available for download. Perhaps even more useful might be to provide a direct link to the ArcGIS compatible Marine Geospatial Ecology Tools (MGET) developed by Roberts et al. (2010) that provides easy-to-use open-source geoprocessing tools to access oceanographic data in addition to other forms of spatial environmental analyses.

The customization of Arc Marine also revealed two areas worth considering for further development of both this customization and the Arc Marine data model. First, because the customization of Arc Marine brings a new user group to the GIS table, it would be useful to develop a tool to enable easy data import into the *geneGIS* Arc Marine data model. Second, the Arc Marine data model is based on an older data structure, the personal geodatabase, for which a number of issues including file size limitations and stability have been identified. Revising the Arc Marine data model to the now Esri recommended standard, a file geodatabase, would resolve these issues and allow for a smoother interface between the Arc Marine customization for genetic data and the *geneGIS* tools.

2.8   Availability

geneGIS is freely available for download from the website http://genegis.org. Source code is hosted on Github (https://github.com/genegis/genegis). The *geneGIS* website contains an online manual, installation instructions, a tutorial with sample data, conference presentations, and a list of relevant literature.

2.9   Acknowledgements

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3 Mapping the Flock: Modeling Multispecies Seabird Foraging Aggregations in the California Current System

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3.1 Abstract

Marine conservation measures such as marine protected areas (MPAs) rely on a robust understanding of the relationships between species and their environment. We developed species-specific, spatially-explicit seabird-habitat association models to identify multispecies foraging aggregations (hotspots) in the California Current System. Using negative binomial regression, we built and validated models for 30 species using 15 years (1997-2012) of seabird survey data from multiple cruises spanning the California Current combined with predictor variables derived from bathymetric and remotely-sensed oceanographic data as well as climate indices. We predicted species-specific abundances during four focal months (February, May, July, and October). Predicted abundances were averaged by month across all years and by year and standardized. Standardized predicted means for all species were averaged for each focal month, for each year, and across all months/years to create scenario-specific multispecies hotspot maps for relative abundance and species richness (number of species). Average depth and sea surface temperature (SST) were the most important explanatory variables in our models, while no distance related variables were included in any final models. Model outputs yielded similar results - where there was high relative abundance there was also high species richness. Peak values of both measures were found along most of the coast, both within and outside National Marine Sanctuaries. Results also predicted high habitat use by seabirds in association with offshore bathymetric features, especially north of the Mendocino Ridge where seafloor complexity increases. Our use of seabirds as indicator species combined with a multispecies approach provides an example of using at-sea seabird data combined with remotely sensed data and spatial modeling techniques to help prioritize protected area designation in the CCS. This approach can be used in other regions of the world where similar data exist, as well as explore the possible effects of climate change on seabird at-sea distribution.

3.2 Introduction

Despite being conspicuous marine predators, seabirds are one of the most threatened marine taxonomic groups (Croxall et al. 2012; Sydeman et al. 2012; Paleczny et al. 2015). They are also considered important indicators of marine ecosystem status and structure because of their global distribution and their wide range of prey items spanning multiple trophic levels (Cairns 1987; MEPS 2007, 2009; Durant et al 2009; Sydeman et al. 2012). Although it is often assumed finding food is problematic in an environment where prey items are dynamic, patchy, and dispersed over large areas (Weimerskirch 2007; Durant et al. 2009), studies show that seabirds consistently return to the same areas to forage in predictable mesoscale features such as shelf edges, upwelling zones, eddies, and fronts where prey is abundant (Weimerskirch 2007; Michael et al. 2013). It is this tight trophic interaction between predator and prey that is perhaps the best reason to use seabirds as ecosystem indicators because behavioral responses (e.g., presence/absence in an area, increased search effort) tend to be more sensitive to change than demographic ones (e.g., breeding success) (Durant et al. 2009). Consequently, data on seabirds and their habitat associations can play an important role in helping to identify and designate sites for marine conservation such as marine protected areas (MPAs) (Lescelles et al. 2012; Ronconi et al. 2012; Lewison et al. 2014). Long-term at-sea datasets from ship-based surveys, for example, used in combination with remotely sensed data (e.g., sea surface temperature, chlorophyll concentration, telemetry) and more refined spatial modeling techniques (e.g., species distribution modeling) will be critical to seabird conservation and MPA development. The California Current System (CCS) is one example where such initiatives are possible.

The CCS, located along the west coast of North America, is a highly productive eastern boundary current system (Hickey 1979). As the eastern portion of the North Pacific Gyre, the California Current moves seawater southward from British Columbia to Baja California and extends out from the coast hundreds of kilometers (Figure 3.1). During the
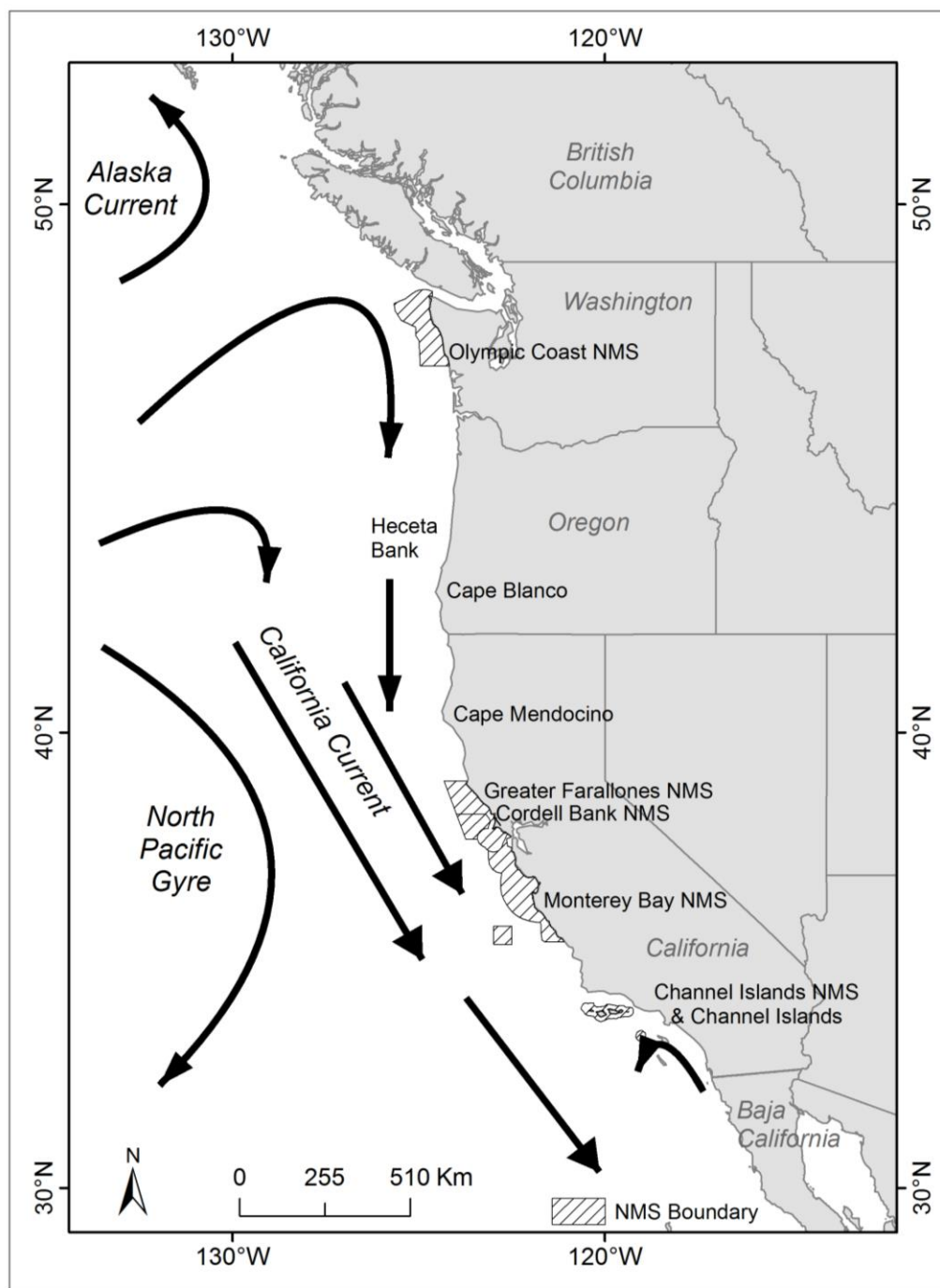
Figure 3.1. The eastern North Pacific Ocean showing the California Current System, the main flow direction and important land/ocean features. National marine sanctuaries (NMS) are also noted. (adapted from Nur et al. 2011).

spring and summer months the CCS is dominated by upwelling, saturating the ocean with nutrients that support an abundance of commercially valuable fish and shellfish species as well as diverse array marine mammals and birds (Hickey 1979; Hyrenbach and Veit 2003; Yen et al. 2004; Ainley et al. 2009). Like most of the world's oceans, the CCS has experienced extensive overfishing in addition to increased variability in oceanographic (e.g., recurring warm water events) and climatic (e.g., frequent El Niño events) conditions (McGowan et al. 1998; Bakun and Weeks 2004). The CCS is also adjacent to several large population centers where direct and indirect anthropogenic impacts are high and not likely to decrease (Halpern et al. 2009). These factors emphasize the need to establish protected areas for species dependent on this region.

The CCS has been well studied for decades with regard to the influence of physical and biological ocean processes on top predators (North: Ainley et al. 2005; Tynan et al. 2005; Ainley et al. 2009; Central: Oedekoven et al. 2001; Ford et al. 2004; Yen et al. 2004; McGowan et al. 2013; Manugian et al. 2015; South: Sydeman et al. 2001; Hyrenbach and Veit 2003). Studies that span the entire system, however, are rare. In 2011, Nur et al. conducted a CCS-wide study in which areas predicted to support foraging aggregations ("hotpots") of multiple seabird species were identified to assist with MPA site selection. The hotspots were developed using habitat-association models for 16 species collected from 11 years of ship surveys (1997-2008) based on three criteria pertinent to MSP: standardized abundance across species, importance of core areas by species, and among year hotspot persistence. They found predicted hotspots matched well to existing MPAs along the California and Washington coasts (the National Marine Sanctuaries at Cordell Bank, Gulf of the Farallones [now the Greater Farallones], Monterey Bay, Channel Islands, and Olympic Coast), as well as identifying three new areas (Heceta Bank, Cape Mendocino, and southern Channel Islands) currently without protective measures (Figure 1). Although no hotspots were detected seaward of 90 km, their study is the first to identify ecologically significant

areas to seabirds across the entire CCS using at-sea seabird distribution and abundance data.

From a marine spatial planning (MSP) perspective, Nur et al.'s (2011) findings are important for laying the groundwork in the development of a comprehensive ecosystem-wide MPA network for both seabirds and the CCS. Clearly, the coastal region, where many nesting/breeding sites are located, is critical to seabirds. However, their findings were unable to identify the potential importance of pelagic habitats for seabirds and therefore cannot address placement of offshore MPAs.

With at-sea threats considered to be the greatest cause of decline for seabirds today (Lewison et al. 2012; Sydeman et al. 2012; Lascelles et al 2012), it is imperative that pelagic regions also be included in the MSP process. Our study seeks to build upon and extend the findings from Nur et al. (2011) in four ways. First, we include additional at-sea data both in the pelagic region as well as in the northern portion of the CCS (e.g., Northern California, Oregon, Washington, and British Columbia) to provide more even spatial coverage across the entire CCS. Second, though they modeled 16 species, there are many more, especially pelagic, non-breeders and species of conservation concern, that were under-represented in their study that we include here. Third, we re-examine the role of dynamic, oceanographic variables (e.g., sea surface temperature, chlorophyll concentration, and sea surface height) which Nur et al. (2011) found to be less important than bathymetric variables in their models. Finally, instead of the data-mining approach (bagged decision trees) taken by Nur et al. (2011), we use generalized linear models, a more commonly used approach to identify significant habitat factors and their effects on species (Oppel et al. 2012; McGowan et al. 2013; Manugian et al. 2015).

Our re-examination of the multispecies seabird foraging hotspots in the CCS seeks to answer the following questions: (1) Across years and seasons, where are the hotspots?; (2)

How do hotspot locations differ across seasons?; (3) How do hotspots differ among years?; (4) Are there locations that were not apparent in Nur et al. (2011) that are now?; (5) What are the factors that determine the location and temporal variability of hotspots?; and (6) Which factors differ in their influence among years? Ultimately, our goal is to determine if the findings and conclusions of Nur et al. (2011) are maintained when a larger, more robust dataset and different modeling approach are used, and hence, what are the important implications for MPAs and in general, marine spatial planning.

3.3   Material and Methods

3.3.1   Data Collection and Processing

3.3.1.1   Survey Area and Seabird Data

Seabird data were obtained from at-sea surveys by eight research and monitoring programs: 1. California Co-operative Oceanic Fisheries Investigation (CalCOFI); 2. California Current Ecosystem Study (National Marine Fisheries Service CCES - National Oceanic and Atmospheric Administration [NOAA] and Point Blue Conservation Science); 3. CSCAPE and ORCAWALE (NOAA Southwest Fisheries Science Center); 4. Line P and other North Pacific surveys (Canadian Wildlife Service [CWS] and Environment Canada); 5. NMFS Rockfish Surveys; 6. NMFS Sardine Surveys; 7. Global Ocean Ecosystem Dynamics Northeast Pacific Northern California Current (GLOBEC NEP NCC); and 8. Ocean Salmon Ecology (OSE), Southern Resident Killer Whale (SRKW) and Ships-of-Opportunity (SoO) surveys (NOAA Northwest Fisheries Science Center). This included the data from Nur et al. (2011) plus newly available data from programs 1, 3, 4, 5, 7, and 8 that filled spatial and temporal data gaps in coastal Northern California, Oregon, Washington, and British Columbia while also adding to the pelagic region (Figure 3.2, right, Appendix A). Similar to Nur et al. (2011), the spatial coverage varied by cruise, some with sparse coverage along the west coast from Baja California, Mexico to slightly north of Vancouver Island, Canada and others with dense
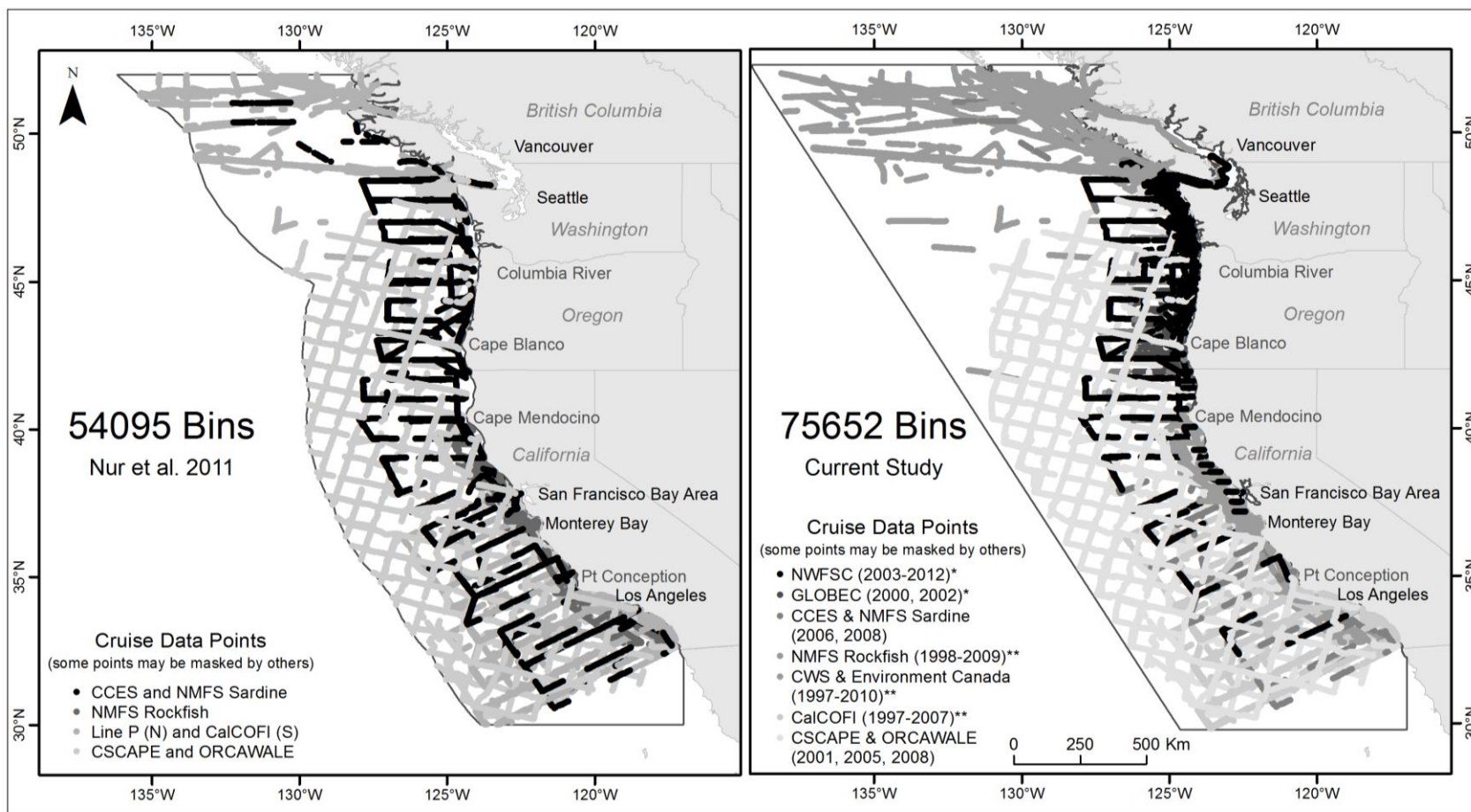
Figure 3.2. Comparison of the at-sea cruise data used in Nur et al. (2011) (left) and the current study (right), noting new data (* = new data, ** = additional years of data). Maps are the same scale.

coverage in smaller, more coastal regions. For analytical purposes, the spatial extent corresponded to the approximate northern (52°N) boundary of the California Current, while survey coverage determined the southern (30°N) and western (~600-800 km from the mainland) boundaries (Figure 3.2, right). The temporal period, also limited by data availability, spanned October 1997 (when remotely sensed data from the Sea-viewing Wide Field-of-view Sensor [SeaWiFS] satellite first became available) through June 2012 (last available survey data).

Seabird abundance and distribution data were collected using standardized strip-survey methods (Tasker et al. 1985; Buckland et al. 2001). While the survey vessel was underway at 8-10 knots, birds were continuously counted and their behavior recorded in a 90° arc from bow to beam on the side of the ship with best visibility (lowest glare) within a survey band. Survey bandwidth ranged between 100 and 400 m (85% at 300 m) depending on the vessel and weather conditions. Though we used the strip survey method to count birds, we did not assume that all birds within a strip were detected and counted by observers, nor did we estimate absolute abundance/density. Instead, we first derived relative abundances from count data and then, to negate species-specific detectability differences during multispecies analyses, we standardized the relative abundances across species (Nur et al. 2011). Furthermore, we explicitly allowed for "false zeroes" (i.e., failure to detect species that are present in the surveyed area; Zuur et al. 2009) as described below.

To account for spatial autocorrelation among seabird observations, ship transect data were divided into 3-km segments (referred to as bins) (Yen et al. 2004; Nur et al. 2011). We used the midpoint of each bin to aggregate counts of individual seabird species by behavior category and only birds foraging, feeding, or sitting on the water surface were included. Flying birds, however, were included if known to be aerial forgers (terns,

kittiwakes, jaegers, and storm-petrels) or not often observed unless flying (gulls and albatrosses) (Clarke et al. 2003; Jahncke et al. 2008; Nur et al. 2011). Bins less than 1 km (occasionally at the end of transect lines) and bins where ship speed was less than 8 knots were removed from the final dataset to avoid inflated counts (Michael et al. 2014). All remaining surveys bins were used in the statistical analysis and included information on GPS position, visibility, species, and number of birds. Bin midpoints were also used to extract values for bathymetric related data, remotely sensed oceanographic data, and climate indices data.

3.3.1.2 Bathymetric Data

We used bathymetric data from the General Bathymetric Chart of the Oceans (GEBCO_08 Grid, version 20100927, http://www.gebco.net) at a spatial resolution of 30-arc seconds (approximately 0.9 km x 0.9 km, slight variation with latitude). All bathymetric data processing occurred in ArcGIS 10.2.2 (Esri, Redlands, CA). Depth (in m) for each survey bin was determined by overlaying the bin midpoints on the bathymetric raster and extracting the depth values at each point. Focal statistics for depth (mean, minimum, maximum and standard deviation) were calculated for each raster cell using a 3 x 3 cell moving window (approximately 7 km x 7 km); we sampled each focal raster at the bin midpoints to extract values. The maximum and minimum values were used to calculate a "contour index" to reflect the topographic relief of the sea floor using the formula: [(max. depth - min. depth)/max. depth *100]. Index values ranged from 0 to 100, with higher values representing steeper bathymetry (Nur et al. 2011).

We used the 30-arc second GEBCO bathymetric raster to derive contour lines representing the western North America coastline (0 m) and the 200-, 1,000-, and 3,000- m isobaths. The choice of these isobaths was based on previous seabird-habitat association studies in which the 200 m isobath is considered the continental shelf break, the 1,000 m

isobath represents the continental slope, and the 3,000 m isobath indicates pelagic water (Yen et al. 2004, 2005; Nur et al. 2011). The nearest distances (in km) from the bin midpoints to land and the three isobaths were calculated in ArcGIS 10.2.2 using the Near tool with the geodesic option to account for the Earth's curvature.

3.3.1.3   Remotely Sensed Oceanographic Data

Chlorophyll-a (Chla) concentration (mg/m^3) data were obtained from two satellite sensors (Sea-viewing Wide Field-of-view Sensor [SeaWiFS] and Moderate Resolution Imaging Spectroradiometer [MODIS-Aqua]) and downloaded from the NASA GSFC OceanColor Group (http://oceancolor.gsfc.nasa.gov/) using the ArcGIS-compatible extension Marie Geospatial Ecology Tools v0.8a56 (MGET) (Roberts et al. 2010). To minimize missing data due to clouds, 8-day composite periods were created with a cell size of approximately 9.3 km x 7.3 km (depending on latitude) for all study years (SeaWiFS: Oct 1997 - Dec 2010; MODIS - Aqua: July 2002 - June 2012). Survey dates and bin midpoints were matched to the corresponding 8-day composite and Chla values were extracted for each survey bin using the Interpolate Time Series of Rasters at Points tool in MGET (Roberts et al. 2010). We used SeaWiFS data when available; when not available, we used a regression-derived estimate of SeaWiFS Chla by using a predictive equation to estimate SeaWiFS Chla as a function of the available MODIS-Aqua data based on the set of cells that had both sensor values (r^2 = 0.6, n = 29,120).

Sea surface height above geoid (SSH) data were obtained from up to four satellite sensors (e.g., Jason -2 + AltiKa or Cryosat or Envisat, Jason-1 + Envisat, Topex/Poseidon + ERS) with the same ground track and downloaded from AVISO (http://www.aviso.altimetry.fr/duacs/) via MGET v0.8a56 (Roberts et al. 2010). Eight-day global composites with a cell resolution of 0.25 x 0.25 degrees (~ 27 km x 23 km depending

on latitude) were created for all study years. SSH (in meters) data were matched with survey dates and bin midpoints and extracted for each survey bin using the Interpolate Time Series of Rasters at Points tool in MGET (Roberts et al. 2010).

Sea surface temperature (SST) data were obtained from the Group for High Resolution Sea Surface Temperature (GHRSST) L4 gridded products (https://www.ghrsst.org/, Martin et al. 2012). The L4 products merge multiple satellite sensors and *in situ* observations together to derive the best quality SST data at various time scales. Despite the loss in spatial resolution (cell size 0.2 x 0.2 degree or ~ 22 km x 18 km varying with latitude), we chose to use this measure of SST over more commonly used measures from AVHRR Pathfinder v5.0-5.2 or MODIS-Aqua L3 for two reasons. First, the GHRSST L4 products are gap-free, thus providing daily cloud-free estimates of SST, and thereby avoiding the problem of missing data over large areas due to cloud cover common in AVHRR Pathfinder and MODIS data. Second, and more importantly, instead of measuring the temperature in the highly variable top 10-20 micrometers (skin) of the sea surface, like AVHRR Pathfinder and MODIS-Aqua, the GHRSST L4 products provide the foundation SST, which is the temperature of the water column without diurnal variability. Because the diurnal variability is removed, this is considered a better measure for predicting the presence or behavior of species (Roberts et al. 2016). Daily GHRSST L4 data were downloaded from NASA JPL PO.DAAC (http://podaac.jpl.nasa.gov/dataset/CMC0.2deg-CMC-L4-GLOB-v2.0, Canadian Meteorological Center 2012; Brasnett 2008) via MGET v0.8a56 (Roberts et al. 2010) and used to create 8-day composites of SST. SST (in °C) data were matched with survey dates and bin midpoints and extracted for each survey bin using the Interpolate Time Series of Rasters at Points tool in MGET (Roberts et al. 2010).

