RESEARCH PLAN

A. Project Title : BSIERP Patch Dynamics Study

B. Proposal Summary

Patches are formally defined as significant spatial variations in oceanic biomass, but are more broadly recognized to reflect significant spatial variation in any feature of prey that is important for exploitation of the resource by the predator. Prey patches may occur at scales of less than 1 m to several kilometers with persistence times of minutes to months. They are also known to vary in species composition, biomass, energy content of prey, and distribution (size of patch, density within a patch, density of patches, and distance from colony/rookery). However, it is not yet known how apex predators respond to variability in prey patches (patch dynamics) and the consequence it has on population dynamics of top-predators in the Bering Sea. Such fundamental information is needed to predict how the Bering Sea ecosystem will respond to global warming.

The goal of our study is to undertake a coordinated fine-scale study of birds and mammals, and their forage base to determine the consequences of spatial patterns (patches) on predator-prey dynamics. We will thereby establish mechanisms that control the abundance and distributions of top predators in the Bering Sea, and provide models with data to predict how and why these species respond to changes in the physical and biological environment.

Concurrent fine-scale field studies will be undertaken during 2008 and 2009 in two geographic areas of the Eastern Bering Sea (St. Lawrence Island from March – May, and at the Pribilof Islands during July and August). The Pribilof Islands region includes a comparison between seabirds and fur seals at St. Paul and St. George islands as part of the large-scale BSIERP research component. Seabirds (thick-billed murres and black-legged kittiwakes) and marine mammals (northern fur seals and Pacific walrus) will be tracked at sea to determine where, when, and how they capture prey. Forage species will be sampled from vessels using nets, bottom grabs, and hydro-acoustics to describe the patches (quality and quantity) and their relationship with physical oceanography. Relative densities of prey patches and foraging success of birds and mammals will be related to regional and interannual differences in population processes. Specifically, we will examine (*i*) how changes in patch dynamics influence diets (species composition and energy content), and (*ii*) how diets affect the nutritional status of individuals, which in turn determines population dynamics (reproductive success and population trends).

This integrated, fine-scale approach that we propose for studying patch dynamics has not been previously undertaken. It will provide needed data to determine how groups of species are controlled by fishing, predators, food availability, the physical environment, or a combination of all four. It will further assist in parameterizing and validating single-species and ecosystem-based models (to be constructed by BSIERP) to predict the effects of global warming on the Bering Sea.

C. **Project Responsiveness**

Biologists generally recognize that ecosystems are affected by both bottom-up and top-down processes, but disagree about the relative importance of each (Stenseth *et al.* 2002). In the Bering Sea, this disagreement manifests itself through the lack of consensus over the relative importance of five controlling mechanisms thought to underlie the linkage between climate and predator-prey interactions:

M1: *Physical environment (climate)* determines where species live (based on their physiological adaptations to water temperatures, salinities, depths, etc.) and influences the transport of nutrients (including phosphate, nitrate, and iron) to the surface that lead to the large blooms of ice algae and phytoplankton that ultimately fall to the ocean floor. The nutrient supply is determined by the degree of upwelling and mixing. Global warming may drive the pelagic and benthic systems towards greater stability, and will likely impact organic matter deposition on the ocean floor (Grebmeier *et al.* 2006a; Grebmeier and Barry 2007a);

M2: *Match-mismatch* between food requirements and food supply affects growth, survival and recruitment. The degree of spatial and temporal overlap between animals and their prey is believed to be particularly important in the early life stages. Significant temporal mismatch may be compensated for by high abundance of prey (Cushing 1980; 1990; Wassmann 1998); Global warming may lead to increased mismatch of predator-prey productivity cycles.

M3: *Foraging arenas* are spatial patches where predation occurs, and where prey must accept predation risk in order to forage. Predation rates under some circumstances may be limited by prey foraging time and refuge occupancy rates rather than by predator satiation. Fishing can reduce the number of adults and release one or more smaller forage species to increase in abundance, which in turn can increase predation of the predator's juvenile life stage (Walters and Juanes 1993; Linehan *et al.* 2001; Walters and Kitchell 2001; Martell *et al.* 2005);

M4: *Bioenergetic constraints* recognize that seasonal and inter-species differences in lipid and energy content of prey, combined with physiological limitations associated with finding, capturing, and digesting prey affects growth and recruitment of all predators. Such limitations can be further compounded by changes in water temperature (that can increase metabolism and food requirements, and affect relative abundance of different prey species that have different energetic content—Hooff and Peterson 2006), or by changes in prey distribution that increase the time and energy predators spend foraging. (Dörner and Wagner 2003; Trites and Donnelly 2003; Litzow *et al.* 2004; Rosen and Trites 2005; Litzow *et al.* 2006; Rosen *et al.* 2007); and

M5: *Competition* between predators (such as large flatfish, pinnipeds, seabirds, and people) that consume similar diets or consume different prey with similar diets can directly and indirectly affect each other's dynamics by altering food web energy flow. (Trites *et al.* 1997; Bystroem *et al.* 1998; Guénette *et al.* 2006).

The relative importance of these five mechanisms (M1-M5) likely depends upon the patchiness of prey. In the narrowest sense, patches are defined as *significant* spatial variations in oceanic biomass (Downes 1990). However, the broader definition we embrace considers patches to include significant spatial or temporal variation in any feature of prey that is important (from the perspective of the predator) for their exploitation. This includes species composition, quality of prey (energy content), and distribution (density within a patch, density of patches, distance from colony/rookery). Patches can occur at spatial scales of less than 1 m (Davis *et al.* 1991) to several kilometers (Mackas *et al.* 1985) and with persistence times of minutes to months (Cushing 1961). Temporal change in the consequences of spatial patterns (e.g., predator-prey interactions) is termed patch dynamics. Patches and patch dynamics (i.e., the development and maintenance of spatial and temporal patterns and the consequences of those patterns for the dynamics of populations and ecosystems) are fundamental themes in ecology (Levin 1992).

Previous ecological research has been unable to test the fundamental hypotheses regarding what controls the Bering Sea ecosystem, or reconcile the control mechanisms that explain variation over the past half-century in the abundance and distribution of important species in Alaska. Nor has large-scale monitoring of bird, mammal, and forage abundances provided a means to assess the combined ecosystem effects of resource harvests and climate change — or predict the consequences of change for Alaska's fishing industry and coastal communities. We will thus undertake concurrent patch dynamic studies on birds, mammals, fish, and invertebrates in two contrasting geographic areas (southeastern Bering Sea—Pribilof Islands; and northern Bering Sea—St. Lawrence Island) to address these pieces of missing knowledge. These fine-scale study sites will be integrated with the broad-scale surveys and results of the BSIERP project.

D. <u>Soundness of Project Design and Conceptual Approach</u>.

The primary goal of our study is to undertake coordinated fine-scale studies of birds, mammals, fish, bivalves, and zooplankton to establish mechanisms (M1-M5) that control their abundances and distributions, and provide models with data to predict the dynamics of the eastern Bering Sea.

Our research involves field studies on a finer temporal and spatial scale than has previously been considered by other research programs. Our work is designed to complement the larger-scale studies being conducted by NMFS and BSIERP by filling in many missing pieces of information required to accurately predict the range of possible effects that climate change will have on the Bering Sea and the people that depend upon it for their livelihoods.

Marine mammals and seabirds—as upper trophic level predators—are expected to be heavily affected by changes in ocean climate (Kelly 2001; Learmonth *et al.* 2006). However, projecting how their numbers and distributions might change over time is not yet possible due to uncertainties in the relative importance of the five controlling mechanisms (M1-M5) thought to drive bottom-up and top-down control of bird and mammal populations. These mechanisms need to be quantified to properly parameterize models that will predict the range of possible future distributions and abundances of upper trophic level organisms under various climate scenarios. The mechanisms must also be described for fish, cephalopods, benthic invertebrates, and zooplankton to properly quantify the models that will predict how the Bering Sea ecosystem will respond to climate change.

Field studies will be undertaken in two regions of the Bering Sea. Seabird, marine mammal, fish, and zooplankton data will be collected in the southeastern Bering Sea (Pribilof Islands); and seabird, benthic and marine mammal data will be collected in the northern Bering Sea.

Zooplankton research is not supported within the Patch Dynamic Study (inquiries have been made with BEST and BSIERP regarding planned research that would complement the Patch Dynamic Study). We chose our focal species groups based on 1) their social and economic importance, 2) the contrast they provide to establish functional relationships, 3) species interactions within each region are complementary and quantifiable, and 4) their life history traits allow comprehensive data to be collected easily. Detailed descriptions and justifications appear in subsequent sections.

Southeastern Bering Sea (Pribilof Islands) — pelagic system. Our field studies are designed to establish the relationships between animal behavior (e.g., diet, length of foraging trips, feeding rates, location of successful feeding), the environment (e.g., oceanographic conditions, relative prey density), and life history parameters (e.g., predation risk, reproduction and survival, animal physiology and nutritional status of individuals). They build upon ongoing studies conducted by government and university researchers with funding from NPRB, NMFS, ADF&G, USGS, USFWS, and the North Pacific Universities Marine Mammal Research Consortium (NPUMMRC). These studies have been monitoring diets, nutritional stress, population abundance and other demographic parameters, and broad scale movement and diving patterns.

The pelagic patch dynamics study (Pribilof Islands) integrates with the seabird component of BSIERP (colony and telemetry studies at the Pribilofs, and broad-scale at-sea distribution surveys), which will provide data on the inter-annual and intra-seasonal changes in foraging distribution of birds, diet, reproductive performance, and population trends. It will expand on past work in the region on marine mammals and seabirds, including long-term monitoring (NMFS, USFWS) and other research (e.g., NPRB Project 320—Regime forcing and ecosystem response in the Bering Sea (ReFER): Phase II) to establish functional links between changes in diets and population dynamics of apex top-predators in the Bering Sea. Although these previous studies have been successful in relating current changes in climate to changes in nutritional stress of apex predators, concurrent measurements of prey patch dynamics and at-sea foraging distribution were not available. This is why these previous studies have not been able to identify a specific mechanism(s) of how climate variability translates into changes in trophic interactions, which are likely to control population dynamics of apex predators in the Bering Sea. Our Patch Dynamic Study will also expand upon thick-billed murre and northern fur seal research initiated in 2004-2006 to determine the second-by-second swimming and hunting patterns of individuals and establish overlap with inter-annual changes in oceanic conditions (Takahashi *et al.* 2007) and commercial fishing (Lestenkof and Trites 2007).