3.3.1.4   Climate Indices Data

We included three climate indices known to influence seasonal and inter-annual variability in oceanographic conditions in the California Current System: 1. the Southern Oscillation Index (SOI), which measures sea level pressure anomalies in the tropical Pacific Ocean to indicate the development and intensity of El Niño and La Niña events (Trenberth 1984; http://www.cgd.ucar.edu/cas/catalog/climind/SOI.signal.ascii); 2. the North Pacific Gyre Oscillation (NPGO),which is correlated to fluctuations in salinity, nutrients, and surface chlorophyll-a along the west coast of North America (Di Lorenzo et al. 2008; http://eros.eas.gatech.edu/npgo/npgo.php); and 3. the Pacific Decadal Oscillation (PDO), which is the key driver of sea surface temperature north of 20°N in the North Pacific (Mantua and Hare 2002; http://jisao.washington.edu/pdo/). We calculated the average of two 3-month time periods for each index: the survey month and the two previous months (i.e., 0-2 months before) and the 3 months prior to that period (i.e., 3-5 months before). Values for each of the two periods were assigned to the bin midpoints based on survey year and month (Nur et al. 2011).

3.3.1.5   Data Related to Annual/Seasonal Variability and Survey Effort

To account for additional annual and seasonal variability in individual species abundances, we included the temporal variables year, month, and Julian date. We also incorporated information on spring transition date anomalies, which are based on deviations of each year's spring transition date (date when winter downwelling changes to summer upwelling) from the long-term mean transition date (calculated as March 29 for the years 1973 – 2012) (Nur et al. 2011). To account for seasonal and interannual variability which can occur within the CCS in a north-south direction (e.g., difference in solar radiation), we included latitude. Finally, the bin area was used as an offset for all models to

incorporate bin length variation and account for differences in detection rates across survey bins (Hilbe 2011; Nur et al. 2011; McGowan et al. 2013; Dransfield et al. 2014).

3.3.2 Statistical Model Development

We used all bins and all environmental, climate, spatio- temporal, and effort related data from October 1997 through June 2012 for model development. Treating seabird counts per survey bin as the dependent variable, species-specific models were developed using negative binomial regression (STATA version 13.0, StataCorp 2013, Statistical Software, College Station, TX). Negative binomial regression is recommended when data have a larger count of zeros than expected from a Poisson-distributed variable (Hilbe 2011). Twenty-one variables of interest (Table 3.1) were selected based on availability and previous seabird-habitat studies conducted within the CCS (Yen et al. 2004; Ainley et al. 2009; Trembley et al. 2009; Nur et al. 2011; McGowan et al. 2013). Linear and quadratic forms were included for all variables except year and distances to land and isobaths. A fourth-order polynomial was used for year over the 15 years to allow for a more flexible curve fit and the inverse natural log was used for all distance measures. All models also included the natural log of the bin area.

Table 3.1. Candidate predictor variables including type of variability, resolution, and the mean, standard deviation, and max/min values for each data set used to model seabird species-specific abundance and distribution in the California Current System using 3-km bins.

Variable	Variability	Resolution	Mean ± SD	Min - Max Value
Bathymetric				
Average Depth (m)	spatial	7km x 7km	-2206.70 ± 1668.60	-5048.2 - 141.1
Contour Index (%)	spatial	7km x 7km	10.20 ± 15.00	0 - 99.0
Distance to land (km)	spatial	NA	152.13 ± 149.57	0 - 601.81
Distance to 200 m isobath (km)	spatial	NA	154.75 ± 157.61	0 - 582.84
Distance to 1 km isobath (km)	spatial	NA	128.36 ± 135.89	0 - 558.49
Distance to 3 km isobath (km)	spatial	NA	148.22 ± 121.46	0 - 543.89
Remotely Sensed Oceanographic				
Chlorophyll a Conc. (mg/m^3)	spatial, temporal	9.3km x 7.3km, 8 days	1.53 ± 2.70	0.03 - 86.94
Sea surface height (m)	spatial, temporal	27km x 23km, 8 days	0.50 ± 0.10	0 - 0.81
Sea surface temperature (°C)	spatial, temporal	22km x 18km, 8 days	14.00 ± 3.03	6.33 - 22.92
Climate Indices				
SOI, 0-2 months before	temporal	3 months	-0.06 ± 1.37	-5.17 - 3.43
SOI, 3-5 months before	temporal	3 months	-0.07 ± 1.67	-5.17 - 4.7
NPGO, 0-2 months before	temporal	3 months	0.69 ± 1.15	-1.46 - 2.66
NPGO, 3-5 months before	temporal	3 months	0.68 ± 1.20	-1.46 - 2.74
PDO, 0-2 months before	temporal	3 months	-0.13 ± 0.96	-1.67 - 2.2
PDO, 3-5 months before	temporal	3 months	-0.01 ± 0.97	-1.94 - 2.63
Data Related to Annual/Seasonal Variability				
Year	temporal	annual	2004 ± 3.33	1997 - 2012
Month	temporal	month	6.29 ± 2.71	1 - 12
Julian Date	temporal	within year	175 ± 82.76	4 - 350
Spring Transition Date Anomalies	temporal	annual	-10.58 ± 14.49	-39.07 - 22.93
Latitude	spatial	NA	39.19 ± 6.57	29.83 - 52.24
Effort Related				
Bin area (log(km^2))	spatial	NA	-0.18 ± 0.24	-2.74 - 1.66

We used a six-step process for model development (Figure 3.3) and repeated it for as many individual species as possible. All candidate predictor variables were included in an initial negative binomial regression (nbreg) model and run through a stepwise backward selection process to remove non-significant terms ($p > 0.1$). Year (up to fourth-order),

- nbreg with all variables
- Stepwise backward selection with removal (p > 0.1)
- If quadratic term kept, always include linear term

1.

- Run nbreg model
- Assess p values of terms, remove term if p > 0.05, one term at a time, until all terms in model are significant

2.

- Stepwise forward selection with addition (p < 0.05)
- Check that no terms inadvertently removed
- Add back terms as needed

3.

- Test nbreg model against zinb model
- Use Vuong Statistic to select best fitted model

4.

- Add most significant interaction term (year with SSH, SST, latitude, average depth, or distance to land)

5.

- Final model for predictions

6.

Figure 3.3. The 6-step process used in during model development.

month (linear and quadratic) and latitude (linear and quadratic) terms were included regardless of significance based on *a priori* information. For other variables with a linear and quadratic component, the linear term was forced in the model if the stepwise process

retained the quadratic term. The nbreg model was re-run to assess the p-value of remaining terms. For each of the climate indices, the more significant of either the 0-2 months before or 3-5 months before terms was selected; if neither were significant, that particular index was left out of the model. Significant quadratic terms ($p < 0.05$) were always retained; if the quadratic term was non-significant it was removed and the linear form was included provided $p < 0.05$. This process was repeated until all terms in the model were significant ($p < 0.05$). A stepwise forward selection process ($p < 0.05$) was then used to ensure no terms had been inadvertently removed during model fitting.

Due to the high prevalence of zero count bins in the dataset, all selected variables were modeled with a zero-inflated negative binomial regression model (zinb). This was done as a precautionary step to account for any excess zeros that might result from failing to detect a species when it is in fact present (false zeros), such as during questionable observation conditions, and may lead to incorrect assumptions regarding the ecological links between species and environment and result in poor prediction models (Zuur et al. 2009). We used the Vuong test statistic to determine model preference between zinb and the standard nbreg (Vuong 1989; McGowan et al. 2013; Dransfield et al. 2014) and the better fitting model was retained.

With the base model generated, we examined potential interactions between year (up to fourth-order) and five a priori identified variables (SSH, SST, latitude, average depth, and distance to land) considered to be influential to seabird presence. To allow for effective model fitting (e.g., model convergence) we did not considered all possible interactions. For each species, we retained the most significant interaction term to create the final model for predictions. Multicollinearity among final variables in each model was examined using variance inflation factor testing (VIF) (Zuur et al. 2009).

3.3.3   Model Validation

We validated the final model fit using k-fold cross validation (k = 10, 10 runs each) based on the predictions to the 3 km bins of the seabird survey data. The data were randomly divided into 10 equally sized but mutually exclusive subsets; each subset was used as a "test" dataset while the remaining nine were combined into the "training" dataset (Fielding and Bell 1997; Franklin 2009). We then evaluated the model using the test data to determine its statistical significance; this process was repeated 10 times (Manugian et al. *In press*).

3.3.4   Model Predictions

We created a prediction grid encompassing the spatial extent of the study area (29°-52°N and 117°-139°W) and matching the spatial resolution of the SeaWiFS Chla data (~ 9.3 km x 7.3 km, latitude dependent). The centroid of each grid cell (n = 29,644) was populated with similar data to that used in model development (Table 3.1). We used the 15th of each month for Julian date and remotely sensed data were based on the 8-day average centered around that date. Based on survey data availability we used the same seasonal approach as Nur et al. (2011) and predicted species-specific distributions to each grid cell for May (spring), July (summer), October (fall), and February (winter) in each year.

3.3.5   Deriving and Mapping Multispecies Hotspots

3.3.5.1   Using Standardized Abundance

Spatial predictions for each species were averaged by month across all years (1997-2012) and by year (1998-2011, using May and July only) for each cell of the prediction grid. October and February were excluded from the yearly means because these months have

reduced productivity and fewer species and our goal was to focus on annual variation when species are more likely to be present in the study area. To ensure no single species' predicted values swamped the others, the seasonal and annual ln-transformed predicted means for each species on a cell-by-cell basis were standardized (to produce an overall mean = 0, standard deviation = 1) using the formula:

$$\frac{[\log(\text{predicted cell mean}) - \text{mean}(\log(\text{predicted cell mean}))]}{\text{Std Dev}(\log(\text{predicted cell mean}))}$$

To represent multispecies hotspots we averaged the standardized predicted means for all species for each focal month (season) and for each year (May and July only). To help discern the locations of high use habitat (highest predicted values), we classified the data into percentiles (top 1, 2, 5, 10, 15, 20, 25 and > 25) and mapped the predictions two ways. First, to identify the location of hotspots in each season independently of the others, we created maps for each focal month using a scale specific to the particular month being mapped. Second, to better understand seasonal/annual hotspots throughout the CCS, we created independent monthly/yearly maps but classified the percentiles of the predicted values from the full, predicted monthly or annual dataset to allow for same scale comparison. We also created an all-inclusive CCS hotspot map by averaging the standardized predicted means across all months and years for all species.

3.3.5.2 Closer Investigation of the Pelagic Region

Based on the maps using standardized abundances, we chose to inspect the pelagic region more closely for potential areas of high seabird use. We used the standardized predicted means across all months and years for all species, classified the values into deciles (10 equal classes), and used the resulting map as a guide to determine a division point

between inshore and pelagic domains. By dividing the predicted maps in this way, we were able to prevent the strong coastal signature from overwhelming any suggested pelagic signal in the hotspot map. The dominant coastal signature (defined as the top two deciles of predicted mean values) fell just beyond the 1,000 m isobath and quickly dropped as one moved offshore (Figure 3.4). To ensure the inshore domain encapsulated the coastal signal for all species, we tried several buffer distances (10, 20, and 50 km) beyond the 1,000 m isobath, and chose the 50-km buffer (Figure 3.4) for the inshore/pelagic cutoff point. We classified the percentiles of predicted values from only the pelagic subset of data for all months/years and created a pelagic map of hotspots.
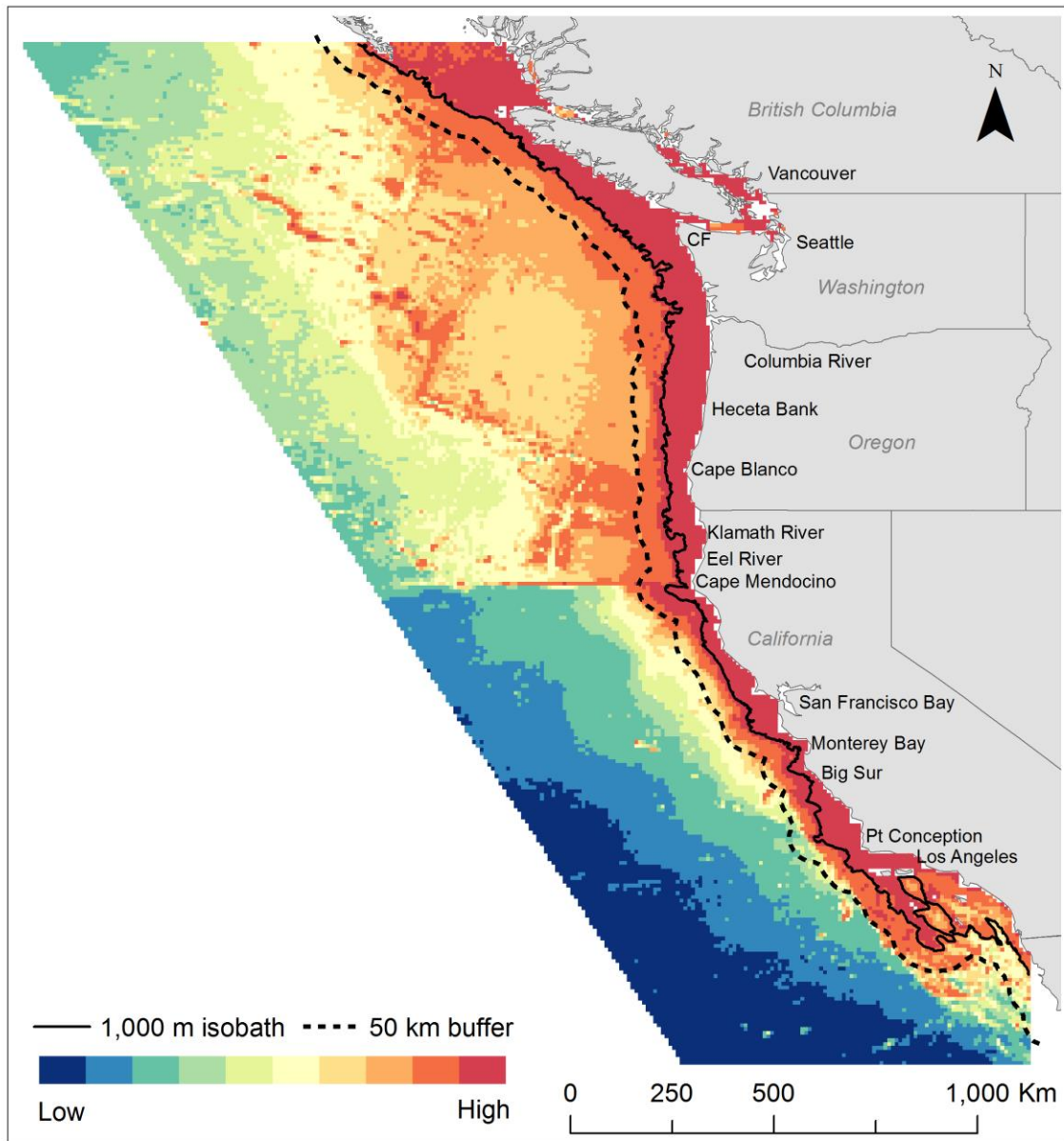
Figure 3.4. Predicted standardized abundance from all months/years for all species classified into deciles (10 equal classes) and the boundaries used to define the inshore and pelagic domains. In general, the top two deciles fall within the 50 km buffer or the inshore domain while the pelagic domain is the region beyond the 50 km buffer.

3.3.5.3   Using Species Richness

To quantify the number of species predicted to occur in multispecies hotspots, we reclassified the standardized abundances for each species into two classes. The predicted values in the top two percentiles were assigned a value of 1, while all remaining values received a value of 0. We tried several other reclassification variations, including the top 20, 10, and 5 percentiles, but none of these options were able to effectively distinguish distinct hotspot areas. The reclassified species-specific layers were added together on a cell-by-cell basis by month and the multispecies hotspots were mapped across months to allow for the same scale comparison. An all-inclusive CCS map was also created by averaging the species-specific maps across all months/years.

3.4   Results

A total of 75,652 3 km bins from at-sea surveys across 15 years (October 1997 to June 2012) were used to develop models for 30 seabird species (non-zero count bins ranged from 227-9,614) (Table 3.2). Vuong tests (STATA 13.0) confirmed that the standard negative binomial regression model was the best fitting model for all species except black-footed albatross (Vuong test $z = 1.94$, $P = 0.026$). For this species, we used a zero-inflated negative binomial regression model. Note we were not able to model variables that may affect probability of detection, due to lack of information (cf. McGowan et al. 2013, Dransfield et al. 2014). No significant multicollinearity was found among variables in the final models (VIF < 10). Cross-validation ($k = 10$, 10 runs) confirmed goodness-of-fit for all 30 final models (Table 3.3). We used 59 months ranging from October 1997 to June 2012 for seasonal and 28 months (May and July only) from 1998-2011 for annual model predictions.

Table 3.2. The modeled seabird species including breeding status in the California Current System, IUCN status and IUCN population trend. Also included are the number of zero and non-zero count bins and the maximum and mean number of individuals counted in a bin (n = 75,652).

Species Code	Common Name	Scientific Name	Breeds in CCS	IUCN Status	IUCN Pop Trend	Zero Count Bins	Non-Zero Count Bins	Mean Count
BRAC*	Brandt's Cormorant	*Phalacrocorax penicillatus*	Yes	least concern	decreasing	75146	506	12.0
BRPE*	Brown Pelican	*Pelecanus occidentalis*	Yes	least concern	increasing	74780	872	3.3
CAAU*	Cassin's Auklet	*Ptychoramphus aleuticus*	Yes	near threatened	decreasing	73169	2483	11.0
CATE	Caspian Tern	*Hydroprogne caspia*	Yes	least concern	increasing	75404	248	3.1
COMU*	Common Murre	*Uria aalge*	Yes	least concern	increasing	70852	4800	14.6
FTSP*	Fork-tailed Storm-petrel	*Hydrobates furcatus*	Yes	least concern	increasing	73371	2281	4.4
GWGU*	Glaucous-winged Gull	*Larus glaucescens*	Yes	least concern	increasing	74173	1479	2.5
LESP*	Leach's Storm-Petrel	*Hydrobates leucorhous*	Yes	least concern	stable	67778	7874	3.5
RHAU	Rhinoceros Auklet	*Cerorhinca monocerata*	Yes	least concern	decreasing	72825	2827	2.3
SCMU	Scripps's Murrelet	*Synthliboramphus scrippsi*	Yes	vulnerable	decreasing	75425	227	2.1
TUPU	Tufted Puffin	*Fratercula cirrhata*	Yes	least concern	decreasing	75405	247	1.8
WEGU*	Western Gull	*Larus occidentalis*	Yes	least concern	increasing	66038	9614	3.4
BFAL*	Black-footed Albatross	*Phoebastria nigripes*	No	near threatened	increasing	71672	3980	2.3
BLKI	Black-legged Kittiwake	*Rissa tridactyla*	No	least concern	decreasing	73722	1930	4.6
BOGU*	Bonaparte's Gull	*Larus philadelphia*	No	least concern	increasing	75207	445	9.5
CAGU*	California Gull	*Larus californicus*	No	least concern	decreasing	71469	4183	4.6
HEEG*	Heermann's Gull	*Larus heermanni*	No	near threatened	increasing	75173	479	4.9
HERG*	Herring Gull	*Larus smithsonianus*	No	least concern	decreasing	73841	1811	2.2
LAAL	Laysan Albatross	*Phoebastria immutabilis*	No	near threatened	stable	75382	270	1.1
LTJA	Long-tailed Jaeger	*Stercorarius longicaudus*	No	least concern	stable	75393	259	1.7
MEGU	Mew Gull	*Larus canus*	No	least concern	unknown	75329	323	5.4
NOFU	Northern Fulmar	*Fulmarus glacialis*	No	least concern	increasing	74105	1547	3.4
PAJA	Parasitic Jaeger	*Stercorarius parasiticus*	No	least concern	stable	75243	409	1.4
PALO	Pacific Loon	*Gavia pacifica*	No	least concern	increasing	75376	276	2.4
PFSH	Pink-footed Shearwater	*Ardenna creatopus*	No	vulnerable	unknown	73829	1823	6.9
POJA	Pomarine Jaeger	*Stercorarius pomarinus*	No	least concern	stable	75092	560	1.3
REPH	Red Phalarope	*Phalaropus fulicarius*	No	least concern	decreasing	74501	1151	11.6
RNPH*	Red-necked Phalarope	*Phalaropus lobatus*	No	least concern	decreasing	74895	757	20.1
SAGU*	Sabine's Gull	*Xema sabini*	No	least concern	stable	75023	629	4.4
SOSH*	Sooty Shearwater	*Ardenna grisea*	No	near threatened	decreasing	70369	5283	35.8

* Species modeled in Nur et al. (2011)

Table 3.3. (i) Species specific model results for the linear (L) trends and quadratic (Q) terms, coefficient sign and significance for all variables, p-values: $*< 0.05$, $\Omega< 0.01$, $\ddagger< 0.0001$, ns = not significant. Significant interaction terms noted with an 'x', (ii) Crossfold validation results from 10 simulations.

Variable	models w/ term	Breeds within the CCS							
		BRAC	BRPE	CAAU	CATE	COMU	FTSP	GWGU	LESP
(i) Best Fit Model									
Average Depth	29	L(+)‡	L(+)‡ Q(+)‡	L(+)‡	L(+)‡ Q(+)$^\Omega$	L(+)‡ Q(+)‡	L(-)‡	L(+)‡ Q(+)‡	L(-)‡ Q(-)‡
SST	27		L(+)‡ Q(-)‡	L(+)‡ Q(-)‡	L(+)‡	L(-)‡ Q(-)‡	L (-)‡ Q(-)‡	L(-)* Q(-)‡	L(+)‡ Q(-)‡
Spring Transition Date Anomalies	25	L(-)‡ Q(-)‡	L(-)‡	L(+)ns Q(-)$^\Omega$		L(+)‡ Q(-)‡	L(+)‡ Q(+)‡	L(+)* Q(-)‡	L(-)‡ Q(+)‡
SSH	20		L(-)‡	L(-)* Q(-)‡			L(+)‡ Q(-)$^\Omega$	L(-)$^\Omega$	L(+)‡ Q(-)‡
Julian Date	18		L(+)‡	L(-)ns Q(+)‡		L(+)‡		L(-)$^\Omega$ Q(+)‡	L(+)‡ Q(-)‡
Chla Concentration	18	L(+)‡ Q(-)‡		L(-)‡	L(+)$^\Omega$ Q(-)‡	L(+)‡ Q(-)‡	L(+)ns Q(-)‡	L(+)$^\Omega$ Q(-)$^\Omega$	L(-)‡
Contour Index	18	L(+)‡ Q(-)*	L(-)$^\Omega$	L(+)*	L(+)‡	L(+)‡ Q(-)‡		L(+)‡	
NPGO, 0-2 months	17					L(-)‡ Q(-)$^\Omega$		L(-)* Q(-)‡	L(+)ns Q(-)‡
PDO, 0-2 months	16		L(-)‡ Q(+)‡	L(-)$^\Omega$ Q(-)‡	L(+)ns Q(+)‡	L(+)‡	L(-)ns Q(-)‡		L(-)‡
SOI, 3-5 months	14	L(-)‡	L(-)‡				L(+)‡		L(+)‡ Q(+)‡
SOI, 0-2 months	12			L(+) ‡	L(+)* Q(-)$^\Omega$	L(-)‡ Q(+)$^\Omega$		L(-)‡ Q(-)$^\Omega$	
PDO, 3-5 months	10							L(+)* Q(-)‡	
NPGO, 3-5 months	8	L(-)‡	L(-)‡	L(-)‡					
Year * SST	8			x				x	x
Year * Latitude	8		x						
Year * SSH	3					x			
Year * Avg Depth	1						x		
Year * Dist. to Land	0								
Dist. to 200m isobath	0								
Dist. to 1km isobath	0								
Dist. to 3km isobath	0								
Dist. to Land	0								
Dist. to Fronts	0								
(ii) Crossfold Model Validation (k = 10), 10 simulations									
Validation F-Statistic (df)		(1, 57635)	(1, 74219)	(1, 56875)	(1, 56875)	(1, 56875)	(1, 56875)	(1, 56875)	(1, 56875)
Median		13	964.9	478.8	47.4	68.7	118.2	771.9	1547.3
Range		9.8-15.6	911.6-995.5	471.3-530.7	32.2-63.8	7.5-181.3	105.7-127	527.8-1005.1	1536.5-1560.8
Sig. runs at p < 0.0001		10/10	10/10	10/10	10/10	10/10	10/10	10/10	10/10

Table 3.3. contd. (i) Species specific model results for the linear (L) trends and quadratic (Q) terms, coefficient sign and significance for all variables, p-values: *< 0.05, Ω< 0.01, ‡< 0.0001, ns = not significant. Significant interaction terms noted with an 'x'. (ii) Crossfold validation results from 10 simulations.

Variable	Breeds within the CCS										Does not breed within the CCS			
	MEGU		RHAU		SCMU		TUPU		WEGU		BOGU		BFAL	
Average Depth	L(+)‡	Q(+)‡	L(+)‡	Q(-)‡	L(+)‡	Q(-)‡			L(+)‡	Q(-)*	L(+)‡	Q(-)‡	L(+)‡	
SST	L(-)‡	Q(+)*	L(+)*	Q(-)‡	L(+)$^\Omega$	Q(-)‡			L(+)‡	Q(-)‡			L(-)‡	Q(-)‡
Spring Transition Date Anomalies			L(-)‡		L(-)‡		L(-)$^\Omega$		L(-)‡	Q(+)‡	L(-)‡	Q(-)‡	L(-)$^\Omega$	
SSH			L(+)ns	Q(+)*			L(+)ns	Q(-)‡	L(-)‡	Q(-)$^\Omega$				
Julian Date					L(-)*	Q(-)*	L(+)‡		L(+)‡					
Chla Concentration			L(-)ns	Q(-)‡			L(+)ns	Q(-)$^\Omega$	L(+)‡	Q(-)‡	L(+)‡	Q(-)*		
Contour Index	L(+)‡		L(+)‡				L(+)$^\Omega$		L(+)*	Q(-)‡				
NPGO, 0-2 months			L(-)‡				L(-)$^\Omega$		L(-)‡	Q(-)‡			L(+)ns	Q(-)‡
PDO, 0-2 months	L(+)‡						L(-)$^\Omega$						L(+)‡	Q(-)‡
SOI, 3-5 months	L(+)ns	Q(-)$^\Omega$	L(-)‡	Q(+)‡					L(+)*	Q(+)‡			L(+)$^\Omega$	Q(+)‡
SOI, 0-2 months							L(-)‡				L(-)ns	Q(+)‡		
PDO, 3-5 months			L(-)‡	Q(-)$^\Omega$					L(+)‡	Q(+)‡	L(+)‡			
NPGO, 3-5 months	L(+)$^\Omega$	Q(-)$^\Omega$									L(-)‡			
Year * SST			x				x				x		x	
Year * Latitude					x									
Year * SSH														
Year * Avg Depth														
Year * Dist. to Land														
Dist. to 200m isobath														
Dist. to 1km isobath														
Dist. to 3km isobath														
Dist. to Land														
Dist. to Fronts														
(ii) Crossfold Model Validation (k = 10), 10 simulations														
Validation F-Statistic (df)	(1, 74219)		(1, 56875)		(1, 74219)		(1, 56875)		(1, 56875)		(1, 56875)		(1, 74219)	
Median	201.8		1729		344.5		3617.8		2044.4		1039.5		1001.5	
Range	129.1-603.3		1680-1745.4		322.8-365.1		3201.7-4000.3		1999.1-2055.3		882-1111.2		963.4-1022.5	
Sig. runs at p < 0.0001	10/10		10/10		10/10		10/10		10/10		10/10		10/10	

Table 3.3 contd. (i) Species specific model results for the linear (L) trends and quadratic (Q) terms, coefficient sign and significance for all variables, p-values: *< 0.05, Ω< 0.01, ‡< 0.0001, ns = not significant. Significant interaction terms noted with an 'x'. (ii) Crossfold validation results from 10 simulations.

Variable	Does not breed within the CCS															
	BLKI		CAGU		HEEG		HERG		LAAL		LTJA		NOFU		PAJA	
(i) Best Fit Model																
Average Depth	L(+)‡	Q(+)*	L(+)‡	Q(-)‡	L(-)‡		L(+)‡	Q(+)‡	L(-)‡		L(-)‡	Q(-)‡	L(+)‡	Q(-)‡	L(+)‡	Q(-)‡
SST	L(-)‡	Q(-)‡	L(-)^Ω	Q(-)‡	L(+)‡		L(+)‡		L(-)‡		L(-)ns	Q(-)‡	L(-)ns	Q(-)‡	L(+)ns	Q(-)‡
Spring Transition Date Anomalies	L(+)^Ω		L(+)‡		L(-)‡		L(+)‡	Q(+)‡	L(+)*	Q(+)^Ω			L(+)‡		L(-)ns	Q(-)‡
SSH	L(+)ns	Q(-)‡	L(+)ns	Q(-)^Ω	L(-)‡	Q(+)‡	L(-)ns	Q(-)‡			L(+)ns	Q(-)*	L(-)‡	Q(-)‡		
Julian Date	L(-)‡	Q(-)‡	L(+)‡	Q(+)‡	L(+)‡	Q(-)*	L(+)*	Q(+)‡			L(+)ns	Q(-)‡	L(+)ns	Q(+)^Ω	L(-)*	Q(-)*
Chla Concentration	L(+)‡	Q(-)‡	L(+)*	Q(-)‡	L(+)ns	Q(-)‡	L(+)‡						L(+)‡	Q(-)‡		
Contour Index	L(+)ns	Q(-)*	L(+)‡				L(+)‡		L(-)ns	Q(-)*			L(+)‡	Q(-)‡	L(+)‡	
NPGO, 0-2 months	L(+)‡		L(-)^Ω	Q(-)‡			L(+)‡						L(+)^Ω	Q(-)‡		
PDO, 0-2 months	L(+)‡	Q(+)‡			L(-)ns	Q(-)‡	L(-)‡	Q(+)‡							L(-)‡	
SOI, 3-5 months	L(+)‡	Q(-)‡											L(+)‡	Q(-)^Ω		
SOI, 0-2 months			L(-)‡	Q(+)‡	L(-)‡		L(-)‡	Q(+)‡							L(-)‡	
PDO, 3-5 months			L(-)^Ω	Q(-)‡							L(-)^Ω	Q(-)‡	L(+)‡	Q(-)‡		
NPGO, 3-5 months					L(-)‡	Q(+)‡			L(-)^Ω	Q(+)*						
Year * SST							x									
Year * Latitude	x										x				x	
Year * SSH			x													
Year * Avg Depth																
Year * Dist. to Land																
Dist. to 200m isobath																
Dist. to 1km isobath																
Dist. to 3km isobath																
Dist. to Land																
Dist. to Fronts																
(ii) Crossfold Model Validation (k = 10), 10 simulations																
Validation F-Statistic (df)	(1, 56875)		(1, 56875)		(1, 56875)		(1, 56875)		(1, 74219)		(1, 74219)		(1, 56875)		(1, 74219)	
Median	143.1		162.6		2639.3		584.3		5574.6		477.3		91		441.3	
Range	122.6-1290.1		114.8-482.8		2445.8-2898.3		550.9-600.4		5379-5685.9		451.8-514.3		68-98.1		428.3-458	
Sig. runs at p < 0.0001	10/10		10/10		10/10		10/10		10/10		10/10		10/10		10/10	

Table 3.3. contd. (i) Species specific model results for the linear (L) trends and quadratic (Q) terms, coefficient sign and significance for all variables, p-values: *< 0.05, Ω< 0.01, ‡< 0.0001, ns = not significant. Significant interaction terms noted with an 'x'. (ii) Crossfold validation results from 10 simulations.

Variable	**Does not breed within CCS**													
	PALO		PFSH		POJA		REPH		RNPH		SAGU		SOSH	
(i) Best Fit Model														
Average Depth	L(+)‡		L(+)‡	Q(-)‡	L(+)‡	Q(-)‡	L(-)‡		L(+)‡		L(+)‡	Q(-)‡	L(+)‡	
SST	L(-)*	Q(-)‡	L(+)‡	Q(-)‡	L(+)ns	Q(-)‡	L(-)‡	Q(-)‡	L(-)‡	Q(-)‡	L(-)*	Q(-)‡	L(-)‡	Q(-)‡
Spring Transition Date Anomalies	L(-)‡				L(-)‡				L(-)‡	Q(+)$^{\Omega}$	L(+)ns	Q(+)$^{\Omega}$	L(+)*	Q(-)‡
SSH	L(-)‡	Q(-)‡	L(+)‡	Q(-)‡			L(-)‡	Q(-)‡	L(-)ns	Q(-)$^{\Omega}$	L(-)*		L(-)‡	Q(-)‡
Julian Date	L(+)ns	Q(+)$^{\Omega}$	L(+)‡	Q(-)‡									L(+)$^{\Omega}$	Q(-)‡
Chla Concentration											L(+)‡	Q(-)‡	L(+)‡	Q(-)‡
Contour Index	L(+)ns	Q(-)*					L(+)‡							
NPGO, 0-2 months	L(-)‡		L(-)‡	Q(-)‡	L(-)‡	Q(-)$^{\Omega}$	L(-)ns	Q(-)‡			L(-)ns	Q(-)‡	L(-)‡	Q(-)‡
PDO, 0-2 months	L(+)‡	Q(+)‡	L(-)‡	Q(+)$^{\Omega}$	L(+)ns	Q(+)‡								
SOI, 3-5 months			L(-)‡	Q(-)‡	L(+)ns	Q(-)‡	L(+)ns	Q(+)‡	L(+)$^{\Omega}$					
SOI, 0-2 months	L(+)ns	Q(+)$^{\Omega}$											L(-)‡	Q(-)‡
PDO, 3-5 months							L(-)$^{\Omega}$	Q(-)‡	L(-)ns	Q(-)‡			L(+)ns	Q(-)‡
NPGO, 3-5 months									L(+)$^{\Omega}$					
Year * SST														
Year * Latitude					x				x				x	
Year * SSH			x											
Year * Avg Depth														
Year * Dist. to Land														
Dist. to 200m isobath														
Dist. to 1km isobath														
Dist. to 3km isobath														
Dist. to Land														
Dist. to Fronts														
(ii) Crossfold Model Validation (k = 10), 10 simulations														
Validation F-Statistic (df)	(1, 74219)		(1, 74219)		(1, 74219)		(1, 74219)		(1, 74219)		(1, 56875)		(1, 56875)	
Median	588.7		166.5		834.7		13.7		190.4		76.1		149.7	
Range	553.1-657		150.6-176.3		809.2-849.9		6.2-28.4		173.2-196.3		45.4-90.4		144.6-154.4	
Sig. runs at p < 0.0001	10/10		10/10		10/10		10/10		10/10		10/10		10/10	

3.4.1 <u>Seabird - Habitat Associations</u>

We summarized seabird-habitat associations by species (grouped by their breeding status in the California Current System) in Table 3.3. The top three predictors (average depth, SST, and spring transition date anomalies) were included in more than 80% of species models (25 or more out of 30 species). Average depth significantly influenced the distributions for all species except tufted puffins. SST was a significant predictor for 27 species (all but Bonaparte's gull, Brandt's cormorant, and tufted puffin) and spring transition date anomalies significantly contributed to 25 models (all but mew gull, pink-footed shearwater, red phalarope, long-tailed jaeger, and Caspian tern). Other local/regional variables (SSH, Julian date, Chla concentration, and contour index) were significant in at least 60% of species models (18-20 out of 30 species). Basin-wide climate indices (either 0-2 months before or 3-5 months before) were significant variables in at least 80% of species models (25 or 26 out of 30 species). No distance variables (including the interaction between year and distance to land) were significant predictors for any of modeled species. Interaction terms were significant between year and SST or latitude in eight species and between year and SSH or average depth in one to three species (Table 3.3).

We tested for linear trends in all variables and 42% of cases proved non-linear. All species had at least two, but no more than nine, variables with significant quadratic relationships. A quadratic relationship was found between depth (19 species), SST (23 species), spring transition date anomalies (14 species), SSH (17 species), Julian date (14 species), Chla concentration (15 species), contour index (7 species), and, for both time periods, NPGO (15 species), PDO (20 species), and SOI (18 species) (Table 3.3).

3.4.2   <u>Predicted Distributions</u>

3.4.2.1   Standardized Abundance

Seasonal Multispecies Hotspots

Predicted areas of high habitat use by seabirds varied by season (Figure 3.5). Mean predicted abundances were consistently high for all months in the following regions: west of San Francisco Bay, in Monterey Bay, and the areas between Cape Mendocino and Cape Blanco (especially at the Klamath and Eel River mouths). The Oregon and Washington coasts also had high predicted abundances in May, July, and October. Peak values varied by season between Cape Blanco and Cape Flattery (denoted as CF in Figure 3.5), however, the Columbia River mouth and Heceta Bank consistently stand out as high use areas (Figure 3.5). The region between Big Sur and the Channel Islands in February and the area north of the Channel Islands in May had high predicted abundances, but they disappeared in July and October (Figure 3.5). Offshore, although predicted abundances were lower, there is less monthly variability and areas of high use tend to align well with seamounts, ridges and other bathymetric features, especially north of Cape Mendocino (Figure 3.5, and see *Pelagic Re-examination* section and Figure 3.9 for additional details).
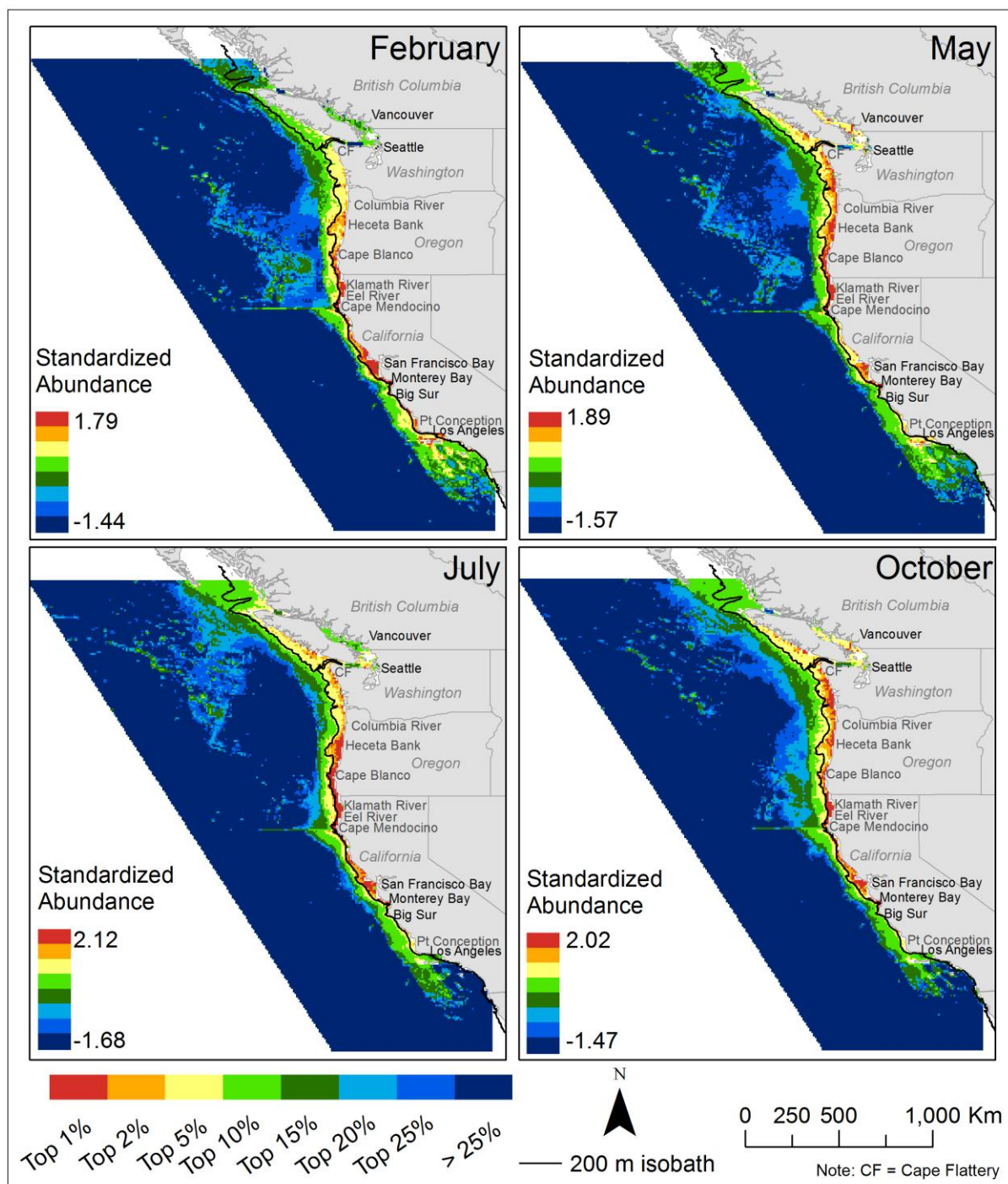
Figure 3.5. Predicted areas of seabird aggregations in the California Current System showing areas of high use by season independent of other seasons where February = winter, May = spring, July = summer and October = Fall. Note: standardized abundance scales differ among months.

Predicted seabird abundance varied across seasons and the amount of high use areas increased in the spring (May), peaked in the summer (July) and declined in the fall (October) (Figure 3.6). February (winter) had the lowest overall mean predicted abundance but had areas of high use located west of San Francisco Bay and Monterey Bay (Figure 3.6). Of the four months, the highest mean predicted abundances occurred in July with high use areas located along most coastal regions from western Vancouver Island to Monterey Bay and, to a lesser extent, from Big Sur to Point Conception (Figure 3.6). A similar pattern also occurred in October but hotspots within the top one percentile were restricted to fewer grid cells, especially west of Vancouver Island and between the mouth of the Columbia River and Cape Blanco (Figure 3.6). Although predicted seabird abundance in May included high use areas at Heceta Bank, Cape Blanco, the areas around the Columbia, Klamath and Eel River mouths, west of San Francisco Bay and Monterey Bay, areas in the top one percentile were reduced in both number and size compared to July or October (Figure 3.6). May, however, was the only month with a few areas of high abundance in the northern Channel Islands (Figure 3.6). In the offshore region, slightly elevated predicted abundances were present across all seasons and aligned well with bathymetric features (Figure 3.6, and see *Pelagic Re-examination* section and Figure 3.9 for additional details).
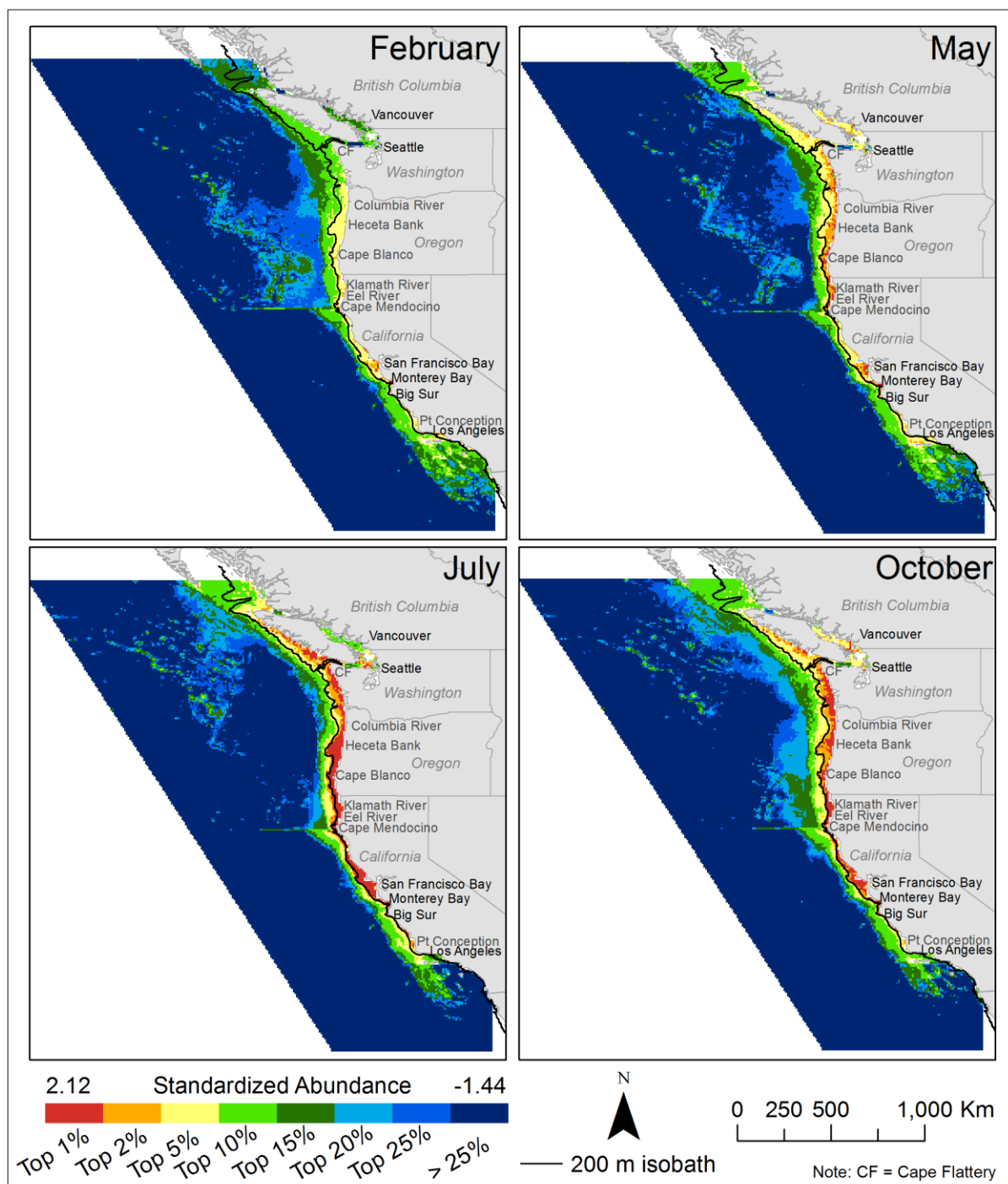
Figure 3.6. Predicted areas of seabird aggregations in the California Current System showing high use areas across seasons, where February = winter, May = spring, July = summer and October = Fall. Note: standardized abundance scales are the same across months.