Our proposed studies will augment the work in progress and incorporate some of the newest technologies developed for other species in other ecosystems, such as mechanistic links between nutritional stress (hormones) and population processes of survival and reproduction (Buck *et al.* 2007; Kitaysky *et al.* 2007), dietary analyses (stable isotopes), and state of the art data loggers (GPS-tracking, CTD-TDR and CTD-SRDL tags—satellite-linked conductivity temperature-depth loggers to measure immediate oceanographic conditions). We will employ these new technologies in the field to quantify the mechanisms (M1-M5) needed to predict the effects of climate change and shifts in species abundance on top predators in the Bering Sea.

Because seabirds raise their chicks on land while meeting their energy requirements at sea, the large-scale seabird component of BSIERP and the Patch Dynamic Study will use a three-pronged approach: colony monitoring, telemetry of breeding birds, and at-sea surveys. At colonies, data on seabird reproductive parameters, diets, body condition, stress level, and colony size will provide information on the types of prey birds are consuming, relative availability of various prey types, and the seabird productivity associated with these foraging conditions. Telemetry data will provide information on foraging location, trip duration, trip frequency, and attendance at the colony. Both of these efforts will focus on seabird response as central place foragers at a relatively fine scale, and will be closely aligned with the fur-seal foraging studies both in design and analyses. At-sea observations will be conducted in concert with fine-scale prey surveys, and will provide data on seabird abundance, distribution, diet, and body condition within the study area around the Pribilof Islands.

Diet studies of birds collected at the patch scale will validate the link between seabird and prey associations, and will define seabird diet relative to characteristics of the prey patches and bird response thresholds relative to prey abundance. While stomach contents of seabirds will inform the link between seabirds and the immediate prey patch, stable isotope analyses from the same seabirds collected and captured at the colony will link the fine-scale processes with broad-scale temporal and spatial shifts in seabirds and their prey. Our Patch Dynamics Study is temporally more constrained (mid-July to mid-August) than the broad-scale surveys of BSIERP, BEST, and BASIS (April-September). Stable isotope analysis of seabird tissues (i.e. red-blood cells with half-life of two weeks, liver and muscle tissues), which integrate seabird diet over a longer time frame, will link the fine-scale process studies of the Patch Dynamics Study to the broad-scale aspects of BSIERP.

Seabird and fur seal foraging locations from at-sea visual surveys and at-sea telemetry will be analyzed and compared in relation to oceanographic data and prey type and abundance data to support detailed predictive models of seabird and fur seal distributions and relative abundance versus prey distributions and oceanographic variables (Redfern *et al.* 2006; Gregr and Trites 2007).

Changes in environmental conditions in the Bering Sea have been implicated in changes in fish population structures. Over the past century, research has illustrated an oscillation of the ocean climate of the Bering Sea and Gulf of Alaska between warm and cold regimes, each lasting from one to several decades (Mantua *et al.* 1997; Anderson and Piatt 1999). These long-term shifts in climatic regime have resulted in dramatic changes in species assemblages, primarily in the epibenthic community (Hollowed and Wooster 1995; Anderson and Piatt 1999). The ocean climate of the Bering Sea and Gulf of Alaska in the late 1970s through the late 1990s was characterized by higher sea surface temperature on average than either prior or subsequent years. The warmer conditions corresponded to increased recruitment of groundfish and salmon and diminished abundance of species such as capelin, herring, and shellfish (Francis and Hare 1994; Anderson and Piatt 1999).

There has been a clear northward shift in the distribution of fishes in the North Sea (Perry *et al.* 2005), and it can be expected that a similar shift will occur in the Bering Sea. Furthermore there is evidence, at least along the Pacific coast, that as ocean temperature rises there is a change in the composition of prey (e.g., copepods; Hooff and Peterson 2006). Associated with this shift in species composition is a shift to poorer quality prey during ocean warming events. Within the context of projected significant increases in ocean temperatures in the eastern Bering Sea, it is important to understand how spatio-temporal shifts in forage base will affect the growth and survival of avian and mammalian predators, as well as predatory fishes. This is particularly true for those species where population success is tied to a particular rookery or colony, such as those found on the Pribilof Islands. If prey patches become too few, too far away, or of poorer quality, those upper-trophic level species will suffer. Understanding patch dynamics within this system forms an important component for modeling ecosystem change under a warming climate scenario.

The ecology and patch dynamics of forage fishes will be studied around the Pribilof Islands in conjunction with bird and mammal studies at St. Paul Island and St. George Island to evaluate possible mechanisms governing the biomass dynamics of forage fish in the Bering Sea and interactions of forage fish with higher level predators, including seabirds, marine mammals, and commercially important fish species. Data will be collected using standardized transect techniques and hot-spot sampling protocols. The fish field study is designed to establish realistic functional relationships for specifying interactions between important upper-level predators and their prey given changing conditions in the physical environment.

The availability of key forage species will be characterized for upper trophic levels in the Bering Sea ecosystem under variable climate conditions (Francis and Hare 1994; Hollowed and Wooster 1995; Mantua *et al.* 1997; Anderson and Piatt 1999). However, availability of prey, in terms of total abundance as well as total energy density will be modulated by individual-based physiological responses to environmental changes. We will measure energy density of prey available for upper trophic level organisms (e.g., Kitts *et al.* 2004; Logerwell and Schaufler 2005). Prey field characteristics can be directly linked to upper trophic level responses (seabird and marine mammal distribution) through concurrent seabird and mammal observations on the survey vessels.

The forage patch component is integrated with the other research components of BSIERP. Understanding forage availability is needed to determine the basis for foraging behavior and develop an understanding of the functional foraging response to shifting prey fields that may occur under changing climate scenarios. Our fine-scale mechanism-based research will provide data for the BSIERP modeling efforts with regard to the dynamics of the forage base available to both avian and mammalian predators in the Bering Sea, and can be scaled up to the broader context of the Bering Sea by overlapping sampling space and ensuring our acoustic sampling scheme is similar to that of the NOAA survey. All research groups (avian, mammalian, forage) will work in real time to conduct transects and focal patch sampling that is informed by the predators to evaluate the results of the decisions that animals make regarding where they feed within the Bering Sea. Examining the quality and distribution of prey will provide insights into the mechanisms that determine foraging effort and allow the available prey fields to be characterized from a bioenergetics perspective. We will thereby work towards developing the predictive power to understand how avian and mammalian population dynamics may be affected as prey fields potentially shift in a changing global climate.

Northern Bering Sea (St. Lawrence Island) — benthic system. Patch dynamics is a conceptual approach to ecosystem and habitat analysis that emphasizes the dynamics of heterogeneity within a system. Benthic-oriented measurements have been taken in the northern Bering Sea for over twenty years (see Grebmeier *et al.* 2006a) in a region known to support highly productive benthic communities and food resources for benthic-feeding apex predators, including gray whales, bearded seals, walruses, and diving sea-ducks—all important in subsistence hunting by local communities. Continued benthic sampling is proposed in the St. Lawrence area to complement the proposed field studies of walrus, and will be expanded southward to St. Matthew Island to evaluate the hypothesized shift of the subarctic-arctic front northward (Grebmeier *et al.* 2006b) that is directly related to the extent of sea ice production of the region.

The Grebmeier *et al.* (2006b) study suggested that climate warming may change the present benthic-dominated northern Bering Sea ecosystem to one more pelagic in nature, similar to the southern Bering Sea—a direct result of changing trophic interactions. Specific evaluation of dominant infaunal prey of walrus (e.g., bivalves, gastropods, and polychaetes), will be undertaken during the benthic field component of the BSIERP walrus-prey patch dynamics study coincident with BEST. We will also endeavor to place these studies in the context of retrospective benthic data sets collected over the last 20 years in the region. We propose to evaluate the spatial heterogeneity of benthic infaunal population and sediment tracers in oceanographic context at coarse scales (20 nm) to evaluate overall effects on ecological processes. We will also strive to develop scaling strategies and limitations for extrapolating information from the small scale (3-5 nm) used for our walrus-prey patch dynamics study to larger (10-20 nm) and even regional (50-100 nm) scales in order to evaluate information from the local ecosystem to overall northern Bering Sea regional scale in which the walrus reside.

SIGNIFICANCE

This proposed research will be the first integrated, comprehensive study of the effects of changing environmental conditions, such as sea ice cover, on top-predators in the eastern Bering Sea (north to south) over varying time scales (days, years). We will depend on other components of the Bering Sea Integrated Ecosystem Research Program (BSIERP) and NSF-funded Bering Ecosystem Study Program (BEST) to provide data on hydrography, primary production, the distribution, abundance and species composition of mesozooplankton, and will obtain data on the reproductive performance and numerical changes of key species through collaboration with other members of BSIERP (seabirds and fish) and established monitoring programs (USFWS, NMFS). Retrospective analyses of data (spanning decades) from these two relatively data-rich study areas will be a critical asset in interpreting the Patch Dynamics Study results. To date, no study has examined the foraging ecology and population dynamics of marine species over the Bering Sea as a whole and under different oceanographic conditions.

SPECIES OF INTEREST & STUDY SITES

Marine Mammals. Two species figure prominently in the Bering Sea because of their cultural, conservation, and ecological importance: northern fur seals and Pacific walrus. In addition to their importance as apex predators, these species have unique characteristics that make them vulnerable to current or potential climate and ecological changes. Northern fur seals have experienced dramatic population declines, hypothesized to be related to changes in their environment, while walrus life histories are intricately associated with sea ice cover (Fay and Burns 1988; Kelly 2001). Both selected study species of marine mammals are biologically tractable (in terms of testing the hypotheses and mechanisms outlined above), as they have been studied in captivity or in the wild (either in the Bering Sea or in other ecosystems) and have relatively long time series to undertake retrospective and comparative analyses (Table 1). Satellite tracking and diving patterns have been previously studied (Gentry 1998; Robson *et al.* 2004), but fine scale foraging studies have only been recently initiated (Lestenkof and Trites 2007).

Almost the entire Pacific walrus population rests on sea ice in the Bering Sea during winter (Fay *et al.* 1997), in contrast to most of the world's population of northern fur seals that returns to the

Pribilof Islands in summer (Angliss and Lodge 2004). Walruses breed in the Bering Sea in January-February and come as far south as Bristol Bay and the Aleutian Islands (Fay 1982; Jay *et al.* 2001), while fur seals breed during July and feed throughout most of the Bering Sea (Robson *et al.* 2004; Sterling and Ream 2004a). The Bering Sea is an important feeding area for pelagic (fur seals) and benthic (walrus) pinnipeds. There is concern that the elevated energy needs of mature females may not be met in an altered Bering Sea and could result in fewer pregnancies and lower survival of newborns and young (Fay 1985).

Location and haul-out behavior data were collected from 39 radio-tagged walruses in the St. Lawrence Island Polynya (SLIP) in March/April of 2006 as part of a range-wide population abundance survey (Table 1). These data have been used in a generalized linear mixed effects model of walrus haul-out status as a response to weather and time of day. The same data will also be used, with coincident sea ice motion data, to assess relations between walrus movements and sea ice drift.