Annual Multispecies Hotspots

Peak seabird abundance values varied annually during spring/summer (May/July), with the highest values found nearshore, within the 200 m isobath, and, depending on the year, stretching between northwest Vancouver Island and Point Conception (Figure 3.7). Peak values were restricted in their latitudinal range in 1998 (Cape Blanco to west of San Francisco Bay), 2004 (Cape Blanco to Point Conception) and 2005 (Cape Blanco to Monterey Bay) (Figure 3.7). Predicted areas of high use expanded latitudinally in most other years, but especially in 2001 (western Vancouver Island to Big Sur), 2007 (northwestern Vancouver Island to Monterey Bay), 2008 (Cape Flattery to Monterey Bay), and 2011 (western Vancouver Island to San Francisco Bay) (Figure 3.7). Finally, although there were no peak abundance values (top two percentiles) located offshore, some alignment with bathymetric features can be seen in most years (Figure 3.7, and see *Pelagic Re-examination* section and Figure 3.9 for additional details).
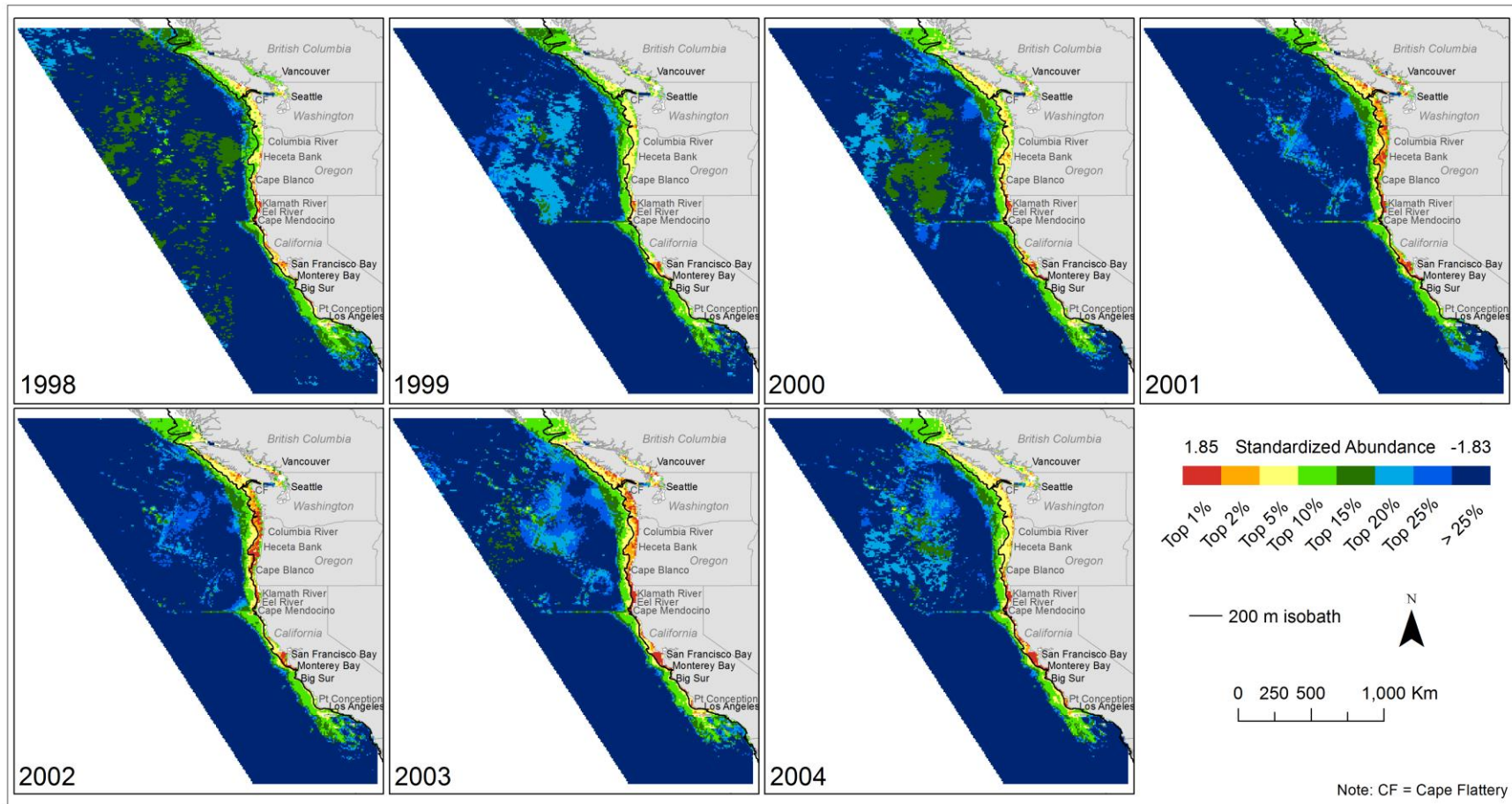
Figure 3.7. Annual spring/summer (May/July) predicted areas of seabird aggregations in the California Current System from 1998 to 2004. Note: standardized abundance scales are the same across years.
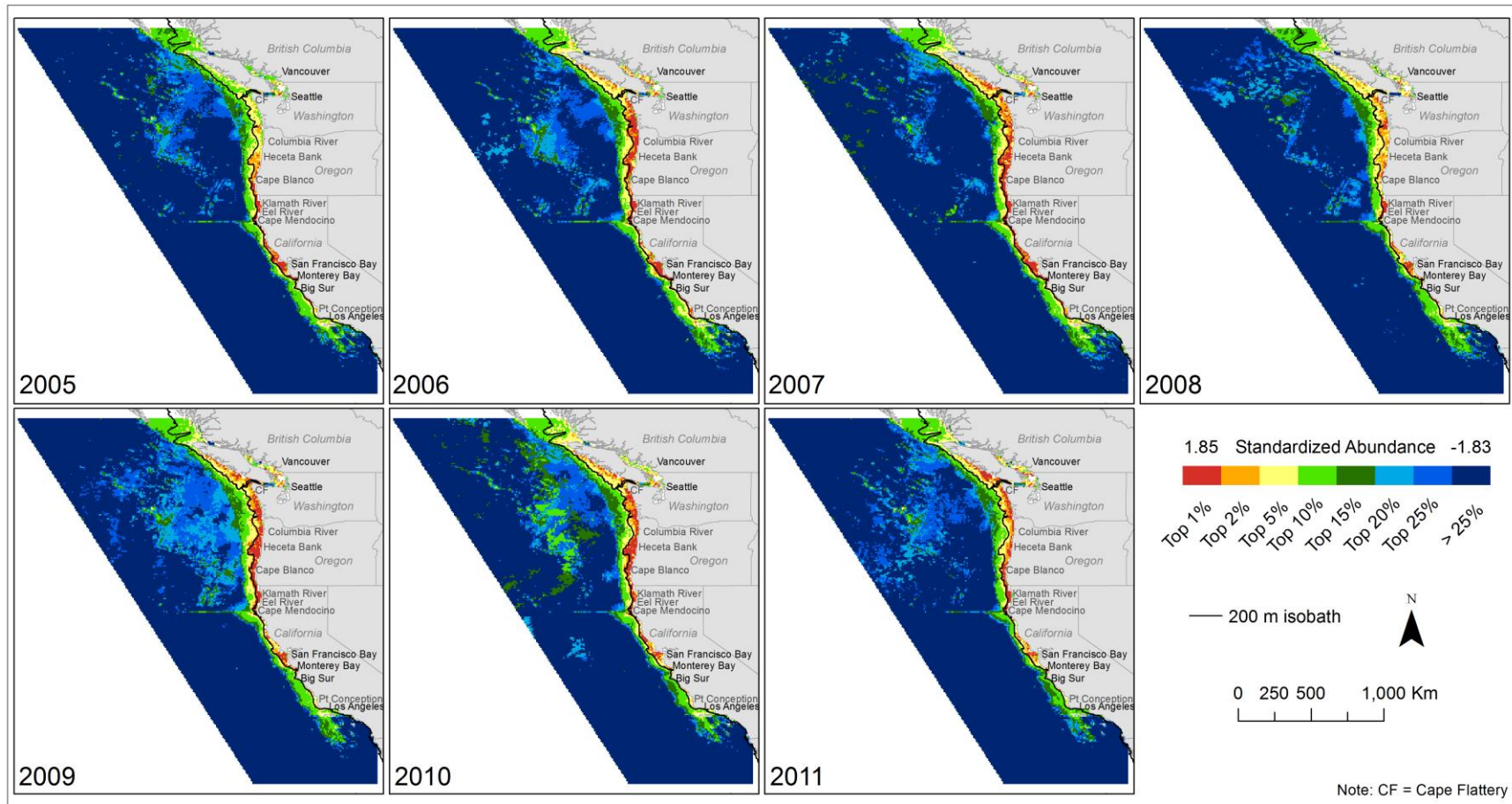
Figure 3.7 contd. Annual spring/summer (May/July) predicted areas of seabird aggregations in the California Current System from 2005 to 2011. Note: standardized abundance scales are the same across years.

All-inclusive Multispecies Hotspots

After averaging the predicted standardized abundance across all months/years, high use areas occurred within the 200 m isobath with peak values at Heceta Bank, between Cape Blanco and Cape Mendocino, west of San Francisco Bay, and Monterey Bay (Figure 3.8). Several smaller areas with more diffuse peak values were located north and south of the Columbia River mouth and between Cape Mendocino and San Francisco Bay (Figure 3.8). Offshore, there were some areas within the top 10- to 20- percentile that match with bathymetric features (Figures 3.8, and see next section for additional details).

Pelagic Re-examination

After the exclusion of the coastal predicted values from the dataset, predicted high use areas in the offshore region were more easily identifiable (Figure 3.9). North of the Mendocino Ridge, peak values were noted at Cobb, Brown Bear, Eickleberg, Warwick, and Explorer Seamounts among others, along Juan de Fuca, Gorda, and Mendocino Ridges, and at the outfalls of Moresby, Juan de Fuca, and Astoria Canyons (Figure 3.9, left). Though there are fewer bathymetric features south of the Mendocino Ridge, areas of high use occurred at the Davidson and San Juan Seamounts, the Patton Escarpment and Sixty Mile Bank (Figure 3.9, right).
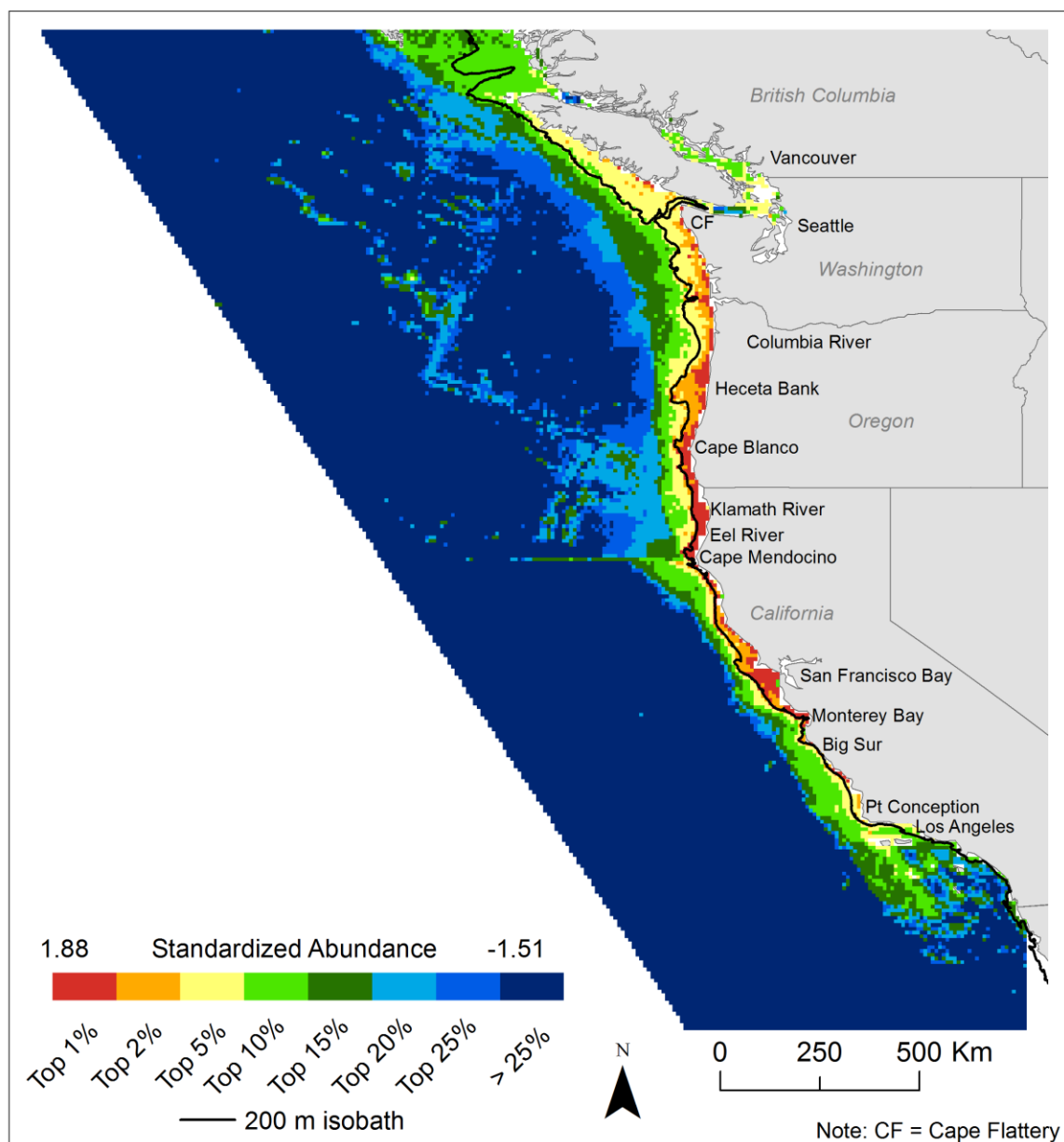
Figure 3.8. Predicted areas of multispecies seabird aggregations in the California Current System for all months/years. Localized peaks occurred at Monterey Bay, west of San Francisco Bay, between Cape Mendocino and Cape Blanco, Heceta Bank and north/south of the Columbia River Mouth.
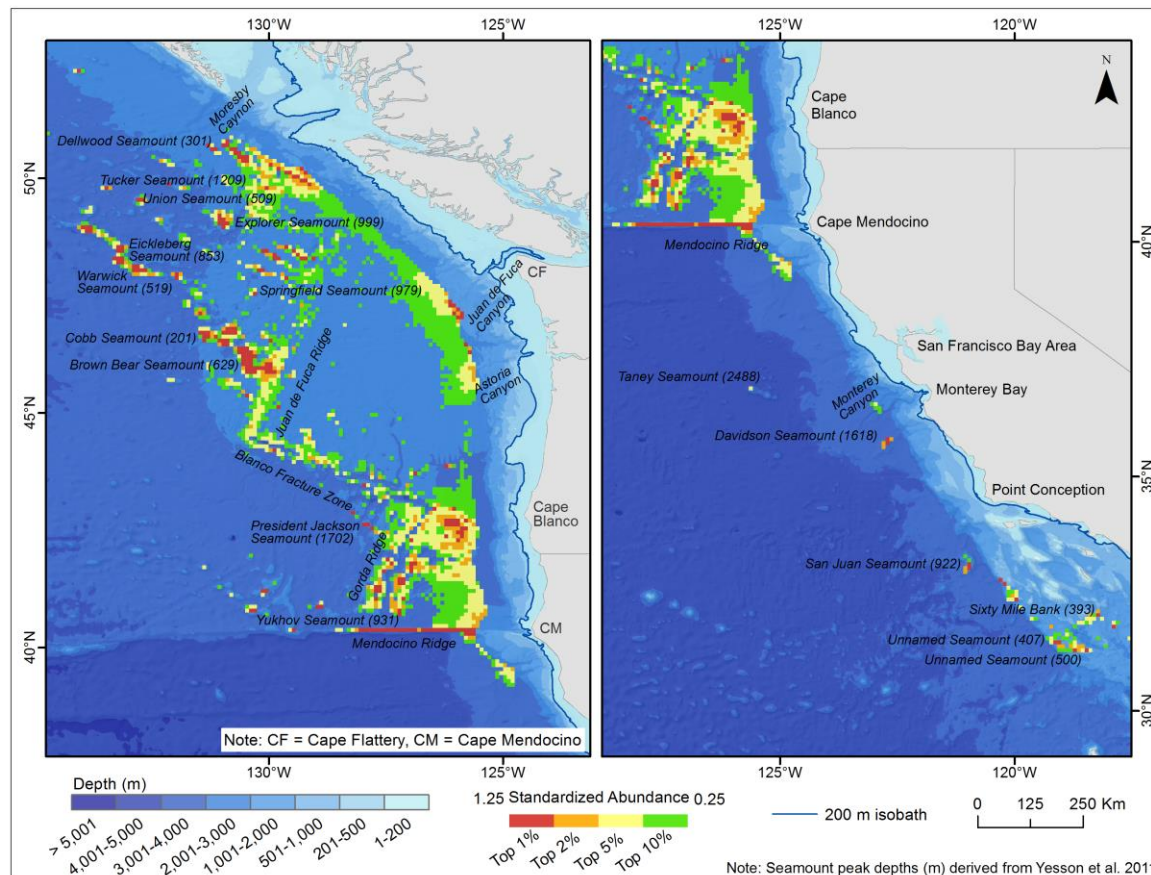
Figure 3.9. The top 1, 2, 5, and 10 percentiles of the predicted standardized abundances for only the offshore region of the California Current System highlighting the alignment of peak values with bathymetric features north (left) and south (right) of the Mendocino Ridge. For geographic context, the Esri Ocean Basemap is used (http://esriurl.com/obm, courtesy of Esri and its partners).

3.4.2.2 Species Richness

Seasonal Multispecies Hotspots

Within the 98th percentile of predicted standardized abundance, the number of species (species richness) predicted to occur ranged from 0 to 17, with the location of peak values varying across months (Figure 3.10). In the winter (February) the highest species richness

occurred south of Big Sur and around the Channel Islands (Figure 3.10). This pattern changed in May (spring) as areas in the north increase in the number of species. For example, although a high species count remained offshore of the Channel Islands, species richness was higher around Point Conception, Monterey Bay, west of San Francisco Bay, and the Klamath and Eel River mouths (Figure 3.10). In the summer (July), the number of species decreases around Point Conception, while the areas of high species richness remained in Monterey Bay, west and north of San Francisco Bay, and between Cape Mendocino to Cape Blanco. Although more diffuse, high species counts also occurred at Heceta Back, north of the Columbia River mouth and along western Vancouver Island (Figure 3.10). Moving into fall, species richness decreases between Vancouver Island and Cape Mendocino, however, the Klamath and Eel River mouths, west and north of San Francisco Bay and northern Monterey Bay continue to have high species numbers (Figure 3.10). For all months, peak species counts were concentrated nearshore, and except for the Cobb and Davidson Seamounts, little to no species richness was noted in the pelagic area.
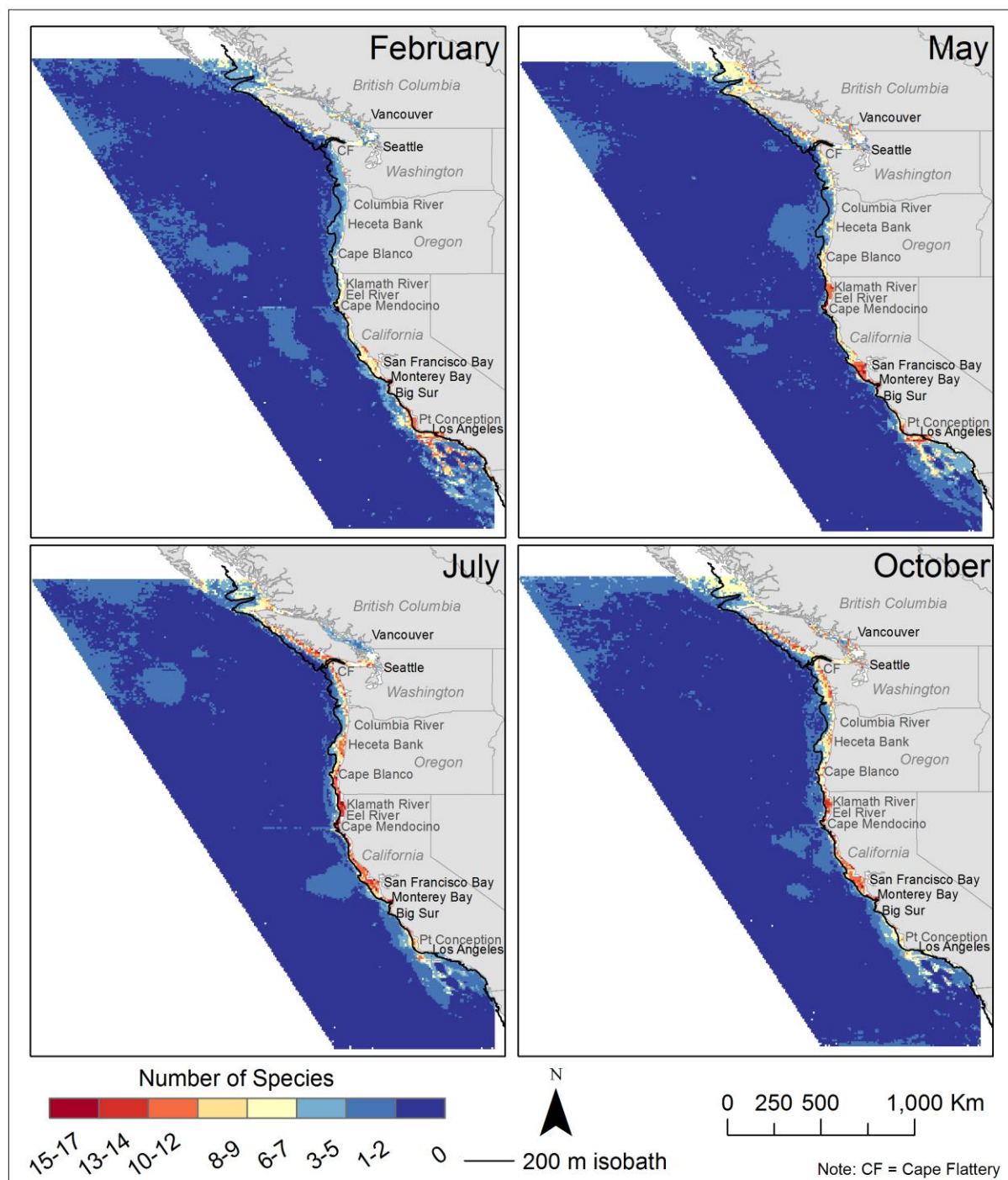
Figure 3.10. Species richness across months for the California Current System derived from the 98th percentile of predicted standardized abundance for each species.

All-inclusive Multispecies Hotspots

After averaging the individual species layers across all months/years, areas of highest species richness occurred within the 200 m isobath north of the Channel Islands, from Big Sur to Point Conception, Monterey Bay, west of San Francisco Bay, between Cape Mendocino and the California/Oregon border with a strong peak at the Klamath and Eel River mouths (Figure 3.11). Although more diffuse, high species counts were also located at Cape Blanco, Heceta Bank, and western Vancouver Island (Figure 3.11). The Cobb and Davidson Seamounts and the areas southwest of the Channel Islands had elevated species counts offshore (Figure 3.11).
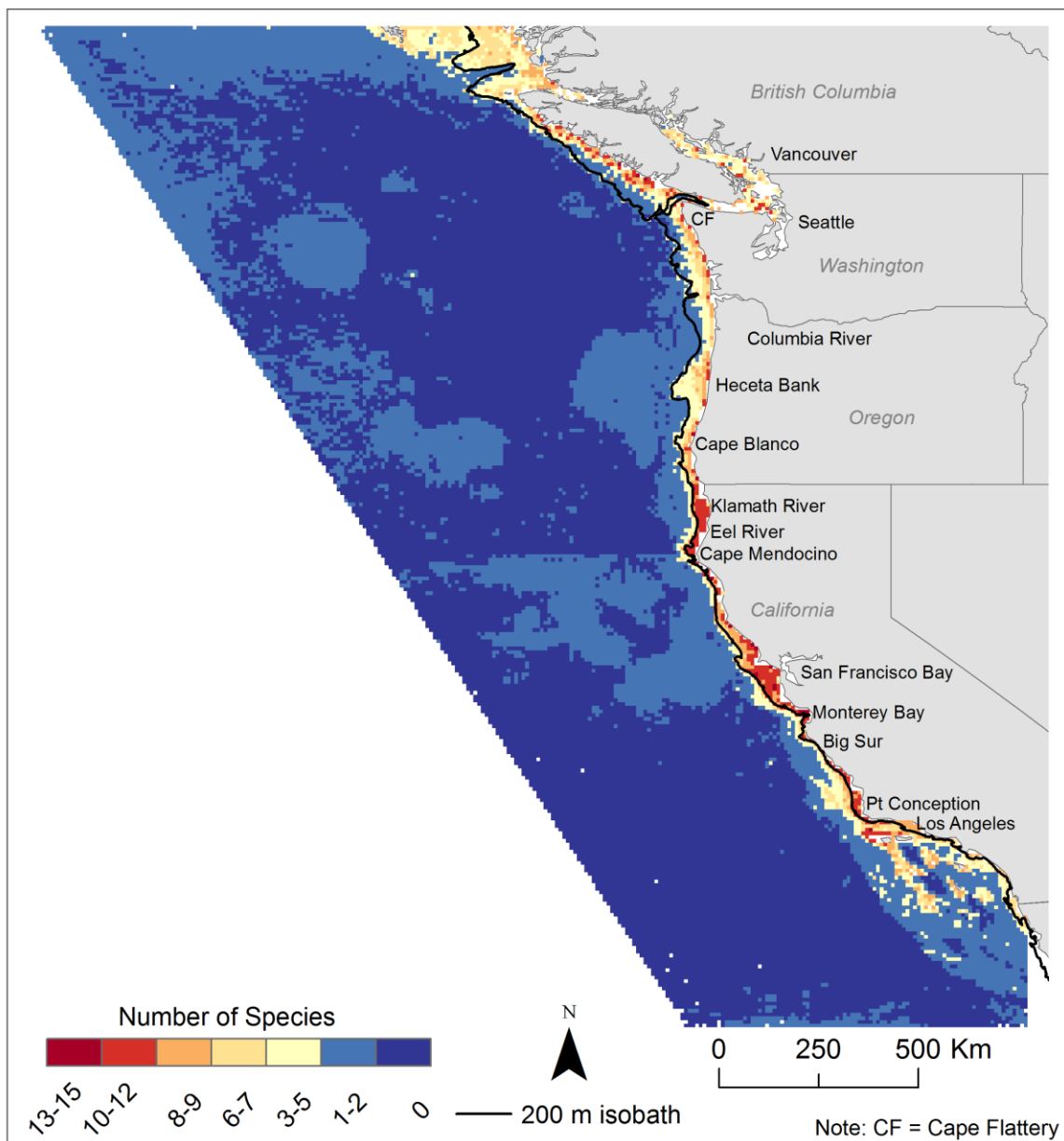
Figure 3.11. Species richness for all months/years for the California Current System derived from the 98th percentile of predicted standardized abundance for each species.