The SLIP is a well studied region of pelagic-benthic coupling dynamics in the Bering Sea. The detection of benthic biological change in the northern Bering Sea coincides with recent observations of larger-scale Arctic environmental changes in water temperature, hydrography, and sea ice regimes. These northern benthic biological communities are known to provide food resources for benthic-feeding apex predators that include gray whales, bearded seals, walruses, and diving sea-ducks, all of which are in turn also used by subsistence based communities along the Bering Sea coast. Walruses consume large quantities of benthic biomass, mostly in the form of bivalves (Fay 1982). The large energy flow from the benthic environment to walruses makes them a good species for studying small scale foraging dynamics and walrus foraging locations can be identified using satellite radio-tags.

Benthic Fauna. During May-June 2006 a full grid of benthic stations was occupied in the SLIP area as part of a separate NSF-funded project, along with hydrographic and ice cover data collections. These data have just been statistically processed and will be evaluated in the context of walrus locations based on tagging data from March-April 2006 in order to guide field sampling operations in spring 2008 and subsequent years. These walrus-prey data sets, in combination with real-time walrus observations via helicopter reconnaissance proposed during the spring Healy cruise, will enable us to focus on a small-scale patch dynamics study within the standard benthic grid to evaluate hot spots, patch utilization, and system heterogeneity to determine the prey and predator response to both “bottom-up” and “top-down” driving factors for the northern Bering Sea ecosystem.

Seabirds. The two most common, and well-studied seabird species in the southeastern Bering Sea are thick-billed murres (*Uria lomvia*) and black-legged kittiwakes (*Rissa tridactyla*). Their sensitivity to changes in climate have been shown at the population and individual levels (Benowitz-Fredericks *et al.* 2007; Byrd *et al.* 2007; Shultz and Kitaysky 2007; Takahashi *et al.* 2007). We have chosen to examine a diving seabird (thick-billed murre) and a surface-feeding seabird (black-legged kittiwake) because temporal dynamics and locations of available food differ at the surface and at depth (Kitaysky *et al.* 2000). To fully characterize effects of climate on foraging resources we need to rely on information obtained for both feeding ecotypes, rather than a single species of piscivorous seabird. Additional data on the distribution and abundance of all seabird species will also be obtained at both the northern and southeastern study sites, by placing seabird observers on the NSF and PDS vessels.

Considerable data on seabirds were collected in the Bering Sea as part of the Outer Continental Shelf Environmental Assessment Program (OCSEAP) during the 1970's. This work forms the foundation of our current understanding of seabird trophic relationships (Hunt *et al.* 1981; Sanger and Jones 1984; Sanger 1986, 1987; Hunt *et al.* 2000). During the late 1980s and 1990s, data on birds at sea were more restricted to specific study sites, but a broad-scale seabird observer program was reinstated in 2006 and 2007 (NPRB #637). The North Pacific Seabird Pelagic Database (NPPSD), maintained by USGS and USFWS, is the repository for at-sea survey data of seabirds (North Pacific Pelagic Seabird Database 2006). Work on seabirds in the Bering Sea has continued with funding by the USFWS (Byrd *et al.* 2007) and NPRB (Kitaysky *et al.* 2007).

We will compare seabirds nesting on two geographically associated islands in the Pribilof group, St. Paul and St. George, where apex predators apparently respond to different environmental regimes. This comparison will allow us to predict how changes in sea ice conditions and associated food-web responses in the Bering Sea may affect apex predators. For central place foraging seabirds, the positions of St. Paul and St. George relative to the typical maximum edge of sea ice and to the edge of the Bering Sea shelf may be important factors in how seabirds breeding on the two islands are affected by changes in climate. The maximum edge of the winter ice on the Bering Sea shelf is generally nearer to St. Paul than to St. George. St. George is nearer the productive edge of the Bering Sea shelf. To the extent that the influence of ice is greater in the vicinity of St. Paul, seabirds nesting on that island might be differentially affected by the loss of that influence if future warming reduces the incidence of ice in the area (Byrd *et al.* 2007).

Hunt et al. (2002) speculated that the Bering Shelf ecosystem may be regulated by different mechanisms during cold vs. warm climate regimes. Although St. George and St. Paul are situated close to each other, they appear to be responsive to different oceanographic processes, potentially driven by proximity to the shelf break and/or movement of water masses across the shelf (P. Stabeno, unpubl. data). The long term consequences of these inter-island differences are striking: since the mid-1990s populations of piscivorous seabirds breeding at the Pribilof Islands have rebounded at St. George (continental shelf-break region), while continuing to decline at St. Paul (shelf region) (Byrd *et al.* 2007). Comparing responses of piscivorous seabirds nesting on these islands may provide insights into whether shelf and oceanic systems respond in tandem (Benowitz-Fredericks *et al.* 2007) or independently to inter-annual climate differences.

The pattern of oceanographic response described above may be driven by climate regime. For example, the shelf and oceanic systems may respond similarly during warm regimes, but are regulated differently during cold regimes. There is a need for a better understanding of the causal links between climate and patterns of productivity among oceanographic regions in the Bering Sea. It is critical to investigate this on a fine scale because responses by nesting seabirds to climate fluctuations are localized. The project proposed here addresses this goal by examining effects of inter-annual climate changes on patch dynamics for seabirds preying on forage fishes (including juvenile walleye pollock) at two major colonies situated in two distinct oceanographic regions on the continental shelf of the southeastern Bering Sea — St. Paul and St. George islands. The telemetry component of BSIERP will determine whether birds nesting on the two islands do indeed utilize different foraging areas.

Seabirds have been widely recognized for their ability to indicate changes in marine ecosystems (Boersma 1978; Crawford and Shelton 1978; Ricklefs *et al.* 1984; Cairns 1987; Croxall *et al.* 1988; Chapdelaine and Brousseau 1989; Monaghan *et al.* 1989; Harris and Wanless 1990;

Hamer *et al.* 1991; Montevecchi 1993). Changes in ocean conditions affects the food supply of seabirds, while a chronic imbalance between energy demands and its availability affects population processes of the seabirds (Kitaysky *et al.* 2007). Seabird response to these changes is reflected in changes in diet composition (Hatch and Sanger 1992; Ballance *et al.* 1997; Bryant *et al.* 1999; Carscadden *et al.* 2002; Suryan *et al.* 2002), foraging behavior (Cairns 1987; Burger and Piatt 1990; Suryan *et al.* 2000), nutritional stress (Kitaysky *et al.* 2007), nesting success (Jodice *et al.* 2006), and survival (Kitaysky *et al.* 2007). Changes in diet composition, foraging behavior, and nutritional stress reflect short-term (hours-days) changes in food availability. Each of these parameters alone, however, would not provide sufficient information to characterize short-term changes in patch dynamics. For example, changes in diets do not always result in shortages of energy (Benowitz-Fredericks *et al.* 2007), and relying on poor quality food is not always nutritionally stressful (Kitaysky *et al.* 1999b). Yet when these three parameters are used together, they can characterize bird responses to changes in patch dynamics. Longer-term changes in food availability (days – weeks) are reflected in reproductive parameters, such as nest initiation date, hatching success, brood reduction, chick growth rates, and fledging success. Population responses of long-lived seabirds are sensitive to long-term changes in food availability and typically reflect oceanographic changes on inter-annual and decadal scales (Thompson and Ollason 2001). However, nutritional status of breeding individuals (assessed by measurements of stress) reflects changes in food availability during the reproductive season and determines post-reproductive survival of adult birds, providing a mechanistic link between changes in forage patch dynamics and population processes in seabirds (Kitaysky *et al.* 2007).

Forage Fishes. The forage base component of the Patch Dynamics Study will sample euphuasiids, all species of squid found, and all species of fish that comprise at least 10% by number of any individual sample with special emphasis on those species identified from the gut contents of the marine mammal and bird predators. For the first analysis, acoustic data will be partitioned into 4 categories (Pollock, Myctophids, Euphausiids, and Capelin) to allow direct comparison to NMFS acoustic surveys, the richest data set for forage species for the area. We anticipate encountering additional species such as Atka mackerel, sand lance, juvenile salmon, kelp greenling and herring, all of which have been indicated as being important to the diet of seals and/or seabirds in this area. The NMFS pollock surveys extensively cover the Bering Sea with transects spaced 20 nm apart that have been conducted every other summer since 1979 (Table 1). These surveys provide incredible information on the inter-annual variability of forage species over the entire Bering Sea but only 3 transects provide information about the waters surrounding the Pribilof Islands. Furthermore, the lack of any repeat sampling within a year does not allow for addressing questions about temporal scales shorter than several years.

We will conduct forage sampling around the Pribilof Islands using a combination of stratified planned sampling covering the shelf, slope, and open water which will be informed by existing tagging data from relevant predators, and adaptive sampling guided in real-time by predator habitat use based on contemporaneously tagged birds and mammals in the area, during a one-month period in July and August 2008 and 2009. As shown in predator prey studies in a range of marine systems (e.g., Swartzman and Hunt 2000; Benoit-Bird and Au 2003a), concurrent sampling of the predator and prey as we will do during adaptive sampling is critical for finding spatial overlap between predators and high-intensity prey. The temporal scales at which prey change make serial sampling ineffective for determining what prey features predators are selecting for or in fact to even find coherence between predator and prey.

SCALES / TIMING / LOCATIONS

Marine Mammals. Northern fur seals return to the Pribilof Islands each summer to give birth, mate and raise their pups. Pupping occurs over a 5-week period beginning in mid June with over 50% of pups being born during the first two weeks of July (Trites 1992). The mean date of birth (based on 4 years of observations between 1951 and 1983) is July 9 (Trites 1992). The rigid harem-breeding structure begins to break down towards the end of July when mating ends. Females give birth to a single pup which they will nurse until late October or early November when the pups wean and all fur seals leave the Pribilofs (Gentry and Kooyman 1986; Baker 2007). Foraging trips by lactating females at the Pribilof Islands last on average about 7-8 days, during which time the pup fasts on shore. Individual females tend to feed at about the same location on different trips to sea, but rookery populations specialize in where they feed (i.e., in their direction of travel away from the island—Gentry 1998; Robson *et al.* 2004). There appears to be feeding segregation between the sexes, with males traveling further and longer than females (Sterling and Ream 2004b). Mean maximum foraging distance of satellite-tracked females was about 250 km from the Pribilof Islands (Robson *et al.* 2004). Diets (based on frequency of prey items recovered from female fur seal scats between 1987 and 2000) were dominated by juvenile walleye pollock *Theragra chalcogramma* and gonatid squid *Gonatopsis borealis/Berryteuthis magister* and *Gonatus madokai/Gonatus middendorffi* (Zeppelin and Ream 2006). Less frequently occurring prey included Pacific sand lance *Ammodytes hexapteus*, Pacific herring *Clupea pallasi*, northern smoothtongue *Leuroglossus schmidti*, Atka mackerel *Pleurogrammus monopterygius*, Pacific salmon (*Oncorhynchus* spp.) and other squid of the genus *Gonatus* (Zeppelin and Ream 2006).