3.5   Discussion

This study collected and modelled long-term, at-sea seabird survey data with remotely sensed biophysical oceanographic data and climate indices to predict seabird foraging hotspots throughout the entire California Current System. Our study improved upon Nur et al. (2011) in several ways. First, we filled temporal and spatial data gaps with newly available at-sea survey data, augmenting the data by thirty-five percent, most notably in the coastal regions of northern California, Oregon and Washington. Second, the inclusion of new data allowed us to almost double the number of species modeled from 16 to 30, including 10 additional pelagic and/or non-breeding species (e.g., black-legged kittiwake, Laysan albatross, long-tailed jaeger, mew gull, northern fulmar, parasitic jaeger, Pacific loon, pink-footed shearwater, pomarine jaeger, and red phalarope). Finally, we used a different modeling approach (statistical: generalized linear models, specifically negative binomial regression vs. machine learning: bagged decision trees) whose outcome emphasized the importance of local/regional static and oceanographic variables and basin-wide climate conditions to seabirds within the CCS (dominant predictors in Nur et al. (2011) were primarily bathymetry related). The advantage of generalized linear models is explicit coefficients and standard errors for each variable, including assessing quadratic curvature. Combined, these analytical differences provide additional insight and understanding of coastal and pelagic multispecies seabird hotspots in the CCS while also informing future marine spatial planning decisions.

3.5.1   <u>Predictors</u>

Given the life history and ecological differences of the 30 species modeled, there was substantial variation among species with respect to important predictor variables. In general, however, we found important predictive variables to differ spatially and temporally at both local/regional and basin-wide scales. Of the top seven predictors, two are associated with static bathymetric features (average depth and contour index), four are linked to oceanographic

processes influencing or related to upwelling and subsequent increased nutrients (SST, Chla concentration, SSH, and spring transition date anomalies), and one is related to within year temporal variability (Julian date).

We found a positive relationship between most seabird species and average depth and contour index (bathymetric relief) predictors suggesting that the number of birds increases in deeper water as the seafloor becomes more complex (e.g., towards the continental shelf break). Depth showed significant quadratic curvature for 19 species implying an intermediate optimal depth value exists and influences seabird abundance. Complex bathymetries (e.g., continental shelf breaks, seamounts, ridges, and submarine canyons) influence water movement, enhance mixing, stimulate upwelling, and lead to nutrient rich water that promotes increased primary and secondary production and subsequent concentrations of prey upon which predators forage (Simrad et al. 1986; Hyrenbach et al. 2000; Genin 2004; Yen at al. 2004). Depth is tied closely to the above processes because primary productivity in the oceans is generally limited to the upper 200 m (euphotic zone) where light penetrates and is available to phytoplankton for photosynthesis. Secondary productivity follows when zooplankton graze on phytoplankton. As a result, productivity is generally highest over the continental shelf (depths 0-200 m) and along the shelf break (200 m isobath), leading to dense prey concentrations that draw large numbers of seabirds to the area to forage (Hyrenbach et al. 2002; Ford et al. 2004; Shaffer et al. 2006; Adams et al 2012; Michael et al. 2013).

The relationships between seabirds and the predictors SST, spring transition date anomalies, Chla concentration, and SSH ranged widely. Varied life histories and feeding habits among the species we modeled could explain these differences. For example, our model results suggest that migratory species are more abundant later in the upwelling season when SST is cooler and Chla concentration is higher. This is consistent with studies that show migrants appear to time their presence in areas when ocean productivity is high such as during peak upwelling in eastern boundary current systems (Schaffer et al. 2006; Block et al. 2011). In

contrast, for species that breed in the CCS, our model results suggest their presence in the area before peak upwelling and become more abundant as productivity increases within and up to some intermediate optimum depth, regardless of increasing/decreasing SST. This is consistent with the idea that breeding seabirds are central place foragers who are constrained to feeding in productive waters (often over continental shelves or shelf breaks) that are near to their nesting sites (Harding et al. 2013).

We found no consistent relationships between seabirds and climate indices. This is not surprising since our study spans a relatively short period (15 years) with respect to the climate indices used in our models. Both the Pacific Decadal Oscillation (PDO) and North Pacific Gyre Oscillation (NPGO) have decadal cycles and together, they have described a "cool phase" in the CCS since 1999 (Hazen et al. 2012). Thus, it is unlikely that our models would pick up any trends in these two indices within our 15-year study. The Southern Oscillation Index (SOI), however, operates on a shorter cycle, and therefore, we expected El Niño Southern Oscillation events would correlate with interannual abundance. Yet, despite several recognized El Niño Southern Oscillation events during our study period (e.g., El Niño: 1997-1998, 2004-2005 and La Niña: 2007, 2010-2011), relationships were generally inconsistent among species. Our annual mapped results of abundance however, suggest that for El Niño years, when upwelling is reduced, lower overall seabird abundance occurs in the CCS. Conversely, in La Niña years, when upwelling intensifies, our maps showed higher overall seabird abundance.

Surprisingly, our models did not include any distance related variables despite being important predictors in previous studies (Ford et al. 2004; Nur et al. 2011; McGowan et al 2014; Yen et al. 2004). This is likely due to the inclusion of other variables that are better at predicting seabird distribution (discussed above). Yet, even without significant distance related variables in our models, our multispecies aggregation maps show peak standardized abundances and species richness tend to occur over the continental shelf and along the shelf break (e.g., 200 m

isobath), corroborating the importance of this region to seabirds (Hyrenbach et al. 2002; Ford et al. 2004; Shaffer et al. 2006; Adams et al 2012; Michael et al. 2013).

3.5.2   <u>Hotspot Location and Variability</u>

Despite the inclusion of at-sea survey data from the offshore region, Nur et al.'s (2011) significant hotspot areas were limited to within 90 km of shore. This is perhaps the most notable distinction between Nur et al. (2011) and our study and is likely the result of additional pelagic data and the inclusion of more pelagic species in our analysis. Our results predicted high habitat use by seabirds in association with offshore bathymetric features, especially north of the Mendocino Ridge where seafloor complexity increases. Six areas (five seamounts and one ridge) stand out: Cobb and Brown Bear Seamounts, Eickleberg and Warwick Seamounts, Explorer Seamount, Davidson Seamount, the areas around Sixty Mile Bank, and the Gorda Ridge. In general, these hotspots showed less seasonal and annual variability than their coastal counterparts did, and we hypothesize this might be due to their submerged nature and distance from coastal influences. Seamounts and ridges alter local currents that in turn upwell nutrients, increase productivity, and support/attract a wide range of organisms, including seabirds (Pitcher et al. 2007; Wessel 2007; White et al. 2007; Thompson 2007; Morato et al. 2010). Our results are consistent with previous studies that found, compared to surrounding waters, some seamounts have higher species abundance and richness within 30-40 km of the summit (Haney et al. 1995; Dower and Mackas 1996; Morato et al. 2010).

To identify areas favorable for multispecies seabird foraging aggregations, we used two measures: predicted abundance and predicted species richness. Model outputs for each measure provided similar results. In general, where there was high seabird abundance, there was also high species richness. Predicted peak values for both measures were observed along most of the coast and fall into one of two categories: (1) areas protected through established National Marine Sanctuaries (NMS) including Monterey Bay, west and north of San Francisco

Bay, and the Olympic Peninsula; or (2) areas without protection including between Cape
Mendocino and Cape Blanco, Heceta Bank, the Columbia River mouth, and western Vancouver
Island. These findings are generally consistent with Nur et al. (2011). Conversely, our model
results did not predict high abundance or species richness around the Channel Islands. This
differs from Nur et al. (2011) who found the area around the Channel Islands NMS to be a
significant and persistent hotspot. Given this location is near Los Angeles, a densely populated
area where direct and indirect anthropogenic impacts occur, further investigation concerning
this difference in findings is needed.

Mapped model outputs for abundance and species richness were are also similar from
month to month and appear to mirror when upwelling is (spring/summer) or is not (fall/winter)
generally occurring. Seasonal variability across months for both measures increased between
February and July before decreasing between October and February. However, it is unclear
from this study whether species resident to the CCS dominate some hotspots, while other
hotspots are dominated by migratory species. Understanding hotspot species composition
could have important implications for management decisions (e.g., whether or not to weigh
species equally vs. placing more weight on some species for MPA designation) and is worthy of
additional research.

3.5.3   Management Implications

Though our final models included bathymetric, oceanographic, and climate variables as
important predictors, our mapped results of multispecies seabird aggregations suggest that
coastal and pelagic static bathymetric features (e.g., capes, the continental shelf, shelf break at
the 200 m isobath, seamounts, and ridges) are critical for predicting seabird habitat use in the
CCS. As previously discussed, these features play an important role in the enhancement of
productivity during active upwelling and prioritizing protected areas based on static benthic
features may be the simplest and most pragmatic method to site delineation (Hyrenbach et al.

2000). In the coastal regions of the United States, we identified areas of conservation importance that fit well with currently established national marine sanctuaries in the coastal regions. The placement of one or more new NMSs between Cape Mendocino and the Columbia River mouth would eliminate current gaps highlighted in this study (and in Nur et al. 2011). Another priority area for consideration occurs around the complex benthic features southwest of the Channel Islands (e.g. San Juan Seamount/Sixty Mile Bank area). Moreover, because such measures cannot track dynamic features upon which seabirds and other top predators exploit, some degree of flexible boundaries should be incorporated (Hyrenbach et al. 2000). For example, dynamic management areas, successfully used for North Atlantic right whales to reduce entanglement in fishing gear (Asaro 2012), could be established as a way to temporarily extend the NMS boundaries when the amount of available foraging habitat increases during La Niña years when upwelling intensifies. Although the current national marine sanctuaries mandate provides limited protection to marine species, their legal framework could be used to develop a future network of MPAs for the CCS (Nur et al. 2011).

Beyond U.S. jurisdiction, we identified areas important for seabird foraging along western Vancouver Island, and in the high seas (areas beyond national jurisdiction [ABNJ]), we identified areas of conservation importance, particularly at the Cobb/ Brown Bear seamount complex which had the largest predicted area of high habitat use perhaps due to its summit located in the euphotic zone. Protection in the ABNJ will require new governance arrangements within the United Nations (Ban et al. 2014).

3.5.4   Conclusion

There is a growing preference for multispecies approaches that use overall abundance and/or species diversity to delineate MPA network sites across large spatial scales (Zacharias and Roff 2001; Campanga et al. 2008; Nur et al. 2011; Lascelles et al. 2012; McGowan et al. 2013). By using a suite of species with varying body sizes, life histories, and ecologies, these

approaches are believed to identify areas important for a functioning ecosystem making them well-suited for marine spatial planning initiatives with an ecosystem-based management framework. Our use of seabirds as indicator species combined with a multispecies approach has provided an example of using at-sea seabird data combined with remotely sensed data and spatial modeling techniques to help prioritize protected area designation in the CCS. This approach can be used in other regions of the world where similar data exist, as well as explore the possible effects of climate change on seabird at-sea distribution.

3.6 Acknowledgements

3.7 Literature Cited

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4   Forecasting the Flock: Evaluating the Effects of Climate Change on Future Seabird Foraging Aggregations in the California Current System

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4.1   Abstract

Marine protected area design in the face of climate change depends on robust understanding of current relationships between species and their environment. This study combined species-specific distribution models with climate envelope models as a first-order approach to examine at-sea distributions and range shifts for multispecies seabird foraging aggregations ("hotspots") in the California Current System. Using distribution models developed in Chapter 3, we predicted species-specific abundances during February, May, July, and October under three scenarios: current conditions and increases of sea surface temperature (SST) by 0.6°C and 2.0°C, based on ocean warming estimates from the IPCC's 5th Assessment. For future scenarios, we assessed current relationships between SST, sea surface height (SSH) and chlorophyll-*a* concentration (Chla), and used these relationships to predict future SSH and Chla while increasing SST. Predicted abundances were averaged across years, standardized, and based on predicted sensitivity to SST increases, species were split at the 50th percentile. Species in the upper 50th percentile were split further by foraging ecotype (diving foragers and surface feeders). Standardized predicted means were averaged by foraging ecotype to create scenario-specific multispecies hotspot maps by month. Results suggest suitable foraging habitat will shift offshore and north, diving and surface feeders will be the most sensitive to a changing climate, and some seamounts may retain suitable habitat in the future. Our projected results suggest some federally designated national marine sanctuaries will become less suitable (Channel Islands) while others will continue to provide suitable habitat in the future (Greater Farallones and Cordell Bank) for seabirds. At least three unprotected regions may become suitable habitat in the future. Despite uncertainty associated with how ecosystems and species will respond to climate change, this study provides an important first step in elucidating the magnitude, direction, and potential mechanisms underlying projected changes in seabird habitat in the California Current System.

4.2 Introduction

Climate variability and change are now accepted to have profound effects on marine ecosystems (Behrenfeld et al. 2006; Harley et al. 2006; Hoegh-Guldberg and Bruno 2010; Doney et al. 2012). Much of the energy from rising global temperatures has been absorbed by the ocean, increasing ocean surface temperatures by ~0.67°C in the last century (Hoegh-Guldburg and Bruno 2010). The latest assessment report (AR5) from the Intergovernmental Panel on Climate Change (IPCC) states the global ocean will continue to warm, though not uniformly, over the 21st century with estimates ranging between 0.6° to 2.0°C for the upper 100 meters depending on the scenario (IPCC 2013). Moreover, though the mechanism remains under debate (e.g. land-sea temperature/pressure gradients [Bakun 1990] or poleward displacement of high-pressure systems [Rykaczewski et al. 2015], it is generally agreed that in a warming world, favorable upwelling winds in eastern boundary current systems (EBCS) will intensify during spring/summer, particularly at higher latitudes and lead to a cascade of effects in the marine environment (Bakun 1990; Bakun and Weeks 2004; Sydeman et al 2014; Bakun et al 2015; Rykaczewski et al. 2015; Wang et al. 2015). Scenarios using empirical data predict increased winds may push nutrients offshore or deeper leading to a decrease in coastal primary productivity that would disrupt lower trophic levels and reduce prey availability for upper-trophic level predators like seabirds (King et al 2011; Bakun et al. 2015)

Seabirds, although conspicuous, are considered one of the most threatened marine taxonomic groups worldwide, with roughly 30% of species threatened, near-threatened, or critically endangered (Croxall et al. 2012, Sydeman et al. 2012). They are long-lived animals with high adult survival, low fertility, delayed sexual maturity, and they breed in colonies in coastal areas or offshore islands, exhibiting strong site fidelity to their natal site (Schreiber and Burger 2002). As wide ranging marine predators, seabirds are found globally in all oceans, feed across multiple trophic levels, and rely on micronekton (forage fish and squids)

and mesozooplankton (copepods and krill) for food (Schreiber and Burger 2002; Lewison et al. 2012; Sydeman et al. 2012). Their dependence on both marine and terrestrial ecosystems and their global range make them particularly sensitive to habitat changes and thus, excellent indicators of marine ecosystem status and structure (Sydeman et al. 2012; Lewison et al. 2014). Consequently, an improved understanding of how climate change might affect seabirds and the locations where they forage will be important for their conservation.

Direct effects of climate change on seabirds are considered rare but not impossible (e.g., seabird deaths from heightened hurricane activity [Hass et al. 2012] or loss of nesting habitat from sea level rise [Sydeman et al. 2015]). It is more likely changing climate will affect seabirds indirectly, via modifications to oceanic processes and the spatio-temporal availability of their prey (Grémillet and Boulinier 2009). Unfortunately, systematic surveys quantifying the abundance of marine invertebrates and fish are scarce, especially for non-commercially exploited species (Durant et al. 2009). Moreover, while land-based seabird demographic and population size studies that focus on food-related mechanisms in response to climate change are common (Sydeman et al. 2001; Dorresteijn et al. 2012; MEPS 2012), studies that investigate at-sea distribution and range shifts due to future climate-related changes are lacking and rarely include multiple species (Sydeman et al.2012; Péron et al. 2012; Hazen et al. 2013). To close this gap, it is imperative to develop better spatial models that test and predict future seabird-climate relationships.

A simple first-order approach to understanding how future seabird foraging aggregations may be impacted by climate change is to use a type of climate envelope model (CEM). CEMs build correlative statistical models using species distribution data to explain the spatial patterns in the present or recent past, assume some type of space-for-time substitution, and project forward in time the locations suitable for species under different climate scenarios (Renwick et al. 2012; Blois et al. 2013; Russel et al. 2015). Although CEMs

have been criticized (Araújo and Rahbek 2006; Hijmans and Graham 2006; Watling et al. 2013), they remain widely used because they provide an empirical method of evaluating species' relative vulnerability to climate change necessary for management decisions (Willis et al. 2009; Renwick et al. 2012).

The availability of at-sea ship surveys conducted in the California Current System from several long-term seabird monitoring programs (additional details in Methods section) provides an unparalleled opportunity to combine species-specific distribution models and CEMs to examine at-sea distributions and range shifts for multiple species. We use the species-specific models developed in Chapter 3 as species' distribution baselines in combination with IPCC estimates of ocean warming to explore the impacts of climate change on multispecies seabird foraging aggregations ("hotspots") in the California Current System. Specifically, we asked: (1) how do the locations of multispecies foraging aggregations shift with increasing ocean temperatures?; (2) Are all species equally sensitive or are some species likely to be more sensitive to climate-related changes?; and (3) Do seamounts (identified as important habitat in Chapter 3) retain suitable habitat in a warming ocean?

Forecasting how future climate change will affect seabird foraging hotspots and communities in the CCS can be used in the marine spatial planning process to ensure marine protected area (MPA) networks will remain appropriate as climate conditions change in the future. This information can also be used to adapt strategies now to alleviate non-climate stressors such as fishery pressures and coastal development in areas projected to be important to seabirds in the future.

4.3   Material and Methods

4.3.1   Survey Area and Seabird Data

We used seabird data collected from at-sea surveys over a 15-year period (October 1997 through June 2012) by eight U.S. and Canadian research and monitoring programs (see Chapter 3, Appendix A). Although the spatial coverage varied by cruise, the combined extent of all cruises spanned the California Current along the west coast of North America from Baja California, Mexico (30°N) to just north of Vancouver Island, Canada (52°N) and 600-800km offshore (Figure 4.1, left). Seabird data were collected using standardized strip-surveys (Tasker et al. 1985; Buckland et al. 2001). We divided transects for each cruise into 3-km bins using methods outlined in prior studies (Yen et al. 2004; Nur et al. 2011; McGowan et al. 2013; Chapter 3). Each bin's mid-point was used to aggregate species counts for seabirds that were observed foraging, feeding, or sitting on the water (Nur et al. 2011; Chapter 3). Additional details of at-sea data collection and survey data processing are described in Chapter 3.

4.3.2   Predictor Variables, Model Development, and Model Validation

We selected 21 variables of interest (Table 4.1) based on availability and previous studies of seabird-habitat associations conducted in the California Current System (Yen et al. 2004; Ainley et al. 2009; Trembley et al. 2009; Nur et al. 2011; McGowan et al. 2013; Chapter 3). For bathymetric related data, we used the General Bathymetric Chart of the Oceans (GEBCO_08 Grid, version 20100927, http://www.gebco.net) and ArcGIS 10.2.2 (Esri, Redlands, CA) to derive average depth, contour index (a measure of sea floor topographic relief), and nearest distance to land and the 200-, 1,000-, and 3,000-m isobaths (Chapter 3). We used the ArcGIS-compatible extension Marie Geospatial Ecology Tools v0.8a56 (MGET) (Roberts et al. 2010) to obtain remotely sensed oceanographic data for chlorophyll-a (Chla) concentration (SeaWiFS and MODIS-Aqua, http://oceancolor.gsfc.nasa.gov/), sea surface
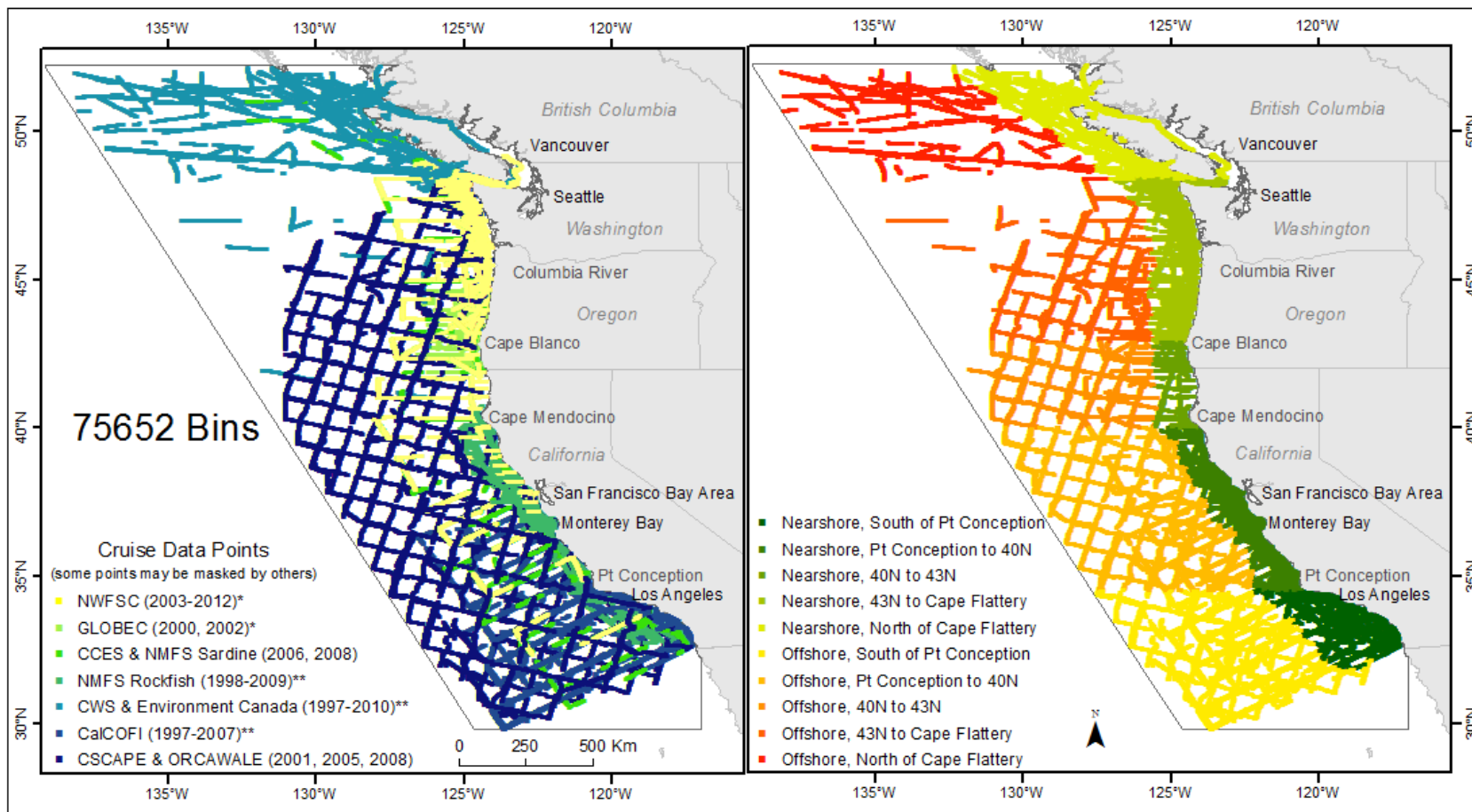
Figure 4.1. The spatial coverage and monitoring programs for the at-sea survey data used in this study (Left). The study area divided into 10 regions based on distinct latitudinal break points where oceanographic processes differ and a nearshore/pelagic component as determined in Chapter 3 (Right).

Table 4.1.The 21 predictor variables, including details on their variability, resolution, mean, range and source, used in model development.

Variable	Variability	Resolution	Mean ± SD	Min - Max Value	Source
Bathymetric					
Average Depth (m)	spatial	7km x 7km	-2206.70 ± 1668.60	-5048.2 - 141.1	GEBCO_08 Grid, version 20100927, http://www.gebco.net
Contour Index (%)	spatial	7km x 7km	10.20 ± 15.00	0 - 99.0	Derived from GEBCO_08 Grid
Distance to land (km)	spatial	NA	152.13 ± 149.57	0 - 601.81	GEBCO_08 Grid, calculated in ArcGIS 10.2.2
Distance to 200 m isobath (km)	spatial	NA	154.75 ± 157.61	0 - 582.84	GEBCO_08 Grid, calculated in ArcGIS 10.2.2
Distance to 1 km isobath (km)	spatial	NA	128.36 ± 135.89	0 - 558.49	GEBCO_08 Grid, calculated in ArcGIS 10.2.2
Distance to 3 km isobath (km)	spatial	NA	148.22 ± 121.46	0 - 543.89	GEBCO_08 Grid, calculated in ArcGIS 10.2.2
Remotely Sensed Oceanographic					
Chlorophyll a Conc. (mg/m^3)	spatial, temporal	9.3km x 7.3km 8 days	1.53 ± 2.70	0.03 - 86.94	SeaWiFS (Oct 1997 - Dec 2010), MODIS - Aqua (July 2002 - June 2012), http://oceancolor.gsfc.nasa.gov/
Sea surface height (m)	spatial, temporal	27km x 23km 8 days	0.50 ± 0.10	0 - 0.81	AVISO, http://www.aviso.altimetry.fr/duacs/
Sea surface temperature (°C)	spatial, temporal	22km x 18km 8 days	14.00 ± 3.03	6.33 - 22.92	GHRSST L4 gridded product, http://podaac.jpl.nasa.gov/dataset/CMC0.2deg-CMC-L4-GLOB-v2.0
Climate Indices					
SOI, 0-2 months before	temporal	3 months	-0.06 ± 1.37	-5.17 - 3.43	Trenberth 1984, http://www.cgd.ucar.edu/cas/
SOI, 3-5 months before	temporal	3 months	-0.07 ± 1.67	-5.17 - 4.7	catalog/climind/SOI.signal.ascii
NPGO, 0-2 months before	temporal	3 months	0.69 ± 1.15	-1.46 - 2.66	Di Lorenzo et al. 2008, http://eros.eas.gatech.edu
NPGO, 3-5 months before	temporal	3 months	0.68 ± 1.20	-1.46 - 2.74	/npgo/npgo.php
PDO, 0-2 months before	temporal	3 months	-0.13 ± 0.96	-1.67 - 2.2	Mantua and Hare 2002,
PDO, 3-5 months before	temporal	3 months	-0.01 ± 0.97	-1.94 - 2.63	http://jisao.washington.edu/pdo/
Data Related to Annual/Seasonal Variability					
Year	temporal	annual	2004 ± 3.33	1997 - 2012	
Month	temporal	month	6.29 ± 2.71	1 - 12	
Julian Date	temporal	within year	175 ± 82.76	4 - 350	
Spring Transition Date Anomalies	temporal	annual	-10.58 ± 14.49	-39.07 - 22.93	
Latitude	spatial	NA	39.19 ± 6.57	29.83 - 52.24	
Effort Related					
Bin area (log(km^2))	spatial	NA	-0.18 ± 0.24	-2.74 - 1.66	derived

height above geoid (SSH, http://www.aviso.altimetry.fr/duacs/), and sea surface

temperature (SST, https://podaac.jpl.nasa.gov/dataset/CMC0.2deg-CMC-L4-GLOB-v2.0)

(Chapter 3). For Chla values, we used measured SeaWiFS data when available and, when

not available, used a regression-derived estimate of SeaWiFS using a predictive equation to

estimate SeaWiFS Chla as a function of the available MODIS-Aqua data based on the set of

cells that had both sensor values (Nur et al. 2011; Chapter 3). We included two time-lagged

periods for three climate indices influential to the seasonal and inter-annual oceanographic

variability in the CCS (Chapter 3): Southern Oscillation Index (SOI, Trenberth 1984), North

Pacific Gyre Oscillation (NPGO, Di Lorenzo et al. 2008), and Pacific Decadal Oscillation (PDO,

Mantua and Hare 2002). Finally, we included additional spatial and temporal variables

related to seasonal and annual variability including year, month, Julian date, spring

transition date anomalies, and latitude. All predictor data were processed using methods

described in Chapter 3. We used bin mid-points and matching temporal period (where

appropriate) to extract predictor variable values for bathymetric and remotely sensed

oceanographic data, climate indices, and additional spatio-temporal data.

All bins and predictor variables from October 1997 through June 2012 were used in

model development. Using seabird counts per survey bin as the response variable, and

because of the larger count of zeros than expected from a Poisson-distributed variable

(Hilbe 2011), we built species-specific models using negative binomial regression (STATA

version 13.0, StataCorp 2013, Statistical Software, College Station, TX) following the six step

process developed in Chapter 3. We validated the fit of all final models using k-fold cross

validation (k=10, 10 runs each) based on the predictions to the 3 km bins from the seabird

survey data (Manugian et al. 2015; Chapter 3).

4.3.3   Future Seascape Scenarios

We developed two future seascape scenarios for the CCS based on a series of informed steps. First, we divided the study area into 10 regions using recognized latitudinal break points at which oceanographic processes change (Huyer et al. 2005; Hickey and Banas 2008; Venegas et al. 2008; Holt and Mantua 2009) and a nearshore or pelagic domain as calculated in Chapter 3 (Figure 4.1, right). Second, we searched for future projections for three dynamic variables (SST, SSH, and Chla) likely to be impacted by climate change and influential to seabirds abundance and distribution. For SST, we used ocean warming estimates from the Intergovernmental Panel on Climate Change Fifth Assessment Report (IPCC AR5). These estimates are the result of a new set of projected scenarios (Representation Concentration Pathways or RCPs) used in the most recent climate model simulations based on the Coupled Model Intercomparison Project Phase 5 (CMIP5) framework from the World Climate Research Programme (IPCC 2013). We used the IPCC's RCP2.6 and RCP8.5 scenarios to represent a "Low" or 0.6°C increase and a "High" or 2.0°C increase (IPCC 2013). We were unable to find future projections for either SSH or Chla, and instead assessed the current relationships between SST and SSH or Chla in each of the 10 regions. Finally, on a region-by-region basis and using the relationships identified, we predicted future SSH and Chla values while increasing SST by either 0.6°C or 2.0°C to build two future seascapes.

4.3.4   Model Predictions

We created a prediction grid spanning the spatial extent of the study area and matching the spatial resolution of the remotely sensed Chla data (~ 9.3 km x 7.3 km, latitude dependent). We populated the centroid of each grid cell (n = 29,644) with the static bathymetric related data, climate indices, and other spatio-temporal and effort data used in

model development (Table 4.1) for the three seascape scenarios (Current, Low, and High).
For the Current scenario we used the 15th of each month for Julian date and remotely
sensed data (SST, SSH, and Chla) were based on the 8-day average centered around that
date. For the two future seascape scenarios, we used the projections derived from
relationships between SST and SSH or Chla. Following the same seasonal approach as Nur et
al. (2011) and Chapter 3, we predicted species-specific abundances to each grid cell for May
(spring), July (summer), October (fall), and February (winter) in each year. On a cell-by-cell
basis for each seascape scenario we averaged the spatial occurrence predictions for each
species by month across all years (1997-2012) and standardized the mean predicted values
(mean = 0, standard deviation = 1) to ensure no single species outweighed another (Chapter
3).

4.3.5   Species Sensitivity to Change - An Index of Combined Effects

To investigate species sensitivity to change, we developed an Index of Combined
Effects (ICE) using the SST, SSH, and Chla model coefficients and their measured means for
each of the 30 final species-specific models. Because the SSH coefficients were much
larger/smaller than their SST and Chla counterparts and the mean SST value was at least an
order of magnitude larger than the other mean values, we used the formula below to
reduce the effect of the differences between mean values in the ICE index calculation.

$$ICE = (SST * \bar{X}_{SST}) + (SST^2 * \bar{X}_{SST}^2) + (SSH * \bar{X}_{SSH}) + (SSH^2 * \bar{X}_{SSH}^2)$$
$$+ (Chla * \bar{X}_{Chla}) + (Chla^2 * \bar{X}_{Chla}^2)$$

In this way, higher ICE values indicated species that are likely to be more sensitive to
changes in SST, SSH, and Chla. We divided the species into two groups: those with the
lowest ICE values (or the bottom 50%) and those with the highest ICE values (or the top

50%). The top 50% were split again into groups based on foraging type (e.g. divers or surface feeders) and whether or not they breed in the CCS.

4.3.6   Multispecies Hotspots Maps

We averaged the standardized predicted means for each ICE-based group by focal month (season) to identify areas of high habitat use (highest predicted values). To help visualize differences between months, we classified the data for each ICE grouping into percentiles (top 1, 2, 5, 10, 15, 20, 25, and >25) to create monthly maps for each seascape scenario.

4.3.7   Difference Maps

We created two sets of difference maps based on the Low and High seascape scenarios. For each ICE -based group, we subtracted the current scenario's average standardized predicted means from either the low (Low - Current) or high (High-Current) scenario's averaged standardized predicted means on a cell-by-cell basis. To help visualize and compare changes from one map to another, we classified the data using the same scale for all difference maps.

4.4   Results

We built models for 30 species for which body sizes, life histories, and ecological needs varied substantially (Table 4.2). Of the 21 variables, SST, SSH, and Chla were important predictors for 27, 20, and 18 species, respectively. Additional details on species-specific model results are discussed in Chapter 3.

Table 4.2. The 30 seabird species modeled in the California Current System, including their CCS breeding status, IUCN status, and current IUCN population trend (IUCN 2016).

Species Code	Common Name	Scientific Name	Breeds in CCS	When Likely to See in CCS?	IUCN Status	IUCN Pop Trend
BRAC*	Brandt's Cormorant	*Phalacrocorax penicillatus*	Yes	Year round	least concern	decreasing
BRPE*	Brown Pelican	*Pelecanus occidentalis*	Yes	Year round	least concern	increasing
CAAU*	Cassin's Auklet	*Ptychoramphus aleuticus*	Yes	Year round	near threatened	decreasing
CATE	Caspian Tern	*Hydroprogne caspia*	Yes	Year round	least concern	increasing
COMU*	Common Murre	*Uria aalge*	Yes	Year round	least concern	increasing
FTSP*	Fork-tailed Storm-petrel	*Hydrobates furcatus*	Yes	Year round	least concern	increasing
GWGU*	Glaucous-winged Gull	*Larus glaucescens*	Yes	Year round	least concern	increasing
LESP*	Leach's Storm-Petrel	*Hydrobates leucorhous*	Yes	Spring - Fall	least concern	stable
RHAU	Rhinoceros Auklet	*Cerorhinca monocerata*	Yes	Year round	least concern	decreasing
SCMU	Scripps's Murrelet	*Synthliboramphus scrippsi*	Yes	Spring - Summer	vulnerable	decreasing
TUPU	Tufted Puffin	*Fratercula cirrhata*	Yes	Year round	least concern	decreasing
WEGU*	Western Gull	*Larus occidentalis*	Yes	Year round	least concern	increasing
BFAL*	Black-footed Albatross	*Phoebastria nigripes*	No	Spring - Summer	near threatened	increasing
BLKI	Black-legged Kittiwake	*Rissa tridactyla*	No	Fall - Winter	least concern	decreasing
BOGU*	Bonaparte's Gull	*Larus philadelphia*	No	Fall - Winter	least concern	increasing
CAGU*	California Gull	*Larus californicus*	No	Fall - Spring	least concern	decreasing
HEEG*	Heermann's Gull	*Larus heermanni*	No	Summer - Winter	near threatened	increasing
HERG*	Herring Gull	*Larus smithsonianus*	No	Fall - Spring	least concern	decreasing
LAAL	Laysan Albatross	*Phoebastria immutabilis*	No	Fall - Winter	near threatened	stable
LTJA	Long-tailed Jaeger	*Stercorarius longicaudus*	No	Fall - Winter	least concern	stable
MEGU	Mew Gull	*Larus canus*	No	Fall - Spring	least concern	unknown
NOFU	Northern Fulmar	*Fulmarus glacialis*	No	Spring - Summer	least concern	increasing
PAJA	Parasitic Jaeger	*Stercorarius parasiticus*	No	Fall - Winter	least concern	stable
PALO	Pacific Loon	*Gavia pacifica*	No	Fall - Winter	least concern	increasing
PFSH	Pink-footed Shearwater	*Ardenna creatopus*	No	Spring - Summer	vulnerable	unknown
POJA	Pomarine Jaeger	*Stercorarius pomarinus*	No	Fall - Winter	least concern	stable
REPH	Red Phalarope	*Phalaropus fulicarius*	No	Fall, Spring	least concern	decreasing
RNPH*	Red-necked Phalarope	*Phalaropus lobatus*	No	Fall, Spring	least concern	decreasing
SAGU*	Sabine's Gull	*Xema sabini*	No	Summer - Fall	least concern	stable
SOSH*	Sooty Shearwater	*Ardenna grisea*	No	Spring - Summer	near threatened	decreasing

* Species modeled in Nur et al. (2011)

4.4.1   Relationships between SST and SSH or Chla

4.4.1.1   SST and SSH

We found a generally positive linear relationship between SST and SSH for all months in both the current (No SST increase) and high (2°C SST increase) scenarios (Figure 4.2). Offshore regions had consistently higher SSH with increasing SST than nearshore regions. For all months, the lowest SSH values present in the current scenario disappear in the high scenario (Figure 4.2). That is, the curves shift to the right and up in the high scenarios and, for July and October, these shifts resulted in the production of SSH values for some locations that were not observed in those locations in the current scenario (as shown by the dashed lines in Figure 4.2).

Figure 4.2. The relationship between SST and SSH in each of the 10 regions for the four focal months for the Current, No SST increase (left), and the High, 2°C SST increase (right), scenarios. Dashed lines were added to help visualize the production of new SSH values in the high scenario that were not present in the current scenario. Relationships for 0.6°C SST increase were intermediate and not shown.

4.4.1.2   SST and Chla

The relationship between SST and Chla was more complex than between SST and SSH for all months in both the current (No SST increase) and high (2°C SST increase) scenarios (Figure 4.3). In general, we found a polynomial relationship with an overall negative trend between SST and Chla, except for May, July, and October when there was a positive relationship up to about 10°C (refer to the dashed line in Figure 4.3). In the current May scenario, Chla increased with increasing SST below 10°C for all regions except offshore between Cape Blanco and Point Conception; for the high scenario, SST < 10°C were not predicted except for offshore north of Cape Flattery. In the current July and October scenarios, Chla increased with increasing SST below 10°C for most nearshore regions, but these increases disappear in the high scenario (Figure 4.3). When controlling for SST, the nearshore regions had consistently higher Chla than offshore areas and Chla decreased moving north and offshore (Figure 4.3).
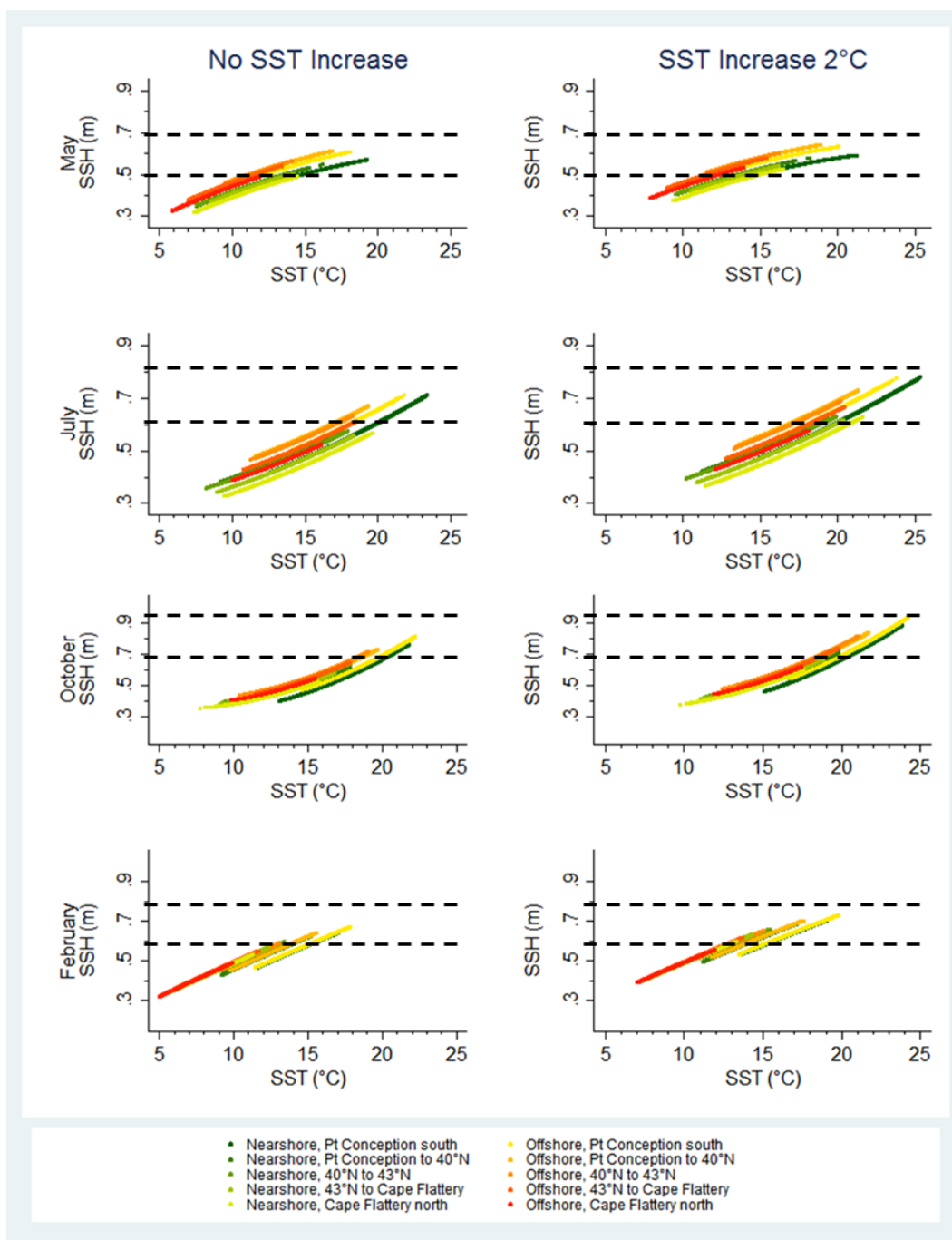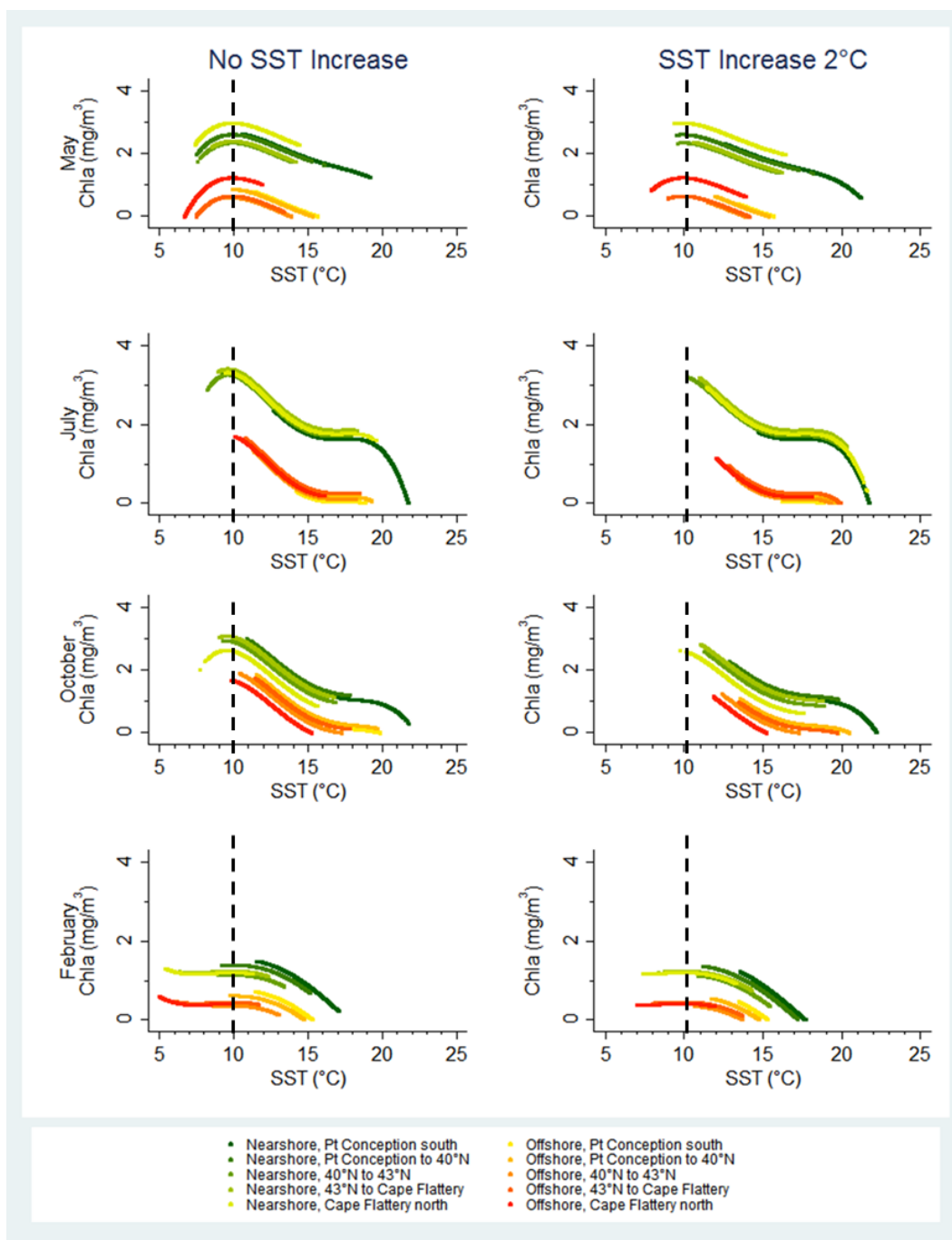
Figure 4.3. The relationship between SST and Chla in each of the 10 regions for the four focal months for the current, No SST increase (left), and the high, 2°C SST increase (right), scenarios. A dashed line was added to help visualize the Chla deflection point at 10°C. Relationships for 0.6°C SST increase were intermediate and not shown.

4.4.2   Index of Combined Effects

Based on the Index of Combined Effects (ICE), species sensitivity to changes in SST, SSH, and Chla ranged from -15.1 to 62.8, with a median value of 7.5, which was used as the breakpoint to divide species into groups that were estimated to be the most/least sensitive to changes in SST, SSH, and Chla (Tables 4.3 and 4.4). For species likely to be most affected by changes in these variables (Table 4.3), SST, SSH, and Chla were significant predictors for 14, 11, and 8 species, respectively. In addition, eight of the 15 species were year-round residents and breed in the CCS. After further splitting the top 50% into foraging types, all divers (n = 7, ICE_{mean} = 27.8) had a greater mean ICE value than surface feeders (n = 8, ICE_{mean} = 17.6) (Table 4.3). For species predicted to be least sensitive (n = 15, ICE_{mean} = 1.1), changes in SST, SSH, and Chla were significant predictors for 13, 8, and 10 species, respectively (Table 4.4). Additionally, 11 of the 15 species were migratory to the CCS and more than half (n = 8) were gulls.

4.4.3   Multispecies Hotspot Maps

Differences between the Current, Low, and High scenarios for the three ICE-based groupings were difficult to distinguish based on visual assessment of predicted abundance maps. Figures and results for these maps are presented in Appendix B.

Table 4.3. The estimated sensitivity of species calculated as an Index of Combined Effects (ICE) to increases in SST and related changes in SSH and Chla for the upper 50% of species modeled (diving foragers and surface feeders). Model coefficients may include linear and quadratic ($_Q$) terms.