The entire Pacific walrus population winters on sea ice in the Bering Sea. Breeding occurs in Jan-Feb and calves are born 15-16 months later in mid April to mid June. Calf body weight triples in the first year and nearly doubles again by the time of weaning, at 2 years of age. Adult males tend to fast during the breeding period and females may fast for several days at estrus and for a week or more at parturition (Fay 1985). While foraging, they select their prey by rooting through the seafloor with tactile exploration from their mystacial vibrissae, which are extremely sensitive, having the ability to identify different shapes with surface areas as small as 0.4 cm^2 (Kastelein and van Gaalen 1988). They feed on a broad range of benthic invertebrates, but primarily bivalves. For deeper burrowing bivalves, such as large *Mya*, they jet water out through their mouth to excavate the clam (Oliver *et al.* 1983; Kastelein and Mosterd 1989). The SLIP bounds the largest of three primary walrus aggregations during the breeding period and early spring. Data from tagged walruses in 2006 indicate that the walruses remained primarily within the SLIP region (roughly 100 km x 300 km) until their departure with the receding ice in spring.

Benthics. The benthic community structure in the SLIP area has been defined through Bray-Curtis similarity multivariate analyses on the 10-20 nm scale. A 5-day dedicated use of the USCGC Healy in the spring as part of the BEST cruise is required for an appropriate small scale (3-5 nm) benthic sampling program for the walrus-prey patch dynamics study, which will also leverage all the ecosystem measurements being conducted on the ship as part of the BEST program. In addition, we will occupy the benthic time-series “hot spot” sites we have maintained south of SLI (Grebmeier et al. 2006a, b; medium scale - 10’s nm) within a larger patch dynamics region where walrus are feeding (large scale - 100’s nm).

The walrus-prey patch dynamics study will occur each March-May during 2008 and 2009, coincident with proposed walrus tagging operations on the USCGC Healy during the BEST cruise.

Seabirds. Black-legged kittiwakes and thick-billed murres spend the summer attending their breeding sites on the cliffs of the Pribilof Islands. Black-legged kittiwakes are surface-foraging seabirds that prey on pelagic fishes and provision their young by regurgitating stomach-loads of partially-digested food. On the Pribilofs, kittiwakes lay their one- or two-egg clutches in mid-June, eggs hatch about mid-July, and chicks fledge around mid-August. Breeding kittiwakes on the Pribilofs provision their young on a daily basis (2 - 3 foraging trips/day; foraging trip duration is generally 4 - 12 hours; Kitaysky *et al.* 2000). Thick-billed murres are pursuit-divers, raise a single chick, and both parents provision their chick with single prey items each visit to the breeding site (3 - 6 foraging trips per day; foraging trip duration generally 3 - 6 hours) (Kitaysky *et al.* 2000). Murres on the Pribilofs initiate nesting about 2 weeks later than kittiwakes and lay their eggs at the end of June; eggs hatch a month later at the end of July. Murre chicks spend only three weeks on the cliff before the flightless young jump into the sea, about a week after kittiwake chicks fledge (Dragoo *et al.* 2003). Murre fathers attend their chicks at sea and feed them for another month. Maximum foraging distance from the breeding colony is highly variable, but most foraging occurs within 100 km of the nest sites (Gaston and Hipfner 2000). Thick-billed murres nesting at the Pribilof Islands consumed primarily juvenile walleye pollock, squid, Pacific sandlance, and euphausiids from the mid-1970's to 2001. Black-legged kittiwakes consumed primarily walleye pollock, Pacific sandlance, myctophids, squid, euphausiids, and copepods during the same time period. Foraging distribution of kittiwakes and murres at the Pribilof Islands suggests that food abundance and/or its availability may differ markedly for black-legged kittiwakes and thick-billed murres (Kitaysky *et al.* 2000). For example, during two years with contrasting oceanographic conditions (1987 and 1988), murres foraged in closer proximity (within a 30-km radius) to the islands and in higher densities in 1987 than in 1988, whereas black-legged kittiwakes foraged in closer proximity (within a 50-km radius) to the islands and in higher densities in 1988 than in 1987 (Kitaysky *et al.* 2000).

Both thick-billed murres and black-legged kittiwakes are present throughout the year in the Bering Sea, although their distribution shifts offshore during the non-breeding season (North Pacific Pelagic Seabird Database 2006). Species composition of the diet changes dramatically with season, and there are spatial shifts in species abundances as well, likely reflecting both changes in their breeding status (shifting from dispersed or 'hot spot' foragers to central place foragers during the breeding season) and changes in prey fields.

Forage Fishes.

Forage patches are variable in both space and time. Overall fish abundance (not just forage species) as measured in the AFSC trawl survey has changed significantly over the last 40 years (Conners *et al.* 2002). These changes in abundance as well as the recruitment success of forage fishes have an important climate component (Hunt *et al.* 2002). With the potential for increased warm years under a warming climate scenario, the Oscillating Control Hypothesis (Hunt *et al.* 2002) would predict increased top-down trophic control and limitations on predator productivity due to a reduced forage base. The forage base component of the Patch Dynamics Study will sample euphausiids, all species of squid encountered, and all species of fish that comprise at least 10% by number of any individual sample with special emphasis on those species identified from the gut contents of the marine mammal and bird predators. For the first analysis, acoustic data will be partitioned into 4 target species categories (pollock, myctophids, euphausiids, and capelin) to allow direct comparison to NMFS acoustic surveys. However, more refined analyses will be conducted based on the quantity and type of the species captured in net tows taken at the same time. As noted above, we also anticipate encountering Atka mackerel, sand lance, juvenile salmon, kelp greenling herring, and northern smoothtongue. Of the four forage categories used by NMFS, we do not expect to find capelin in significant numbers based on their previous surveys in the same area. Euphausiids and myctophids are likely to cover a great vertical range in the water column with a strong vertical movement as a function of light level. For both groups, we anticipate more individuals being found over deep water. The NMFS long-term surveys show that pollock abundance is highly variable but pollock can be found in the area surrounding the Pribilof Islands at depths less than 300 m within the shelf and slope regions. Little is known about the fine-temporal scale distribution of any of these prey species. We cannot yet address if patches of these species form in the same place between days or years or if, once they are formed, they are maintained for hours or weeks or longer.

FORAGING STUDY METHODS

Marine Mammals. Foraging studies will be conducted on both northern fur seals (Pribilof Islands, in cooperation with St. Paul Tribal Eco) and Pacific walruses (St. Lawrence Island Polynya–SLIP, in cooperation with USGS and the Eskimo Walrus Commission) to ascertain the relationship between duration of foraging trips, density and location of prey, foraging success, and the physical properties of the water column or sea ice conditions where animals travel.

For northern fur seals (Marine Mammal Task MM#1), data will be collected annually from 30 lactating females on St. Paul Island (Jul–Sept, 2008 and 2009) carrying combinations of fine-scale tracking devices that record timing of activities of fur seals and the physical oceanography of the water column where animals search for food. Ten sets of instruments will be re-deployed three times per year (on 30 fur seals in total) for three years. Instruments include a VHF-radio tag (to locate animals on shore), a GPS tag (to locate animals at sea in real time), a Dead-Reckoning tag (to reconstruct activities in 3-D during the entire foraging trip), and a CTD-SRDL tag (to measure salinity, depth, and water temperature). Data will be collected as frequently as every 2 seconds at a spatial resolution of 5 cm. Instruments must be recovered from the fur seals to download the data and redeploy the instruments. Sample size is based on the number of animals we feel we can reasonably study at one time and on a general statistical rule of thumb of $n = 30$, given that data are unavailable to undertake a proper power analysis. We propose to capture our first 10 females starting July 15 using a wooden box to enter the rookery. Subsequent captures and recaptures will be done by crawling into the rookery beginning August 1. Field work will require about 8 weeks and is expected to conclude by September 15. Captures will require 3 people using a protective box or hoop nets, and restraining the animals on a restraining board. Data analysis will reveal the locations of feeding events, the foraging strategies employed, length of time in patches, foraging habitat, length of feeding trips, oceanographic characteristics of the water column, and activity budgets of foraging fur seals.

For walruses (Marine Mammal Task MM#2), satellite-linked transmitters will collect data on foraging locations and time spent foraging. The tags are deployed with a crossbow and sub-dermally anchored to the walrus, alleviating the need for animal capture. Similar tags have been deployed on over 75 walruses since 2004 and have a longevity of ~6-8 weeks (Table 1, Jay *et al.* 2006). Kernal estimation methods will be used to estimate the utilization distributions of tagged walruses. Randomization tests will be used to assess variation in area use among years. These data will be linked to benthic prey density estimates from extended NSF-funded benthic studies, proposed by Grebmeier and Cooper (see BENTHICS section below).

These fine-scale foraging studies of marine mammals build upon walrus research funded by USGS, USFWS, and MMC (Jay and Hills 2005; Jay *et al.* 2006) and fur seal research funded in 2005 and 2006 by NPRB and NPUMMRC to identify spatial overlap between foraging fur seals and fisheries (Lestenkof and Trites 2007). They will establish the relationships between length of foraging trips, feeding rates, location of successful feeding, oceanographic conditions, relative prey density, and the risk of predation. It will thus elucidate and quantify three controlling mechanisms thought to underlie climate and predator-prey interactions (M1-physical environment, M2-match-mismatch, M3-foraging arena), which the models need to predict the consequences of climate change on marine mammals. The study of northern fur seals and walruses contrasts two apex predators with differing trophic pathways (pelagic- versus benthic-based).

Seabirds. Foraging routes and locations, depth, water characteristics, trip duration and frequency, diets, and stress levels will be monitored for breeding thick-billed murres and black-legged kittiwakes at St. George and St. Paul islands. The forage fish component, in conjunction with the at-sea seabird component of the Patch Dynamics Study will allow us to describe the characteristics of the prey patches utilized by breeding birds foraging at sea. Foraging locations will be analyzed in relation to data on oceanography, prey type and abundance, and fur seal foraging location to determine the habitat characteristics and prey densities for prey patches used by foraging seabirds and fur seals, and look for temporal and spatial overlap in use areas.