Species	Model Coefficient Value						Model Coefficient Value * Mean Variable Value						ICE Value Sum
	SST	SST_Q	SSH	SSH_Q	Chla	$Chla_Q$	SST*14	SST_Q*14^2	SSH*0.5	$SSH_Q*0.5^2$	Chla*1.58	$Chla_Q*1.58^2$	
Species expected to be MOST sensitive to changing SST, SSH, and Chla													
Diving Feeders - Year-round resident, breeds in CCS													
CAAU	2.201	-0.052	58.522	-60.512	-0.077		30.809	-10.240	29.261	-15.128	-0.122		34.610
XAMU	3.151	-0.105					44.110	-20.610					23.501
TUPU			112.324	-133.124	0.227	-0.010			56.162	-33.281	0.359	-0.025	23.215
RHAU	2.414	-0.056	-2.306	4.364	0.071	-0.004	33.796	-10.902	-1.153	1.091	0.113	-0.010	22.934
Diving Feeders - Migrates to CCS													
PFSH	1.731	-0.051	143.766	-92.803			24.232	-10.048	71.883	-23.201			62.867
NOFU	1.989	-0.079	13.047	-21.447	0.239	-0.008	27.848	-15.387	6.524	-5.362	0.377	-0.020	13.980
PALO	2.664	-0.121	22.708	-45.352			37.303	-23.666	11.354	-11.338			13.653
												Divers ICE$_{mean}$	27.823
Surface Feeders - Year-round resident, breeds in CCS													
LESP	3.346	-0.068	35.203	-30.797	-0.342		46.840	-13.261	17.602	-7.699	-0.540		42.942
FTSP	2.566	-0.111	26.744	-22.907	0.181	-0.009	35.928	-21.821	13.372	-5.727	0.287	-0.023	22.015
CATE	0.853				1.237	-0.078	11.942				1.955	-0.194	13.702
BRPE	1.771	-0.046	-7.598				24.801	-8.920	-3.799				12.082
Surface Feeders - Migrates to CCS													
LTJA	1.312	-0.052	32.535	-31.819			18.362	-10.217	16.268	-7.955			16.458
CAGU	2.146	-0.086	8.642	-6.855	0.140	-0.006	30.048		4.321	-1.714	0.221	-0.015	16.050
PAJA	1.406	-0.051					19.690	-9.972					9.718
REPH	1.243	-0.055	8.858	-14.007			17.399	-10.761	4.429	-3.502			7.565
												Surface Feeders ICE$_{mean}$	17.565

Table 4.4. The estimated sensitivity of species calculated as an Index of Combined Effects (ICE) to increases in SST and related changes in SSH and Chla for the lower 50% of species modeled. Model coefficients may include linear and quadratic ($_Q$) terms.

Species	Model Coefficient Value						Model Coefficient Value * Mean Variable Value						ICE Value Sum
	SST	SST_Q	SSH	SSH_Q	Chla	$Chla_Q$	SST*14	SST_Q*14^2	SSH*0.5	$SSH_Q*0.5^2$	Chla*1.58	$Chla_Q*1.58^2$	
Species expected to be LEAST sensitive to changing SST, SSH, and Chla													
Year-round resident, breeds in CCS													
WEGU	0.463	-0.011	3.131	-6.451	0.106	-0.002	6.478	-2.100	1.565	-1.613	0.167	-0.005	4.492
COMU	0.465	-0.030			0.205	-0.004	6.512	-5.889	-0.762		0.323	-0.010	0.936
BRAC					0.312	-0.011					0.493	-0.027	0.466
GWGU	0.873	-0.071	-1.524		0.099	-0.003	12.222	-13.925	-13.371	5.669	0.156	-0.008	-2.317
Migrates to CCS													
HERG	0.369		13.473	-18.063	0.053		5.169						7.473
SOSH	0.368	-0.023	31.306	-41.930	0.192	-0.005	5.158	-4.517	15.653	-10.483	0.303	-0.013	6.102
RNPH	0.663	-0.034	11.018	-14.776			9.282	-6.668	5.509	-3.694			4.429
BFAL	0.801	-0.035					11.209	-6.923					4.286
POJA	0.571	-0.021					7.999	-4.047					3.952
SAGU	0.661	-0.030	-3.784		0.342	-0.010	9.259	-5.799	-1.892		0.541	-0.026	2.083
BLKI	0.659	-0.053	18.418	-25.338	0.272	-0.013	9.227	-10.468	9.209	-6.335	0.429	-0.032	2.031
HEEG	0.577		-26.742	22.676	0.666	-0.059	8.077		6.736	-4.516	1.053	-0.147	1.280
BOGU					0.299	-0.008					0.473	-0.019	0.454
LAAL	-0.329						-4.601						-4.601
MEGU	-1.813	0.052					-25.382	10.256					-15.126
											Bottom Spp ICE_{mean}		1.063

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4.4.4   Current Predicted Abundance and Difference Maps

4.4.4.1   Top 50% - Divers

For the Current scenario, predicted areas of suitable habitat for diving seabirds estimated to be the most sensitive to changes in SST, SSH, and Chla were primarily within the 200 m isobath for all months (Figure 4.4, left column). The area between Heceta Bank and the west coast of Vancouver Island was consistently in the 98th percentile for May, July, October. Other areas with suitable habitat occurred at Cape Blanco (May and July), near the Klamath/Eel River mouths (July), and west of San Francisco Bay and Monterey Bay (May and February). The area north of the Channel Islands and near Point Conception was also predicted to be suitable in May and February, and, for the latter month, extended west of the 200 m isobath.

Compared to the current scenario, our models predicted a decrease in suitable habitat within the 200 m isobath from Cape Mendocino to Cape Flattery for May, July, and October in both the Low (Figure 4.4, middle column) and High (Figure 4.4, right column) scenarios. This decrease was most pronounced around the mouth of the Columbia River on either side of the 200 m isobath in July and October. A decrease in suitable habitat was also predicted south of San Francisco Bay in May, October (High scenario only), and February. Suitable habitat was predicted to increase in a narrow band beyond the 200 m isobath in May, whereas increases for July and October were noted on both sides of the 200 m isobath between Heceta Bank and San Francisco Bay, Monterey Bay, and Big Sur. For all months our models predicted an increase in suitable habitat along the west coast and north of Vancouver Island as well as into the northern pelagic regions, especially for the High scenario.
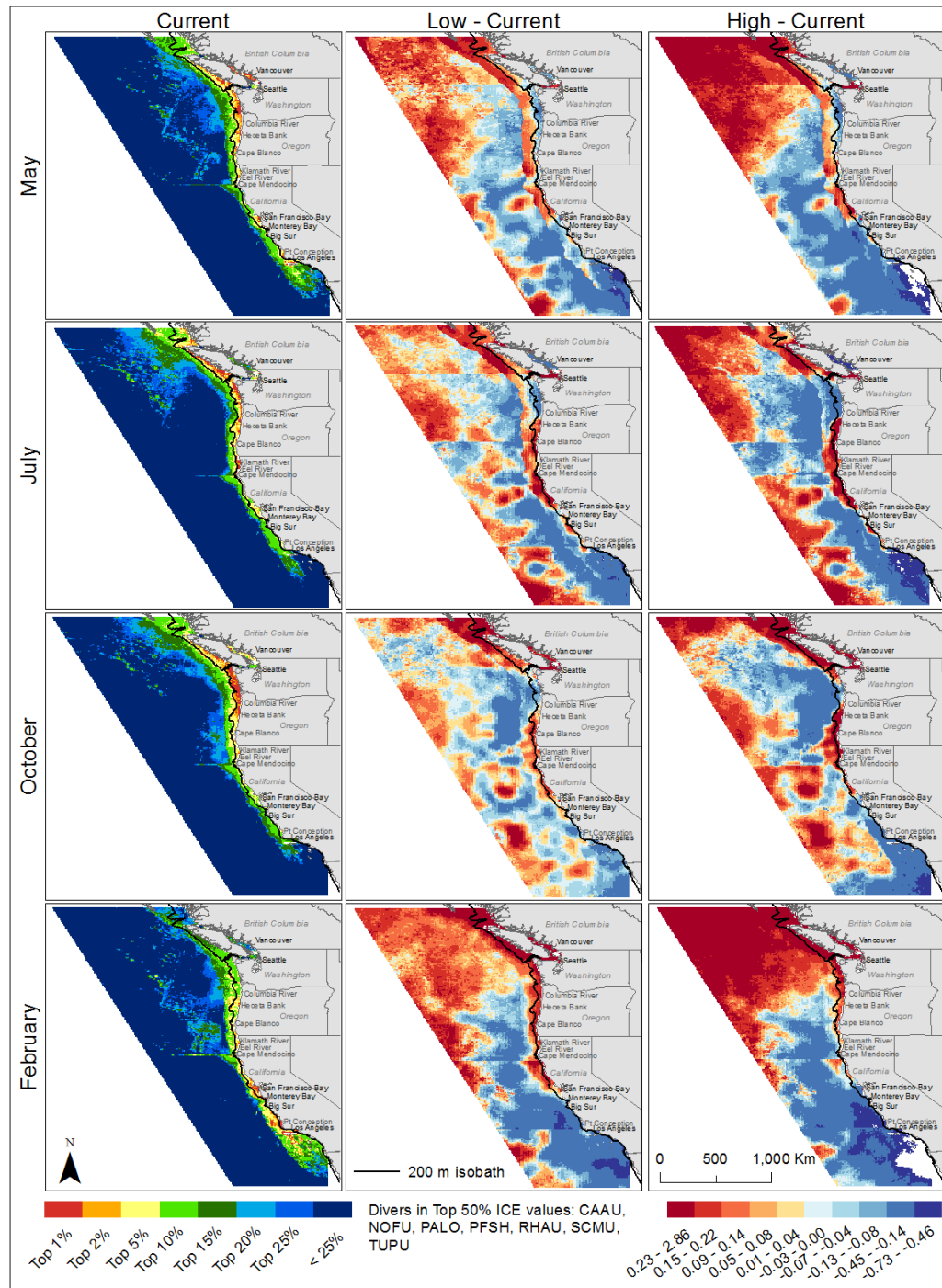
Figure 4.4. Predicted areas of suitable habitat for diving seabird foraging aggregations in the California Current System across seasons (left column). Difference maps between the Low and Current (middle column) and High and current (right column) scenarios showing locations of projected increases (red) and decreases (blue) of suitable habitat.

4.4.4.2   Top 50% - Surface Feeders

For the Current scenario, predicted areas of suitable habitat for surface feeders estimated to be more sensitive to changes in SST, SSH, and Chla varied among months and areas in the 98th percentile were observed primarily within the 200 m isobath (Figure 4.5, left column). Areas west of San Francisco Bay area and Monterey Bay were consistently in the 98th percentile for all months. Suitable habitat in the 98th percentile also occurred at the mouth of the Columbia River, Heceta Bank, and Cape Blanco for May, July, and October (around the Columbia River mouth only); between Cape Blanco and Cape Mendocino in July and February; and south of Point Conception (north of the Channel Islands) in February and May. Suitable habitat was also predicted at the Cobb Seamount (circled in pink).

Compared to the Current scenario, the increases/decreases in suitable habitat of our predicted models varied among months and between scenarios (Figure 4.5, Low, middle column, and High, right column). A decrease within the 200 m isobath, with some variation among months and scenarios, was predicted from Cape Blanco to Cape Flattery for all months, particularly around the Columbia River mouth. Decreases in suitable habitat were also predicted west of San Francisco Bay and Monterey Bay in October. Predicted increases in suitable habitat occurred in a band on either side of the 200 m isobath for most of the coast but not in the areas west and south of San Francisco Bay in February. For all months, but especially in the High scenario, our models predicted an increase in suitable habitat along the west coast and north of Vancouver Island as well as into the northern pelagic regions. Cobb Seamount remained or became more suitable for most months (circled in black).
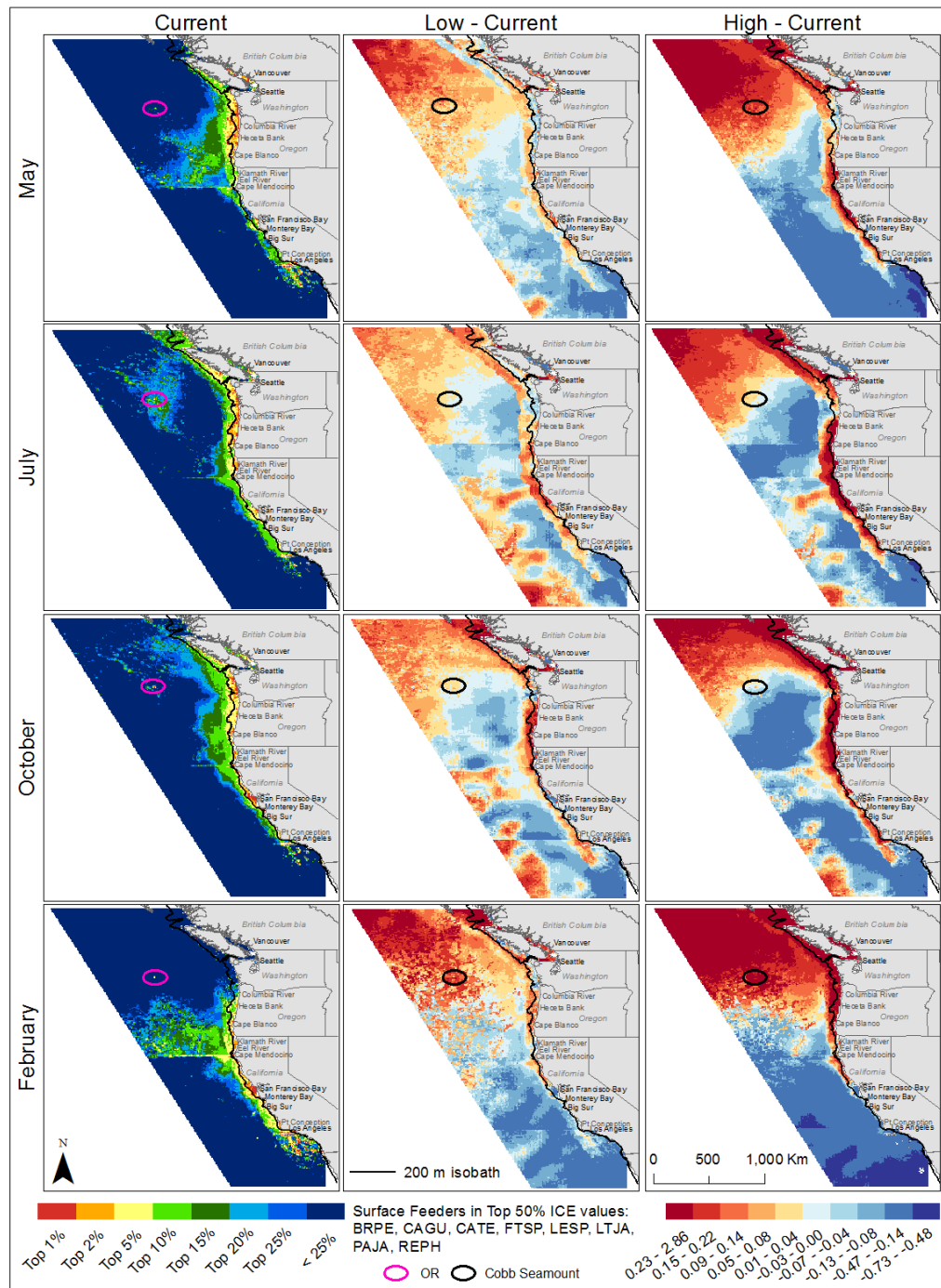
Figure 4.5. Predicted areas of suitable habitat for surface feeding seabird foraging aggregations in the California Current System across seasons (left column). Difference maps between the Low and Current (middle column) and High and current (right column) scenarios showing locations of projected increases (red) and decreases (blue) of suitable habitat.

4.4.4.3   Bottom 50% of Species

For the Current scenario, predicted areas of suitable habitat for species estimated to be the least sensitive to changes in SST, SSH, and Chla varied little among months and did not extend west of the 200 m isobath (Figure 4.6, left column). The area between Monterey Bay and Heceta Bank was consistently in the 98th percentile for all months. Suitable habitat areas in the 98th percentile were also observed north of Heceta Bank to Cape Flattery in May, October, and July as well as north of Point Conception in May.

Compared to the Current scenario, our models predicted a decrease in suitable habitat within the 200 m isobath along much of the coastal region for all months in both the Low (Figure 4.6, middle column) and High (Figure 4.6, right column) scenarios. This decrease was most pronounced in May and July during which coastal areas at San Francisco Bay, Monterey Bay, and north of Cape Mendocino become less suitable. In these areas, an increase in suitable habitat was predicted in an almost continuous narrow band west of the 200 m isobath for May and July. A similar increase in suitable habitat west of the 200 m isobath was predicted in October and February, though it was not continuous and absent in February south of San Francisco Bay. For all months in both scenarios our models predicted an increase of suitable habitat west and north of Vancouver Island.
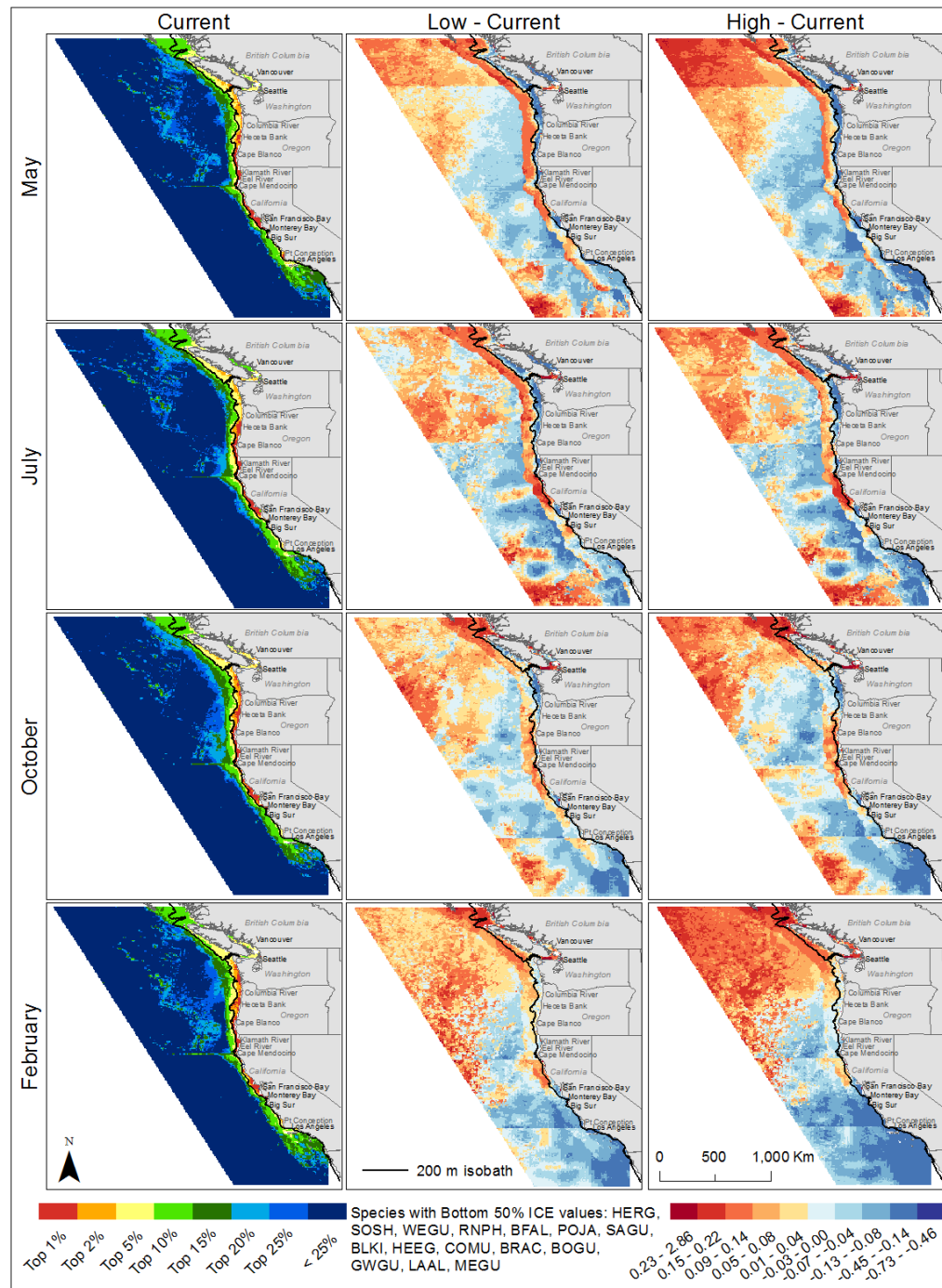
Figure 4.6. Predicted areas of suitable habitat for the lower 50% seabird foraging aggregations in the California Current System across seasons (left column). Difference maps between the Low and Current (middle column) and High and current (right column) scenarios showing locations of projected increases (red) and decreases (blue) of suitable habitat.

4.5   Discussion

Our results suggest that seabird foraging aggregations in the California Current System will shift offshore and north as suitable habitat locations decrease within the 200 m isobath due to climate change. Although we predicted all modeled species would be affected, we estimated that diving foragers and surface feeders, particularly those that are year-round residents and breed in the CCS, will be the most sensitive to a changing climate. In addition, some offshore seamounts may retain suitable habitat for some seabirds, particularly migratory surface feeders.

4.5.1   <u>Offshore and Northward Shift of Hotspots</u>

The occurrence of upwelling and its subsequent impacts on the marine food web are clearly important components of suitable foraging habitat for seabirds. Despite the lack of inclusion of any wind-related variable in our models, our results appear to capture the spatial patterns of where upwelling is likely to occur in the CCS and generally corroborate mechanistic models focused on how climate change may affect upwelling in eastern boundary current systems (EBCS). The decline of suitable habitat over the continental shelf in our projections is consistent with the hypothesis that upwelling-favorable winds will intensify, particularly at higher latitudes, in EBCS in a warming world (Bakun 1990; Sydeman et al. 2014). Increased upwelling may initially appear to counteract the effects of habitat warming in these regions; however, the strength of offshore advection could push nutrients and primary productivity beyond the continental shelf, shift upwelling intensity offshore, and disrupt the nearshore trophic interactions upon which seabirds and other organisms rely (Bakun and Weeks 2004; Sydeman et al. 2014; Bakun et al. 2015).

In addition, our projections suggest a northward shift of suitable habitat as well as a decrease in suitable habitat in the southern CCS. This is consistent with recent studies by

Rykaczewski et al. (2015) who predict that upwelling-favorable winds near the poleward boundaries of EBCS will intensify while winds nearer to the equator will weaken with climate change. The reduction of upwelling from weakening of winds causes additional warming, a deepening of the thermocline, and nutrient-depleted water (Oedekoven et al. 2001). Specifically in the CCS, Rykaczewski et al. (2015) showed a general lack of upwelling intensification during the summer months from Cape Mendocino south, except for a portion between Cape Blanco and Point Conception in the spring that had increased upwelling. Shifts in the timing or location of upwelling could lead to spatio-temporal mismatches between nutrient availability necessary for lower-trophic level productivity and the subsequent prey concentrations needed to maintain stages of seabird life history such as breeding (Sydeman et al. 2105)

4.5.2   Species

Although our models predicted that all species would be sensitive to changes in SST, SSH, and Chla, we estimate diving foragers and surface feeders will be the most affected by climate-related changes. Overall, our difference maps showed projected decreases in suitable habitat for diving foragers and projected increases in suitable habitat for surface feeders in the CCS with climate change. A decrease in suitable habitat for diving foragers may be the result of a reduction in prey and/or from prey becoming inaccessible. Ocean warming, for example, increases thermal stratification and reduces the amount of nutrients upwelled to the euphotic zone, ocean productivity, and prey resources (Oedokoven et al. 2001; García-Reyes et al. 2015). Moreover, because the thermocline is deeper, any prey within the euphotic zone could be beyond the diving limits of these species (e.g. 40 m for Cassin's auklets, Burger and Powell 1990 and 60 m for rhinoceros auklets, Burger et al. 1993). Conversely, the projected increase in suitable habitat for surface feeders may reflect their ability to exploit wider prey types across a variety of habitats. This is consistent with other North Pacific studies that show diving species prefer areas with cool ocean

temperatures, high productivity, and dense prey patches necessary to support their high energetic requirements, while warmer lower productive areas are dominated by surface feeders who can exploit more patchily distributed prey (Hyrenbach and Veit 2003).

We also found that species who are year-round residents and breed in the CCS would be more sensitive to changes in SST, SSH, and Chla than migratory species. Seabird colonies are frequently located near areas with reliably high productivity in order to sustain the large energetic requirements of breeding and chick provisioning. A change in timing or location of upwelling induced productivity would reduce nesting success. Wolf et al. (2010), for example, projected an 11-45% population decline in the Farallon Island Cassin's auklet population due to climate change by the end of the century. Conversely, for migrating species their presence in the CCS coincides with upwelling. The migration of shearwaters, for example, is timed to take advantage of highly productive upwelling periods in both the northern and southern hemispheres (Shaffer et al. 2006). Nevertheless, shifts in suitable habitat caused by warming oceans and changes in the timing of upwelling are likely to lead to changes in the distribution and migratory routes of these species (Oedekoven et al. 2001; King et al. 2011).