Three diet parameters are likely to shift in response to climate variation: i) composition (prey type), ii) quality (energy content), and iii) availability (abundance and distribution). Changes in any or all of these parameters will reflect changes in patch dynamics and have consequences for seabird productivity. Stress hormone (corticosterone) levels in blood of individual seabirds are one indicator of difficulty in maintaining energy balance during foraging. We will be able to more precisely identify and address the nature of short-term diet changes for seabirds at different colonies by employing a combination of corticosterone data and measures of diet composition (direct: regurgitations, stomach contents; and indirect: stable isotope signatures of seabirds from samples of blood and other tissues).

Foraging distributions – at sea surveys. In conjunction with the BEST and PDS prey surveys, a seabird observer will record all birds and marine mammals in a 90^0 arc out to 300 m from the vessel using handheld binoculars during transits (consistent with large-scale BSIERP surveys). Data will be entered directly into a GPS-integrated computer using the DLOG data entry program. Observations can be binned into selected transect lengths to calculate densities, typically 1 – 3 km, depending on the distribution of prey and seabirds.

Foraging distributions – telemetry. Each year of the study, 30 birds of each species at each location (St. Paul and St. George islands) will be fitted with a GPS data logger during the period July 1 to August 15, just before and concurrent with the fine-scale forage fish cruise and northern fur seal studies. These birds will also be used to collect diet samples, when possible. Irons (1998) used a similar sample size of 26 birds to successfully identify foraging locations and habitats of black-legged kittiwakes in Prince William Sound. Each GPS data logger will record latitude and longitude every 5 minutes during a foraging trip. Data logger batteries last only a few days because of their small size, so loggers will be retrieved after one or two foraging trips. Tagging with GPS instruments and monitoring chick diet of seabirds will be conducted by corresponding components of BSIERP. Conventional VHF telemetry has been successfully used for many seabird studies (Benvenuti *et al.* 1998; Irons 1998; Daunt *et al.* 2002), but is limiting for the objectives of this study (i.e., to track a wide-ranging seabird at sea). In 2007 the size of GPS data loggers was reduced to 7 g, which will permit us to attach GPS data loggers on seabirds < 900 g total body mass without negative effects on the bird's behavior. Thick-billed murres and black-legged kittiwakes will be captured while at their nest site with an 8-meter noose-pole — a method used successfully on both seabird study species (Irons 1998). The GPS data loggers will be attached to the birds' back or tail feathers by means of cyanoacrylate glue, Tesa tape, and/or cable ties (see Benvenuti *et al.* 1998; Irons 1998; Daunt *et al.* 2002).

Seabirds nesting at the Pribilof Islands have never before been tracked at sea and, therefore, foraging locations, as determined from birds fitted with GPS data loggers, are a critical data gap for this major seabird breeding area. The foraging locations of tagged birds can also be used to help direct fine-scale surveys of prey patch dynamics, where at-sea bird observers can determine the level of seabird occupation in those areas in conjunction with characteristics of the prey patch. The seabird telemetry component ties the colony of origin to foraging behavior and prey availability/patch use. Knowing colony of origin is critical to the focal research on the Pribilof Islands and its relevance to testing BSIERP hypotheses regarding effects of climate change.

Also concurrent with the prey studies, a separate group of 30 thick-billed murres will be captured and fitted with a time depth recorder (TDR) to characterize the foraging behavior of pursuit-diving murres (diving depth > 100 m, Takahashi et al. 2007). The TDRs will record information on depth (1-m accuracy with 0.05-m resolution) and temperature (0.1°C accuracy with 0.02°C resolution) every second, as well as surge (tail-to-head) and heave (ventral-to-dorsal) accelerations at 16 Hz (Takahashi *et al.* 2007). A detailed study of foraging behavior of murres on the Pribilofs using TDRs was initiated in 2004 by Prof Y. Watanuki, Hokkaido University. Adult thick-billed murres will be captured with noose poles and the TDRs will be attached to the ventral side of the murres using attachment techniques similar to those used for the GPS data loggers (Tremblay *et al.* 2003).

Diet. We will employ three techniques to assess the nature of changes in seabird prey availability: 1) identification of prey items collected directly from birds (regurgitations and stomach samples), 2) measurement of stable isotope signatures from red blood cells and other tissues of birds, and 3) quantification of circulating stress hormones (corticosterone) in blood. We will collect blood samples (for stable isotope analysis and corticosterone analysis) and regurgitations from 30 adult, actively-breeding seabirds of each species at each location.

Direct sampling. PDS is an integrated component of BSIERP, and it is critical to the PDS to collect seabird diet information in conjunction with the fine-scale at-sea work, in order to determine seabird diets in relation to available prey and to the characteristics of the prey patches. The data on instantaneous adult diet composition at the patch will supplement diet sampling at the colony, which is primarily for prey delivered to chicks. We will sample equal numbers (maximum of 3 each per prey patch) of thick-billed murres and black-legged kittiwakes associated with a minimum of 20 prey patches during the first field season of the project (total = 120 birds). Samples of ingested food will be removed from the foregut of collected birds, preserved on-site, and sent to UAF for identification of prey species present, percent frequency of occurrence, and percent volume. Three tissue samples will also be taken from each collected bird for stable isotope analysis (whole blood, liver, and muscle). This is necessary to integrate immediate and longer time-frame diet composition (Hobson and Clark 1992; Sydeman *et al.* 1997). Stomach contents samples from collected seabirds will be compared directly to the prey composition of the forage patch as assessed by hydro-acoustics and direct sampling. In this way we will validate assumptions of predation at each patch and determine prey threshold effects and prey selectivity.

Regurgitations have been widely used in seabird diet studies and prey can often be identified to species and age class (Hunt *et al.* 1996a; Hunt *et al.* 1996b). This technique has been used successfully in the Bering Sea (e.g. Springer *et al.* 1986; Hunt *et al.* 1996a; Hunt *et al.* 1996b; Benowitz-Fredericks *et al.* 2007). However, because murres almost never regurgitate, diet samples will be obtained using the water off-loading technique (Wilson 1984). This is a non-destructive technique that involves inserting a 15-mm diameter soft silicon tube with a funnel on one end down the esophagus and into the stomach. Warm water is poured into the tube, and when water starts to seep through the gape, indicating that the stomach and esophagus is full, the tube is removed. The bird is then inverted and gentle pressure is applied to the abdomen several times. Food that was in the foregut, along with ingested water, is off-loaded into a sample bucket. This method is safe and will not injure birds (Wilson 1984) and has been used successfully for diet studies in many seabird species, including thick-billed murres on the Pribilof Islands (Takahashi *et al.* 2007; for other species see — common murre: Wilson et al. 2004, king penguin: Cherel et al. 1996, gentoo penguin: Bost et al. 1994).

Stable isotopes. We will use stable isotope analysis to identify the presence and nature of inter-annual, inter-colony, and inter-specific diet changes. Blood samples will be taken from all instrumented birds (*n* = 30 species^{-1} island^{-1}) and all birds collected at sea (*n* = 60/species). Stable isotope signatures (ratio of heavy to light isotopes for nitrogen (∂^{15}N) and carbon (∂^{13}C)) can be used to detect changes in diet composition (trophic level changes; Hobson *et al.* 1994; Sydeman *et al.* 1997; Post 2002), prey quality (lipid content: Focken and Becker 1998) and potentially, origin of prey production. In particular, ∂^{15}N increases with trophic level, while ∂^{13}C can reflect both proximity to nearshore habitats in marine systems (Thompson *et al.* 1999) and lipid content of the diet (Focken and Becker 1998; Polischuk *et al.* 2001). SIA is commonly used in seabird studies to compare diets among species (Thompson *et al.* 1999), colonies (Thompson *et al.* 1999), years and age-classes (Forero *et al.* 2002; Forero *et al.* 2004). SIA will also provide information about the relative trophic levels of prey consumed throughout the season. Colony-based studies of birds will define their diet relative to characteristics of the prey patches. While the stomach samples will inform the link between seabirds and the immediate prey patch, stable isotope analyses from the same birds will link the fine-scale processes with broad-scale temporal and spatial shifts in seabirds and prey. Our Patch Dynamics Study is temporally more limited (occurring mid-July to mid-August) than the broad-scale surveys of BSIERP, BEST, and BASIS (April-September). Stable isotope analysis, which integrates a longer time series of seabird diet, will link the fine-scale process studies of the Patch Dynamics Study to the broad-scale aspects of BSIERP.

Previous field and captive studies have demonstrated that taking the proposed blood volume for stable isotope analysis (less than 1% of a bird's body mass) is harmless to birds and does not affect the long-term physiological condition or behavior of birds (A. Kitaysky and J. Wingfield, University of Washington, personal observations). Adult kittiwakes and murres in Lower Cook Inlet and south-eastern Bering Sea were sighted at their nests within 1-10 min after release.

Blood samples collected from black-legged kittiwakes (30-50 per colony/year) and thick-billed murres (30-50 individuals sampled per colony/year) during 2003-2005 at the Pribilof Islands are available for the SIA analyses proposed here, and in a combination with data obtained during 2008 and 2009 would provide sufficient sample sizes to examine intra- and inter-seasonal changes in the diet composition.

Stress hormones. The use of corticosterone (CORT) concentrations in blood as an indicator of prey availability to breeding seabirds has been extensively validated using simultaneous, intensive, direct sampling of food abundance (Piatt 2002) and corticosterone concentrations in the field as well as with controlled experiments in the laboratory (Kitaysky *et al.* 1999a; Kitaysky *et al.* 1999b; Kitaysky *et al.* 2001a; Kitaysky *et al.* 2001b; Kitaysky *et al.* 2002; Wingfield and Kitaysky 2002; Kitaysky *et al.* 2007). Blood can be collected for analysis of baseline CORT levels from all instrumented birds (n = 30 species^{-1} island^{-1}). Decreased prey availability is consistently associated with increased CORT. CORT levels can be standardized for a species such that relative CORT production (compared to the maximum ever observed – "nutritional stress index") is comparable across species. For all birds, initial blood samples will be taken within 3 minutes of capture. Catecholamine hormones such as adrenaline are stored and released into circulation almost immediately in response to a stressor like capture. In contrast, elevations in steroid hormones like CORT are not manifest in circulation for several minutes, because they must be synthesized in response to the stressor (reviewed in Sapolsky *et al.* 2000). It has been demonstrated that for birds, blood samples obtained within 3 minutes of initial capture are a reliable reflection of baseline (pre-capture) levels (reviewed in Romero and Reed 2005).

PREY STUDY METHODS

Benthics. Shallow, high latitude ecosystems are particularly vulnerable to climate change, and there are indications that the northern Bering Sea shelf is shifting towards an earlier spring transition between ice-covered and ice-free conditions (Grebmeier *et al.* 2006b). Detection of benthic biological change in the northern Bering Sea coincides with recent observations of larger-scale Arctic environmental changes in water temperature, hydrography and sea ice regimes (Overland and Stabeno 2004; Meier *et al.* 2005; Stroeve *et al.* 2005). Thus, ecosystem change on the shallow northern Bering Sea shelf is likely to be directly linked to the south (E. Bering Sea shelf) and north (north of Bering Strait to the Arctic Basin). The region south of St. Lawrence Island is a seasonally-varying carbon system, being an "export" system in the spring and directing labile carbon to the benthos, but turning to a "retentive" system and supporting a pelagic, zooplankton-focused system in the summer (Grebmeier and Barry 2007b). There is a strong potential for negative impacts from warming seawater and a reduced sea-ice system in the north with climate warming, resulting in a reduction in the winter-produced cold pool extent for the benthos. However, in the short-term the pelagic system may benefit until nutrient limitation occurs and reduces annual primary production.

The benthic field program will include collections of benthic infaunal populations and biomass, along with sediment tracers, and parameters to identify oceanographic conditions. (M1-physical environment, and M2-match-mismatch) The walrus-prey patch dynamics study will be developed in the context of walrus feeding sites (M3-foraging arena), both historical and tagged in 2006 onwards. Through ongoing collaborative programs, we will evaluate prey caloric and

DNA levels (pilot project) relative to those of walrus, along with continued measurement of bivalve growth rates (M3). As time and funding permit, we will further compare our 2008 and 2009 field results with past data (1988-2006) collected in exactly the same manner as in the current proposal. As part of our field program we will develop a small scale benthic sampling grid (3-5 nm) within the walrus collection sites that will be nested inside our standard benthic grid (20 nm) for the walrus-prey patch dynamics study. We will use a benthic camera system for observations of the benthos in areas closest to St. Lawrence Island where both van Veen grabs and benthic trawls are prohibited due to the rocky substrate. A camera system will allow for the identification of infaunal siphons and tubes (clams and polychaetes) in areas of walrus feeding, based on our use of a camera system in the SLIP area in summer 2007 (Canadian IPY collaboration)

Grebmeier and Cooper have received a recommendation for funding from NSF to continue a subset of benthic-oriented measurements in the northern Bering that has been studied for over 20 years (see Grebmeier *et al.* 2006a) and known to support highly productive benthic communities and food resources for benthic-feeding apex predators, including marine mammals and diving sea-ducks. We also proposed to expand sampling southward to St. Matthew Island to evaluate the hypothesized shift of the subarctic-arctic front northward (Grebmeier *et al.* 2006b) that is directly related to the extent of sea ice production in the region. Studying the benthic infaunal community composition and biomass will allow us to evaluate climate change impacts on the Bering Sea ecosystem and the walrus-prey patch dynamics project will evaluate the dominant bivalve/polychaete community structure within the northern Bering Sea. In order to evaluate changes in these benthic communities we will utilize the same sampling methods as historically used. The vast majority of published benthic infaunal collections accomplished since the 1970’s in this region used a 0.1 m^2 van Veen grab (Grebmeier *et al.* 2006a) followed by separation of organisms from sediments on a 1-mm screen mesh. This standardized methodology is most practical and efficient for the wide variety of sediments encountered in the Bering Sea, from fine muds to coarse sand and gravels, where corers cannot sample. We use coring techniques for sediment oxygen respiration incubations, and all these uptake measurements have used standardized shipboard incubation methods with Winkler and/or dissolved oxygen probe determinations of oxygen utilization (see Grebmeier et al. 2006a for methodology). We will also collect a suite of sediment indicators (sediment grain size, metabolism, organic carbon content, natural and anthropogenic isotope content, and sediment chlorophyll inventories) to compare with historical data from the northern study region (seasonal and interannual data) collected in a consistent manner (same equipment, techniques) over the last 22 years (see Grebmeier et al. 2006a for methodologies).

These benthic measurements will be collected using the USCGC Healy in the spring, as the sea ice retreats northward, over three years. Joint involvement in BSIERP (walrus-prey patch study) and BEST will allow access to hydrographic and water column data that, combined with the benthic data and evaluated by modeling efforts, will allow a synergistic, system-level evaluation of the driving factors influencing observed changes in the Bering Sea and ecosystem response. The joint collaboration across the boundaries of the NPRB BSIERP program and the NSF - BEST program indicates the importance of the benthos as part of a systems approach to understanding the Bering Sea ecosystem *in toto*. The benthos are an integrator of the overlying water column processes that may be used to evaluate inter-annual pelagic-benthic coupling and ecosystem health on this shallow, productive continental shelf in the context of ongoing sea ice retreat and associated ecosystem change. These proposed field studies are integrated into the upper trophic level studies of the BSIERP research program (marine mammals, seabirds, and ecosystem modeling) and are integral to the science goals of the NSF-BEST (Bering Ecosystem Study).

Forage Fish. The formation, persistence, and movement of forage fish patches are hypothesized to be important determinants of foraging success by upper-level marine predators. These patch processes are presumed to be influenced by both the physical and biological components of the environment.

Our objectives for this component of BSIERP are: 1) to understand why animals show observed distributions and to determine whether these distribution patterns affect foraging by fur seals and marine birds; and 2) to understand the mechanisms by which prey affects the foraging of fur seals and marine birds in order to predict the effects of environmental change on these interactions. To achieve these objectives, we will: i) determine if prey are patchy; i) describe patchiness within a season and between years (spatial extent, quality, predictability, persistence); iii) determine if foragers are correlated with patches; and iv) determine what it is about a patch that affects foraging.

We will also cross-reference our work with the current NOAA Fisheries Bering Sea acoustics survey in order to (1) establish the scale of survey necessary to capture ecosystem variability, with the aim of determining whether the current NMFS survey is sufficient to capture spatio-temporal variation in prey patches, and (2) ensure that our detailed acoustic work and directed sampling can be extrapolated to the scale of the eastern Bering Sea.

Forage sampling (FF#1). Our at-sea sampling of forage fish, squid, and euphausiids — the "prey base," and basic physical oceanographic structure will combine both planned transects and adaptive sampling guided by synoptically tagged predators, with a planned 30 days of sea time in July/August of 2008 and 2009 around the Pribilof Islands. For both the planned and adaptive surveys, we will stratify our sampling with respect to inshore, shelf, slope, and oceanic regions (see Benfield et al., NPRB project 401), as well as by island.

Planned transects. At least 3 planned transects will be located in each of the sampling strata based on habitat use by fur seals in previous tagging studies. In addition, transects will be conducted along sections of the NMFS regular pollock survey lines (located 20 nm [37 km] apart), where they fall within the sampling region as defined by maximum foraging distances of avian and mammalian predators. A subset of the transects, including the sections of NMFS lines, will be repeated 3 times during the day, and 3 times at night during each sampling year to observe both the diel patterns in patch distribution and the persistence of observed features within a feeding season. In addition, overlapping the lines from the coarse-scale NMFS pollock survey will provide important information for the interpretation of the larger spatial scale, longer time series surveys, as well as harmonizing results from both datasets for incorporation into ecosystem models. This overlap will be critical for placing our smaller-scale, finer spatial and temporal resolution surveys in the larger context of the regular NMFS acoustic surveys and allow application of our work under the auspices of the BSIERP project toward understanding spatiotemporal patterns in the overall eastern Bering Sea ecosystem.

Adaptive sampling. Approximately half of each cruise will be dedicated to adaptive sampling of prey near predators, both those that are thought to be foraging based on their behavior as observed by real-time remote sensing (see bird and mammal sections) and those that appear to be transiting an area. The duration and area of sampling will be dictated by the behavior of the predators. Similar to the planned transects, areas that are sampled in response to predator behavior will be re-sampled several times during the cruise to observe potential differences in a given area when predators were present and when they were absent. We plan to have daily satellite phone communication with the bird and mammal telemetry crews and will receive reports on the location of foraging predators. While these will not be truly instantaneous "real time" data, the delays in point locations are short and should allow sampling of focal areas within hours of when the animal was actually on site. In addition, we will collaborate with a bird and mammal observer aboard the vessel to guide the adaptive samples more directly.

Echosounders. Along all transects, we will continuously sample using echo-sounders to provide a two-dimensional view of prey in the water column. We will combine several frequencies of split-beam scientific echo-sounders (38, 70, 120, and 200 kHz EK 60s) to map the water column from the research vessel traveling at a speed of ~2.6 m/s (5 knots). The use of split beam technology permits measurement of target strength as well as echo integration measurements. The settings that will be employed will permit the vertical resolution and range shown in Table 1. Echo-sounders will be calibrated using an indirect procedure incorporating reference targets. Target strengths at each frequency will be calculated for all individual targets. In addition, the size and geometry characteristics of aggregations of fish will be quantified, correcting for beam effects (Reid and Simmonds 1993; Diner 2001). Catch data will be used to make density estimates using echo energy integration techniques (MacLennan and Simmonds 1992).

Table I. *Technical capabilities of the split-beam echo-sounder system at each frequency*

Frequency	**Vertical resolution**	**Estimated range**
38 kHz	0.8 m	750 m
70 kHz	0.4 m	350 m
120 kHz	0.2 m	200 m
200 kHz	0.1 m	150 m

Physical Oceanography. In order to characterize the physical environment, vertical casts with a self-contained Conductivity Temperature Depth (CTD) package with a fluorometer (SeaBird 25 equipped with an Eco-flnturt) will be conducted at the beginning and end of each transect and after each net tow. This will provide information on the vertical structure of the habitat that can be compared with the measurements provided by the CTD tags that will be affixed to both the birds and seals tagged during the BSIERP Patch Dynamics Study. The Oceanographic Research Technician (Benoit-Bird's group) has extensive experience in deploying this instrument package and conducting post-cruise processing and quality control. A graduate student interested in the coupling of physical processes and biological distributions will be involved in both the data collection and will be working on the interpretation of the physical oceanographic data collected in conjunction with the acoustic and biological samples as well as the predator distribution and tag data. The student will be under the supervision of Kelly Benoit-Bird and Assistant Professor of Physical Oceanography R. Kipp Shearman at Oregon State University.

Survey Data Analysis — Acoustic Analyses (FF#2). Survey data will be used to characterize aggregations of acoustic scattering. In near real-time, raw echosounder data will be plotted as calibrated scattering strength versus depth for each frequency. In addition, a combined-frequency echogram utilizing each of the four discrete frequencies will be produced as in Korneliussen and Ona (2002). These synthesized echograms will allow rapid quantification of the relative contribution of each frequency to the total backscattering and will permit preliminary separation of scatterers by class using the methods developed for the Bering Sea by the NMFS acoustic survey group (DeRobertis et al., personal communication).