4.5.3 Seamounts

Our results suggest some seamounts, e.g. Cobb Seamount, may retain suitable habitat for species like surface feeders even under warming conditions. Seamounts attract both a high abundance and a diverse array of large predators due to high productivity resulting from upwelled nutrients around them (Pitcher et al. 2007; Wessel 2007; White et al. 2007; Thompson 2007; Morato et al. 2010). Although not all seamounts have high productivity, those whose summits reach within the 200 m euphotic zone, such as Cobb Seamount, can have relatively persistent productivity (Dower et al. 1992; Genin and Dower 2007) and may provide reasonably reliable foraging areas to seabirds. Although it remains

unclear how Cobb Seamount might be impacted by climate change, there is some evidence that productivity may increase in pelagic regions of the Pacific Ocean in the future (Cheung et al. 2010), and could benefit species like seabirds.

4.5.4   Caveats

Often used to predict relationships between variables, models are representations of reality and it is prudent to remember this in studies such as ours. This chapter was based upon species distribution models developed in Chapter 2 that rely on statistical correlations between species and static (e.g. average depth, distances to isobaths) as well as dynamic (e.g. SST, SSH, and Chla) environmental factors. The relationships among SST, SSH and Chla may not be stationary, and may change in the future. Identifying the causal relationships between multispecies seabird foraging aggregations, chlorophyll, and upwelling in a particular location, for example, will require process based or mechanistic models. In addition, the climate envelope modeling approach used here simply shifts variables to future conditions according to current relationships. It does not consider adaptation, plasticity, or intra/inter species-specific interactions, and it presumes that seabirds will respond over time according to the ways they respond today to spatial variation in environmental factors. However, climate-related changes are leading to unprecedented oceanographic conditions and the responses of seabirds to these changes are likely to be novel and difficult to predict.

Despite these limitations, only few studies to our knowledge investigate future climate-related changes in at-sea distributions of seabirds. Recent studies (e.g., Péron et al. 2012; Hazen et al. 2013) rely on satellite data from a few individuals to gain a better understanding of how a population may respond to future conditions. Yet, long-term ship surveys, as used in this study, are important tools to investigate changes in species distributions (range contractions or expansions) by capturing information on species that

are inaccessible on land and on nonbreeding portions of populations (Ballance 2007; Péron et al. 2010). Analyses of long-term ship-based surveys, such as the present study, will complement understanding of climate change impacts on demographic parameters and population sizes obtained from land-based monitoring programs. Together these types of studies will be critical to understand the effect of climate change on seabirds.

4.5.5   Management Implications

Our mapped results have several important implications for federally designated national marine sanctuaries (NMS) (Figure 4.7). First, the most southern sanctuary, the Channel Islands NMS, may become less suitable for seabirds as climate change progresses. Habitat suitability for seabirds also may decline in the Monterey Bay NMS, although it appears to retain some suitable habitat for surface feeders. Second, several NMS appear to be resilient to climate-related changes and will continue to be important habitat for all seabirds, including locations west and north of San Francisco Bay (Greater Farallones and Cordell Bank). The Olympic Coast NMS (west of Cape Flattery and denoted as CF in Figure 4.7) is projected to also retain suitable habitat, especially for surface feeders. Finally, there are at least three unprotected regions that may become suitable habitat in the future; these include the area between Point Conception and Big Sur, Cape Mendocino and Heceta Bank, and the west coast of Vancouver Island.

The inherent uncertainty associated with how ecosystems and species will respond to novel oceanographic conditions from climate-related changes makes projecting into the future especially tricky. Despite limitations, this study provides an important first step in elucidating the magnitude, direction, and potential mechanisms underlying projected changes in seabird habitat in the California Current System. This study can also help to identify species or groups of species at risk and prioritize management decisions. With continually limited resources available for conservation actions and management decisions,
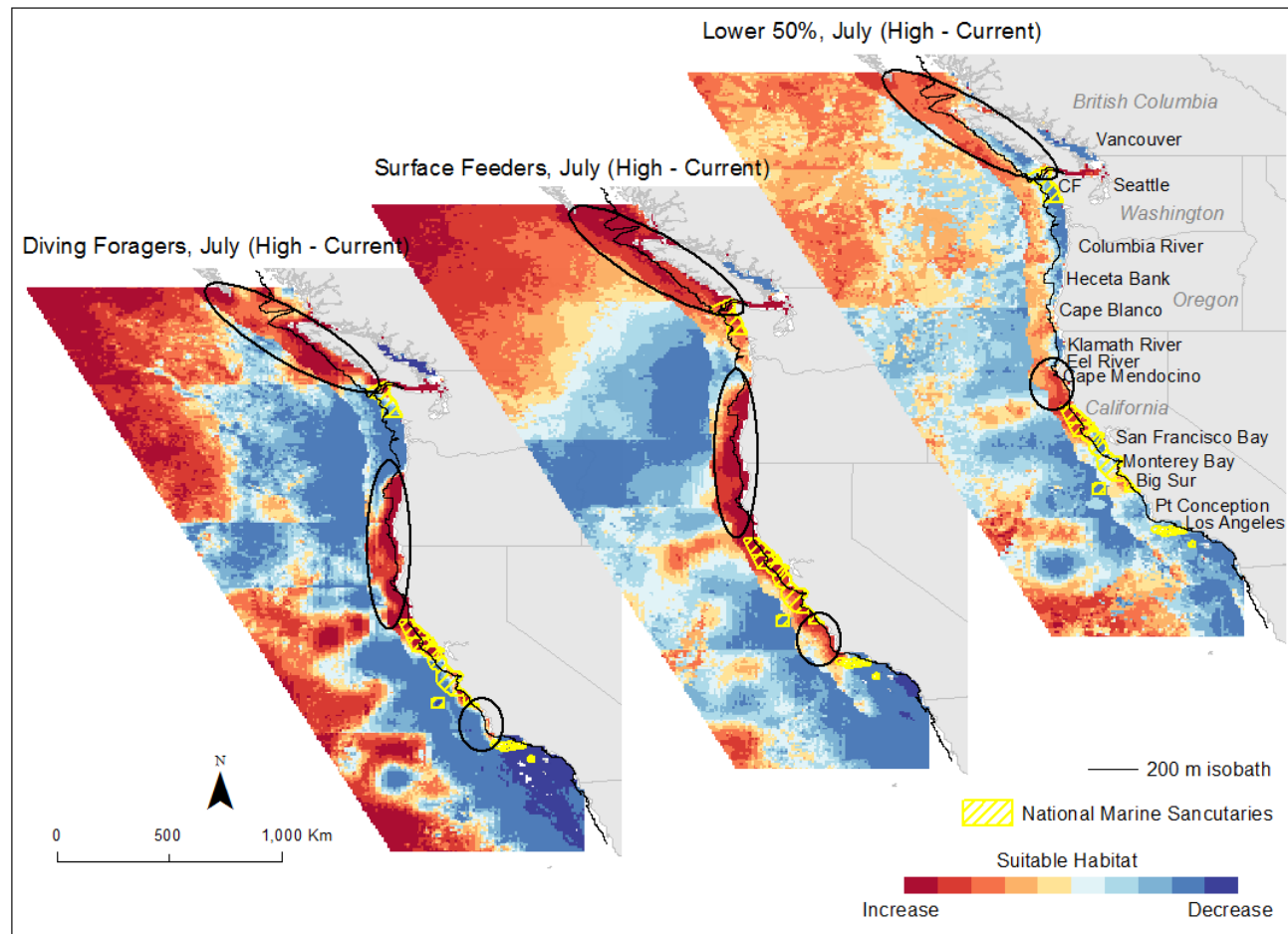
Figure 4.7. Example locations with projected increases and decreases of suitable habitat for seabirds in the California Current System compared to current National Marine Sanctuary boundaries.

multispecies studies such as this can help to prioritize ecosystem based marine spatial planning decisions including marine protected area placement.

4.6   Conclusions

This study provides an important first step in elucidating the magnitude, direction, and potential mechanisms underlying future changes in suitable seabird foraging habitat in the California Current System. Results suggest three key findings: (1) suitable foraging habitat will shift offshore and north; (2) diving and surface feeders, particularly those who are residents and breed in the CCS, will be the most sensitive to a changing climate; and (3) some seamounts may retain suitable habitat in the future. Our projected results also suggest some federally designated national marine sanctuaries will become less suitable (Channel Islands) while others will continue to provide suitable habitat in the future (Greater Farallones and Cordell Bank) for seabirds. At least three unprotected regions may become suitable habitat in the future. Given the recognized issues with climate envelope models and the uncertainty associated with how ecosystems and species will respond to climate change, future research should couple species distribution models with regional ocean models developed for the CCS to better capture upwelling and other oceanographic processes important to seabird foraging habitat.

4.7   Acknowledgements

4.8   Literature Cited

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5   Conclusions

As a way to maintain productive and resilient oceans, ecosystem-based management approaches that incorporate marine spatial planning (MSP) have gained traction in marine management and policy. To be effective, MSP requires sound scientific information to identify the spatial distribution of ocean activities to maintain existing and emerging uses, reduce use conflicts, and protect and maintain ecosystem health and services for future generations (Foley et al. 2010). MSP incorporates place-based protection through the creation of marine protected areas (MPAs) which are used to enhance conservation of marine resources through varying levels of protection from exploitive and extractive activities (Norse and Crowder 2005). Although the benefits of such protective measures are now well recognized, MPAs remain challenging to design and implement in such a large, fluid and dynamic environment. Targeting areas of ocean that are ecologically significant to marine megafauna (top predators) is one technique for MPA designation. By treating top predators as ecological indicators, this approach assumes two things: (1) the ocean areas most important for the survival of these species can be used to delineate MPA boundaries that will safeguard the marine environment and other species dependent on that area; and (2) the subsequently established MPA(s) will benefit the marine megafauna (Hyrenbach et al.2000, Hooker et al. 2004; Ronconi et al. 2012).

The marine spatial planning process requires spatially explicit information resulting in the development of map products used in planning and decision making. The crux of the mapping process is georeferenced species occurrence data. The research presented here explored and analyzed spatially explicit marine megafauna data to inform the marine spatial planning process and to help in the design of MPAs in the North Pacific. Chapter 2 focused on the development of computational ArcGIS tools to explore, analyze, and visualize spatially explicit individual-based records from North Pacific humpback whale photo-identification and genetic data. Unlike most occurrence data, this presence-only dataset is

enriched by the addition of genetic information enabling mangers to factor in population structure and genetic diversity, and thus maximize species resilience, when designing MPAs. Chapters 3 and 4 used 15 years of at-sea survey data to predict seabird hotspots in the California Current System now and under two future seascape scenarios. Key to both components is an improved understanding of what factors influence the presence of a species and/or its genetic variability to enable present day planning and design of MPA networks to ensure adequate protection will be in place now and as climate change progresses. This information can also be used to inform policy decisions by adapting strategies to reduce non-climate stressors such as fishery pressures and coastal development in areas predicted to be important to marine species in the future.

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7   APPENDICES

APPENDIX A: AT-SEA SURVEY COVERAGE BY YEAR AND RESEARCH PROGRAM.

Table A1. Survey coverage by year including number of bins used in the current analysis.

Year	Number of Bins	Percent
1997	393	0.5
1998	4373	5.8
1999	2876	3.9
2000	3982	5.3
2001	8224	10.9
2002	5074	6.7
2003	5869	7.8
2004	5282	7.0
2005	11448	15.1
2006	7657	10.1
2007	3978	5.3
2008	12275	16.2
2009	2004	2.6
2010	1234	1.6
2011	321	0.4
2012	662	0.9
Total	75652	100.0

Table A2. Survey coverage by research monitoring program.

Name	Principal Investigator(s)	Affiliation	Years Available	# of Bins Included
CalCOFI	Jaime Jahncke	Scripps Institution of Oceanography; Point Blue	1997-2007	25,018
CCES	Jen Zamon, Jaime Jahncke	Northwest Fisheries Science Center; Point Blue	2008	3,437
C-SCAPE, ORCAWALE	Lisa Ballance	Southwest Fisheries Science Center	2001, 2005, 2008	15,042
Line P, WCVI, CPR, EGOA, QCI, BS, HE, AT, PGC	Ken Morgan	Canadian Wildlife Service, Environment Canada	1997-2010	11,325
NMFS Rockfish	Bill Sydeman		1998-2009	8,737
NMFS Sardine	Lisa Balance, Bill Sydeman	Southwest Fisheries Science Center	2006	1,504
GLOBEC	David Ainley	H.T. Harvey and Associates	2000, 2002	1,856
Ocean Salmon Ecology, S. Resident Killer Whale, ships-of-opportunity	Jeannette Zamon	Northwest Fisheries Science Center	2003-2012	8,733

APPENDIX B: MULTISPECIES HOTSPOT MAPS USING PROJECTED ABUNDANCES FOR CURRENT, LOW, AND HIGH SEASCAPE SCENARIOS.
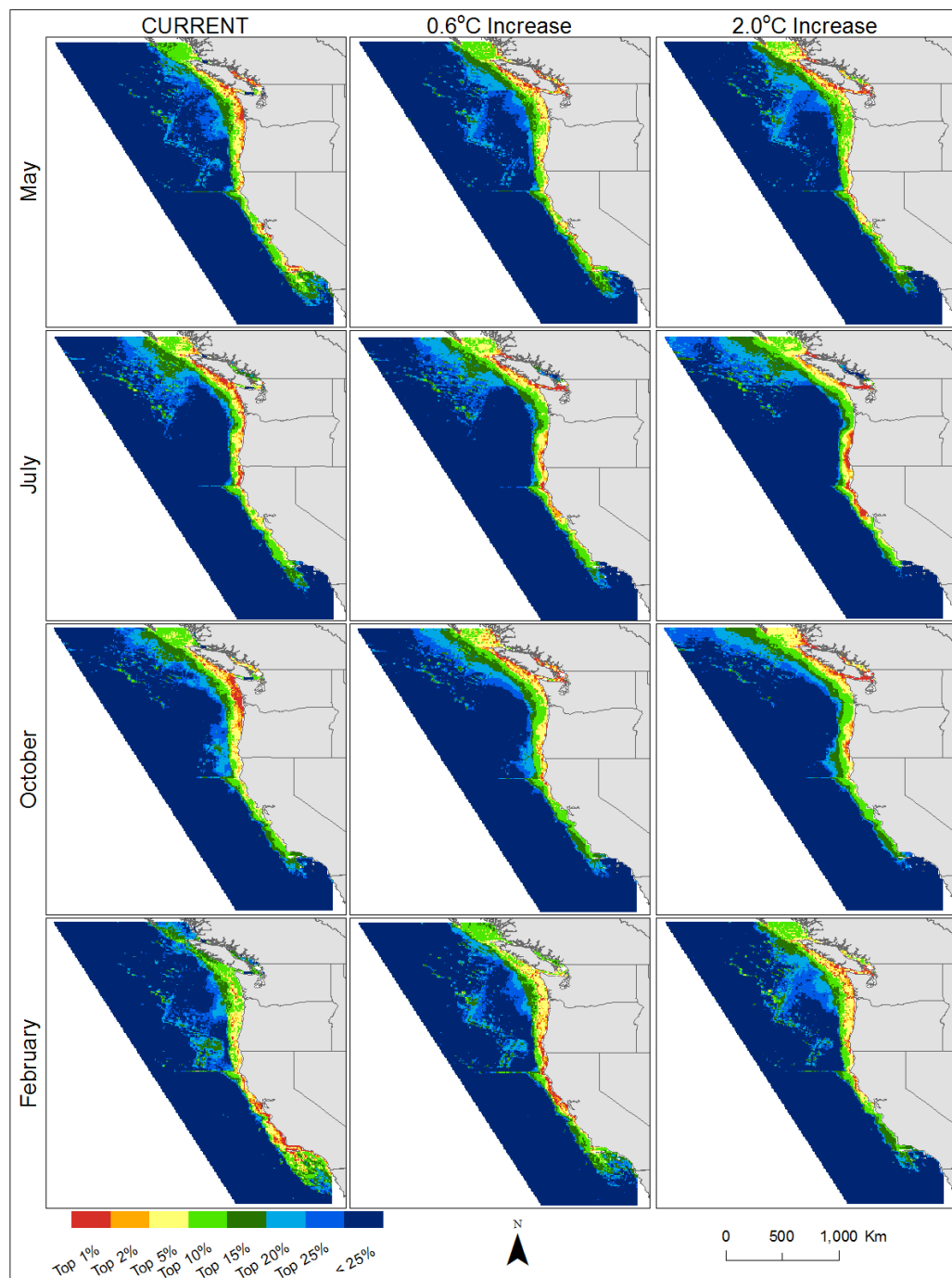

Figure A1. The averaged predicted standardized abundances for the diving seabird species (n = 7) within the top 50% ICE value group.
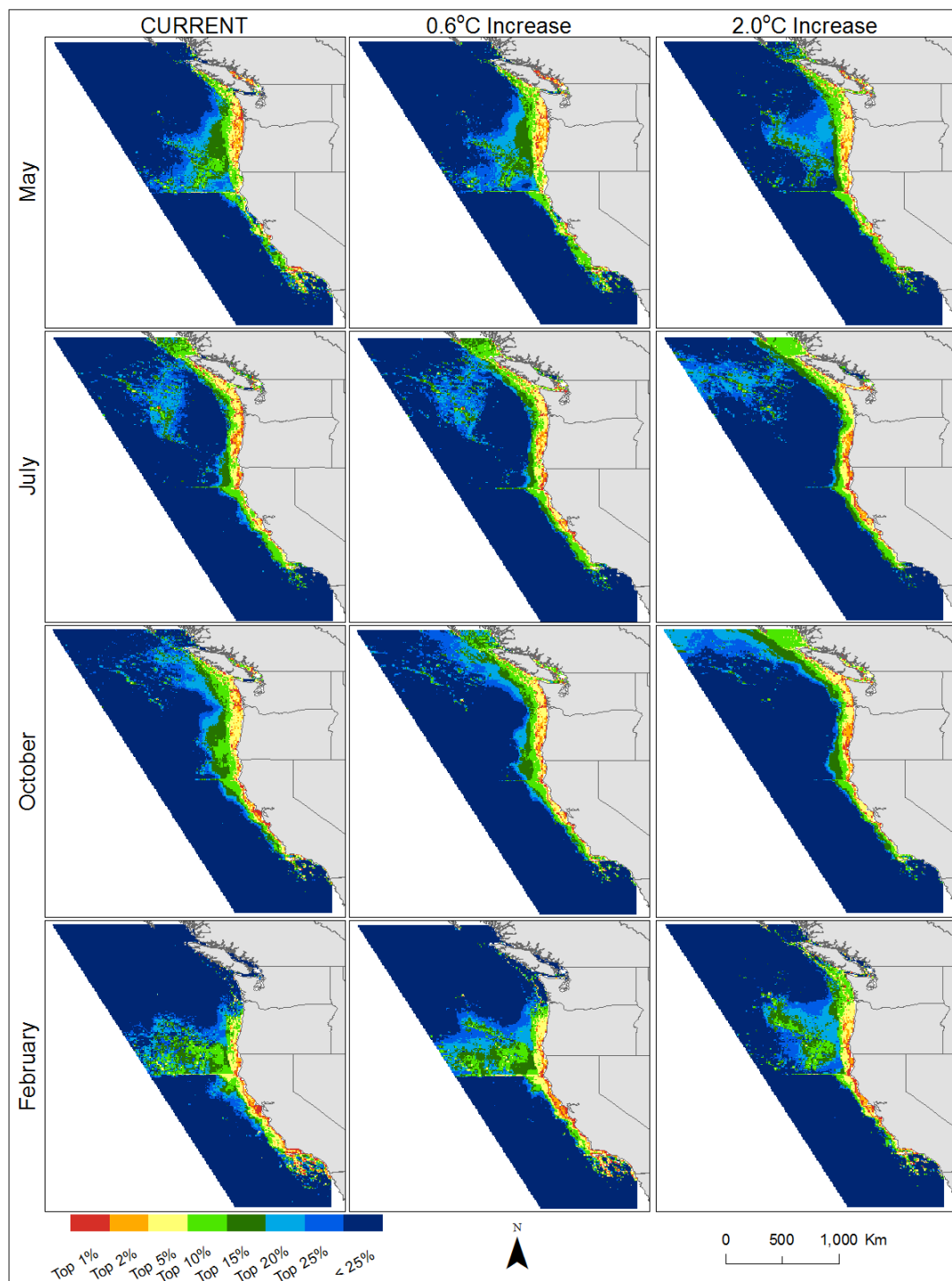
Figure A2. The averaged predicted standardized abundances for the surface feeding seabird species (n = 8) within the top 50% ICE value group.
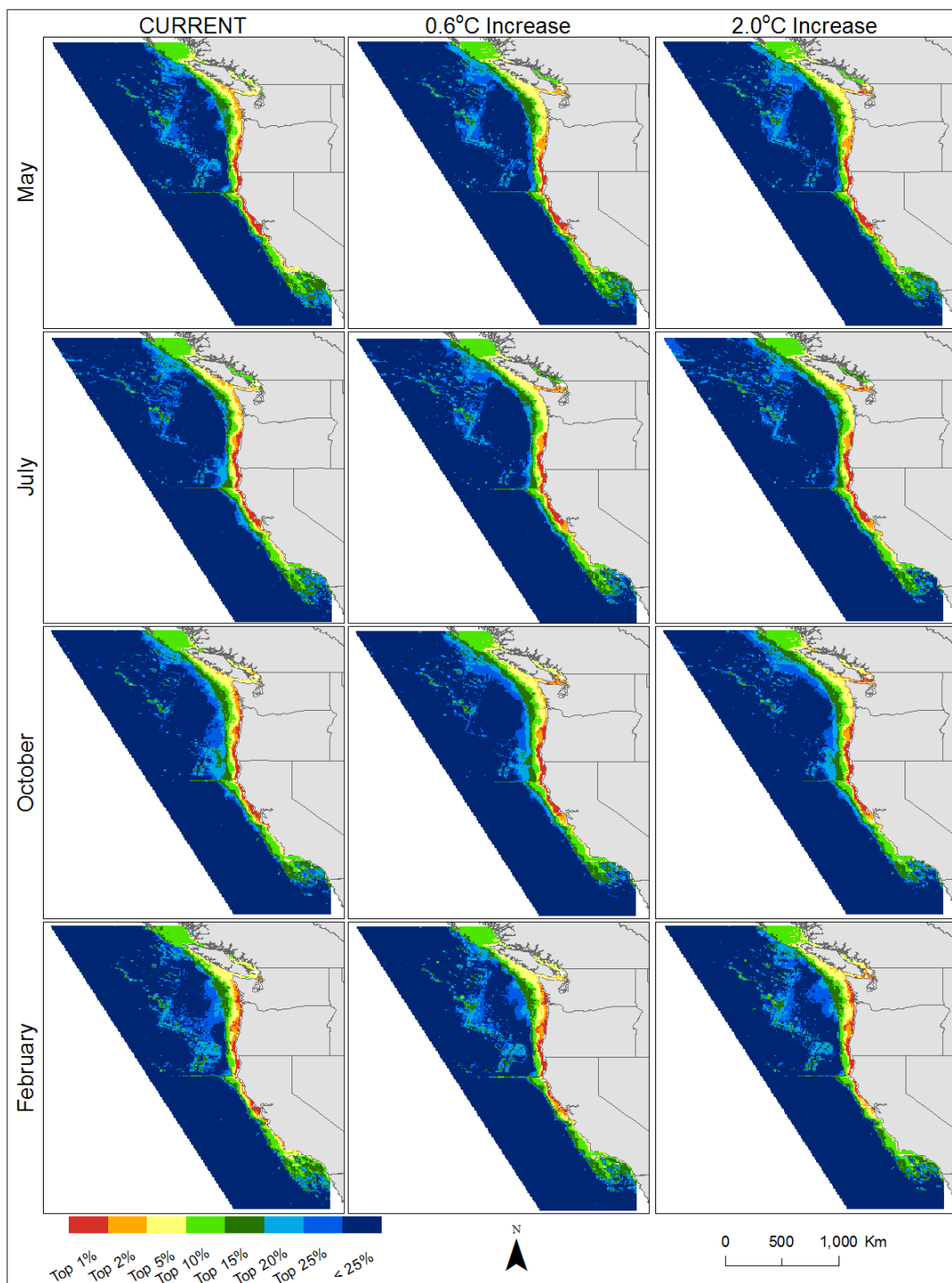
Figure A3. The averaged predicted standardized abundances for the 15 seabird species within the bottom 50% ICE value group.