Our next analysis approach will be to identify patches in the acoustic data. Because a patch is defined as a significant spatial variation in oceanic biomass (Downes 1990), we will use geostatistical techniques post-cruise to characterize the scales of individuals and aggregations, their spacing, and the features of edges. On both the single frequency and synthetic data, the Webster method (Webster 1973) will be used to determine the edges of aggregations. A 1 m + 1 m horizontal or vertical window will be employed to determine discontinuities in density. This technique averages the density observed in each 1-m window, reducing the statistical fluctuation in the scattered field, and then looks for differences between the windows with a *t*-test. Areas of significantly higher density will be used to define both external boundaries (edges) and internal variations (patchiness). The boundaries will then be mapped in a geographic information system. This method results in sharp patch boundaries (Benoit-Bird and Au 2003b), allowing patches to be easily determined using the centroid method (Legendre and Legendre 1998).

The mean, minimum, maximum, and variance in the depth, vertical extent, horizontal extent, scattering strength at each frequency, and total scattering strength for detected patches will be calculated. In addition, combining the acoustics and the direct samples from net tows will allow us to calculate the total number of individuals in a patch, the total calories in a patch, the number of meals for a given predator in a patch and the density and caloric density of prey in a patch (see FF#5, below). These measures of patch "quality", along with patch size, will be combined into spatial maps that can be compared with predator distributions from ship-board observers and from the avian and mammalian tagging effort, along with maps that can be compared across time. This will provide information not only on the patch characteristics, but on the predictability of patches for a given predator and the persistence of individual patches once they are formed. It is critical to understand these features to model energy acquisition for predators. The approach of stratifying all samples with regard to the bottom depth will be important for integration with these models as the characteristics of each stratum have been shown to vary significantly in other areas of the Bering Sea and each predator likely spends a different proportion of their time in each stratum. A robust model will need to take those differences in residence time in each stratum into account, and have a reasonable estimate of the prey parameters and their variance for each stratum.

Integration with NMFS Surveys (FF#3). An important component of this small-scale prey survey work is the integration of the results with the much broader scale, longer time series information provided by the NMFS Bering Sea pollock surveys. The equipment used in both the NMFS surveys and the work proposed here share 4 identical instruments. The first step of data analysis will be to follow the analysis protocol developed by the NMFS team led by Chris Wilson including the frequency differencing approach for separating animals into 4 groups: Pollock, Myctophids, Euphausiids, and Capelin, as developed by Alex DeRobertis. We will be in close contact with the acoustics team at the Alaska Fisheries Science Center including the lead of the BSIERP program, Mike Sigler, to ensure complementary sampling and analysis.

The NMFS pollock surveys extensively cover the Bering Sea and have been conducted biennially since 1979. The surveys will be conducted during both of the survey years proposed here because of an additional commitment of NOAA resources. This will allow us to determine how representative the small scale patterns observed in the BSIERP Patch Dynamics Study are in the Bering Sea both in space and over time and to scale up the relevant findings.

The results obtained through the repetition of transects within a season will provide important information for the interpretation of the NMFS surveys. Our goal is to identify how short term processes impact patch dynamics. The NMFS survey takes nearly 2 months. It is unknown at what time scale significant changes in patches occur, so it is difficult to discern what temporal "smearing" is occurring by only having a single transect in a given year. Some apparently inter-annual differences, for example, may in fact be from differences occurring at shorter temporal scales that are only sampled yearly.

Direct Sampling (FF#4). During the acoustic surveys, direct sampling will be performed along sections of each transect. We will specifically target prey aggregations both horizontally and vertically using the acoustics to guide sampling. We will use both a mid-water trawl for fish and a tucker trawl for euphausiids. The nets will be equipped with a General Oceanics (Inc.) flowmeter to calculate sampling volume. We will also use a real-time pressure sensor (Simrad PI-32) to provide second-by-second depth information of the sampling gear to facilitate targeted sampling. The pressure sensor communicates with the vessel acoustically using a small, towed hydrophone, eliminating the need for a conductive cable. Samples will be sorted by species, counted, and measured at sea. Subsamples will be preserved for further analysis. A power analysis (based on average lipid levels collected from a set of fish in the Gulf of Alaska in 2006) indicates that we should collect a minimum of 28 individuals of each species in order to detect differences in average lipid content at an alpha = 0.05. As such we will attempt to collect n = 30 individuals of each species represented in at least 75% of all samples or at least 10% of the biomass in any sample from each collection event, with the understanding that not all forage species will be represented in each sample. We anticipate collecting around 5,000 prey samples over the two years of field sampling.

Squid have been identified as an important food resource for many of the focal predators in this study. Far from being acoustically transparent, squid present scattering strengths similar to other animals without a swimbladder but with a frequency spectra unlike most measured species (Benoit-Bird *et al.* 2007). Benoit-Bird *et al.* (2007) have shown that individual squid can be identified and tracked by using multi-frequency sonar techniques to a depth of at least 200 m. Whenever the unique signature of squid is detected, direct sampling will also include jigging for squid using hand-lines. The depth of jigging will be targeted using the acoustics to increase the probability of catch success, and all efforts will be made in a quantitative fashion to allow comparisons of abundance through catch-per-unit-effort (CPUE) estimates combined with acoustic density estimates, as well as identification of species present.

Prey Sample Analysis (FF#5): We will measure the energy density (KJ/g) and total caloric content (total KJ) of each prey type encountered during the directed forage patch sampling of the BSIERP study. Proximate analysis will follow the protocols of Anthony and co-workers (2000) and Ball and co-workers (2007). These techniques were used by Feldhaus (2006) at Oregon State University and all necessary equipment is present on site. Briefly, individual samples will be collected, identified, and frozen at sea at -20C. Samples will be weighed in the laboratory to the nearest 0.0001 g, measured to the nearest 1 mm TL (we will measure mantle length for squid, and carapace length for euphausiids), and then placed in a drying oven at 60C until a constant mass is achieved. Some wet mass will be lost during the freezing/storage process (Ball *et al.* 2007), but we cannot conduct the analytical weighing at sea so our wet weights will be slightly underestimated (~4% according to Ball *et al.* 2007). Because of small body size, some species (particularly euphausiids) may require pooling of individuals in order to allow us to work with sufficient masses. Total body water content will be calculated as: (wet mass – dry mass), and percent water is calculated as: [(wet mass - dry mass)/ wet mass * 100].

Fish are then homogenized with mortar and pestle and lipids are extracted from dried samples with a Soxhlet apparatus and a 7:2 (v/v) hexane/isopropyl alcohol solvent system. Extracted lean samples are then dried and re-weighed, total lipid is calculated as: (dry mass – lean dry mass) and percent lipid is calculated as: [(dry mass – lean dry mass)/dry mass · 100)]. Lean dry samples are then baked at 550-600°C for 24 h to generate ash, which is assumed to be composed primarily of skeletal minerals. Ash mass is then weighed, the ash free-lean dry mass (AFLDM, equivalent to protein content; Montevecchi *et al.* 1984) is calculated as: (lean dry mass- ash mass), and AFLDM percent as: (lean dry mass – AFLDM)/lean dry mass · 100). Energy density (KJ/g wet mass) for each prey item will be calculated as (1 – water fraction) · ([lipid fraction · 39.3] + [AFLDMF · 17.8]) (Anthony *et al.* 2000). The energetic content of lipids (39.3 KJ/g) and proteins (17.8 KJ/g) are the same as those used by Anthony and co-workers (2000). Total caloric content of an average individual prey item in a given patch is then calculated as: (Average energy density for that species in that patch · average prey weight for that species in that patch).

We will compare the energy density and total caloric content of individual patches across our stratified and adaptive sampling locations in order to estimate total calories (or KJ) available to apex predators. To scale up to the energy density and caloric content of the patch will require estimates of patch species composition, prey density, and total patch volume, which will be based on the acoustic surveys. Energy density within a patch for a given species will be based on the [average individual caloric content for that species * the relative proportion of that prey species in the patch * the average density of that species in the patch]. Total caloric content of the patch will be the [summation of the energy density of each species within the patch* the overall volume of the patch itself]. In addition, working with bioenergetics models associated with the feeding needs of fur seals, kittiwakes, and thick-billed murres, we should be able to calculate the total number of "meals" available to these upper-trophic-level predators. We will work to correlate energy density with the physical oceanographic parameters collected both on board the sampling platform (salinity, temperature, chlorophyll) as well remote sensed parameters including sea surface temperature and chlorophyll fronts. Finally, we will work with the BSIERP modeling group to evaluate the distribution of calories throughout the Bering Sea in proximity to the Pribilof Islands, and to evaluate whether patch caloric density or total patch caloric content are useful predictors of foraging behavior of the upper trophic-level predators. One-way ANOVA will be used to test for differences in patch energy content within a sampling year, and two-way ANOVA will be used to test for differences between year and location. A Tukey-Kramer multiple comparison test will be applied when significant differences are found (SAS Institute 2003). Other tests may be incorporated to test for spatial correlation in energy density associated with the results of the physical oceanography component.

POPULATION PROCESS STUDY METHODS

Marine Mammals. A fundamental goal of our study is to relate changes in foraging patches to population processes such as diet, attendance patterns, hormone levels, and population trends.

Dietary information will be gathered concurrent with the foraging data from a variety of sources such as scats (for hard part remains and prey DNA analysis), whiskers (stable isotope analysis), and stomach contents. Simulation studies indicate that 70 scats need to be collected for dietary analysis (Trites and Joy 2005). Scats will be collected for fur seals and walrus. Dietary analysis of fur seal scats will be funded by NPUMMRC or conducted in collaboration with NMML. Walrus scats will be archived and separate funding will be sought to identify the DNA of prey species contained within it. DNA dietary analysis has been developed for other species of marine mammals but has yet to be developed for walrus (Deagle and Tollit 2007). Collecting scats is necessary because concurrent access to walrus stomach samples is not possible. Native subsistence hunting occurs north of the SLIP in late spring, so stomachs collected at that time would not be representative of prey consumed within the study area. A measure of prey quality and bivalve production will be obtained from a separate ongoing project analyzing the calorie content of a wide variety of benthos species and via bivalve growth rates that are being investigated through length-weight analyses of dominant bivalves collected on previous SLIP cruises (Lovvorn *et al.* 2003). Changing environmental and benthic conditions in the Bering Sea will likely impact walruses by affecting their distribution and foraging success rates.

Body condition will be assessed for walrus from the lipid content of adipose tissue to relate changes in body condition with changes in foraging behavior, climate and prey distribution (Thiemann *et al.* 2006). Lipid stores in the blubber of walruses will reflect walruses' nutritional status after wintering in the Bering Sea. We will measure the lipid content of walruses taken during subsistence hunting in late spring as walruses migrate northward from the SLIP study area. Samples collected from walruses in spring will reflect animal condition after wintering in the Bering Sea, and hence winter prey availability and walrus foraging success. Blubber samples from 33 walruses were collected in spring 2007 to determine the best place to sample from the walrus and recommend a sampling protocol for future sampling. The study was supported by USGS, USFWS, and Eskimo Walrus Commission in collaboration with Dalhousie University. We are proposing to sample up to 100 walruses in spring in each of the study years to track inter-annual differences in walrus condition. An estimate of the number and density of walruses within the SLIP study area will be obtained by helicopter surveys based from the USCG Healy as part of marine mammal surveys supported by BEST

Blood samples will be drawn from fur seals and stored for meta-population analyses (life expectancy from telomere lengths, and population discreteness). One of the newer molecular techniques that can be applied to mammals involves measuring the telomere length in blood cells to address questions related to age-dependent physiological responses, survival, and life expectancy in individuals of unknown history (e.g., Haussmann *et al.* 2003a; 2003b). Lengths of telomeres (portions of repeating DNA that form the ends of chromosomes) indicates relative age in birds and mammals, and can serve as an indicator of an organism's age, life expectancy, and residual fitness (Watson 1972; Haussmann and Vleck 2002; Haussmann *et al.* 2003b). Telomere lengths are also related to environmental conditions and are shortened by oxidative stress (Epel *et al.* 2004; Zglinicki 2006). Thus, climate-induced physiological stress characterized by increased secretion of stress hormones and oxidative stress is likely to result in reduced longevity and lifetime reproductive success of individuals (Paulini *et al.* 2006), which in turn determines population dynamics (Stearns 1992). Funding will be sought from other sources to undertake the telomere analyses.

Fecal samples from walruses and northern fur seals will be analyzed to assess physiological stress via cortisol, and isolate nutritional stress therein via triiodothyronine (T3) and corticosterone. The analytical techniques for both hormones have been developed and validated for sea lions through previously funded NPUMMRC and ASLC studies (Trites *et al.* 2003; Hunt *et al.* 2004; Mashburn and Atkinson 2004, 2007). The integration of thyroid analysis can isolate the stress source, given that various acute and chronic environmental factors may affect physiological stress levels. The analytical combination of adrenal and thyroid hormone analyses will provide specific measures of the physiological health of these pinnipeds and the relationship with diet, timing of birth, and duration of foraging trips. Funding for the hormonal portion of this study is anticipated from NPUMMRC.

The mean date of birth and seasonal and annual shifts in the duration of foraging trips can be determined from behavioral observations (e.g., Milette and Trites 2003; Soto *et al.* 2006). Such data can be compared with historical data sets (e.g., Trites 1992) to determine the relationship between these variables and annual variations in the extent of ice cover in the Bering Sea or annual changes in the Pacific Decadal Oscillation (Mechanism – M1). It would be advantageous to undertake behavioral observations concurrently with the fine-scale foraging study to establish functional relationships between timing of birth and lengths of foraging trips relative to changes in prey density and annual differences in ice cover and ocean climate. Funding for this study portion will be sought from NPUMMRC.

Seabirds. Diet, foraging behavior, and levels of nutritional stress provide a mechanistic link between patch dynamics and population processes (Kitaysky *et al.* 2007). Many studies have related changes in foraging conditions directly to changes in seabird foraging behavior, reproductive success, and population trends (Piatt *et al.* 2006). This integrated study of the Bering Sea will document how foraging conditions change and how seabirds respond to those changes at various spatial and temporal scales., Seabirds respond immediately when food availability changes by altering their diets, foraging locations, and trip durations. Such changes are reflected in stress level. These parameters will be monitored by GPS data loggers and by examining the diets and baseline corticosterone levels of the instrumented birds. If food availability levels persist throughout the breeding season, seabirds indicate this through reproductive parameters, such as nest initiation rate, clutch size, hatching success, brood reduction, chick growth rates, fledgling success, and overall reproductive success, and through body condition of adults. Changes in size of seabird breeding colonies indicate these foraging conditions over years and decades. Methods for assessing foraging behavior using data loggers, corticosterone levels, stable isotope ratios, and diet samples are described in the previous section. Data on reproductive parameters and colony trends will be collected by the US Fish and Wildlife Service using standardized protocols that have been used for decades (Williams *et al.* 2002).

The foraging distribution of seabirds is one indicator of the distribution and availability of the prey base, and can vary seasonally and among years, with repercussions for seabird reproductive performance. The distribution of seabirds while foraging at sea will be determined at both the broad scale and fine scale. The broad scale surveys are part of BSIERP and will be conducted in conjunction with NSF-funded cruises in the northern Bering Sea (Grebmeier *et al.* 2006b) and onboard NOAA fish surveys in the central Bering Sea. The broad scale surveys encompass a greater temporal scale than does the Patch Dynamics Study, but they will overlap the two Patch

Dynamics Study sites, providing additional data on distributions of predators and prey, as well as the larger context.

SYNTHESIS OF FORAGING & POPULATION PROCESS STUDIES

Functional relationships (Holling 1965; Brown 1999; Middlemas *et al.* 2006) will be derived to relate patchiness of prey (species, densities, quality, distribution, availability) with ice conditions, oceanographic conditions, feeding conditions, and the population biology (processes) of marine mammals and seabirds. These relationships will be used in bioenergetic and ecosystem models to predict the consequences of ecosystem change.

Concurrent sampling of seabirds and fur seals, their prey, and ocean conditions will support detailed predictive models of predator distribution and relative abundance in response to prey distribution and oceanographic variables (Redfern *et al.* 2006).

RETROSPECTIVE ANALYSES

In addition to the data we propose to collect in 2008 and 2009, we would like to undertake a retrospective analysis of existing data (Table 2) to quantify the relationships we believe exist between the biological environment (prey densities) and population attributes (diet, foraging trip characteristics, energy budgets, animal size, condition, and fecundity).

Marine Mammals. (Task MM#3). Existing time series data on abundances of prey of fur seals will be analyzed to determine whether relationships exist between marine mammal populations and the biological environment. Available data include the distribution, productivity, feeding, and demographic composition of northern fur seals (NMFS, DFO, Trites 1990). Other data include fur seal diets, pup weights, pup mortality rates, mean date of birth, at-sea travel and foraging locations, duration of foraging trips, juvenile survival rates, pregnancy rates, and numbers of pups born (NMFS, DFO, Trites 1990). These measures will be correlated with data on stock sizes and prey densities obtained by NMFS and our BSIERP collaborators.

A second set of retrospective analyses will investigate the relationship between physical environment and individual behavior and population attributes (foraging behavior, offspring size, future survival and locations of breeding and foraging habitat). Differences in foraging efforts from the walruses using ice haulouts in 2008 and 2009 (preferred substrate) will be compared with those of walruses using land haulouts in the Chukchi (by Russian researchers with independent funding) to address effects on walruses when forced to abandon the ice and use terrestrial haulouts (Kelly 2001). Juvenile survival, birth rates, and pup weights (an indication of maternal foraging success) of fur seals at St. Paul Island (Trites 1990) may be indirectly related to the primary measures of the physical environment (i.e., the southern extent of ice cover, the timing of ice retreat, the PDO, mean seasonal water temperature) (e.g., Trites and Antonelis 1994). Correlations will be sought between these abiotic measures and the biology of fur seals and walruses (described above). Oceanographic data collected by our field studies will also be used to define physical conditions associated with optimum foraging and identify hotspots that might be altered by climate change. Analyzing these data sets in this context is expected to yield predictive equations to estimate the biological consequences of climate change on pinnipeds.

Seabirds. It is difficult to conduct a conclusive climate change study without long-term data. A tremendous advantage of working on seabirds at the Pribilof Islands is that there is a data-rich history of studies on population trends, reproductive parameters, and diets. Recently, Byrd and others (2007) began to examine the seabird data in relation to climate change. They found that the timing of kittiwake breeding progressed earlier as sea ice retreat occurred earlier in the spring. They also found that population trends of murres and kittiwakes at the two Pribilof islands were different, with seabirds at St. Paul declining and seabirds at St. George stable or increasing. This retrospective analysis led to the hypothesis that we propose testing in this study, namely that seabirds nesting on St. Paul are declining because of lower productivity north of St. Paul due to reduced sea ice, and seabirds at St. George are unaffected because they feed primarily at the shelf break southwest of the island. The Patch Dynamics Study will allow us to test this hypothesis by determining the foraging locations and success of seabirds nesting at each island. We will collect three years of data on oceanography, ice, forage fish, seabird diets, foraging locations, productivity, and population changes with which to examine the mechanisms behind these long-term divergent population trends.

Historic data on at-sea distribution of seabirds in both PDS sites are available through the NPPSD (primarily 1970s-1980s), and from the Pribilof Islands during 1990s-2002 (NPRB #609). More recently, NPRB #637 conducted seabird surveys in 2006-2007 in conjunction with BEST, SLIP, and NOAA research cruises. Although most of these surveys were broad-scale in design, they fill a gap in the long-term data set with which to compare the fine scale results from the PDS. We will test for spatial and temporal changes in seabird species composition at sea, from the 1970s to the present, with respect to regime shifts and changes in the prey base.

PRODUCTS

The multi-faceted approach proposed here will yield a more complete understanding of the potential effects of climate change on seabirds, marine mammals and their prey in the Bering Sea. We will predict and test the interactions between changes in the abiotic (ice cover, oceanography) and biotic environment (LTL biology, prey density and distribution) on individual animals (foraging behavior, diet, habitat preference, physiology, bioenergetics) to draw population level conclusions (births and deaths).

The forage patch dynamics component of the overall BSIERP effort is inherently well integrated with the work being conducted at both higher and lower trophic levels by our collaborators in the eastern Bering Sea. As such, our work will provide critical data for the long-term BSIERP modeling efforts with regard to the dynamics of the forage base available to both avian and mammalian predators in the Bering Sea. By making a component of our acoustic sampling scheme similar to that of the NOAA survey, as well as creating overlap in sampling space, our fine-scale mechanism-based work can be scaled up to the broader context of the Bering Sea. By working directly, in real time, with the avian and mammalian telemetry groups and by conducting both random transects and focal patch sampling as informed by the predators, we can evaluate the results of the decisions that these animals make with regard to where within the Bering Sea they feed. By examining both the nature of prey distribution as well as the quality of prey we aim to understand the mechanisms by which foraging effort is distributed and to initially characterize the current prey field available from a bioenergetics perspective. From this effort we can work toward developing the predictive power to understand how avian and mammalian population dynamics may be affected as prey fields potentially shift in a changing global climate.

The Patch Dynamic Study will contribute to understanding how the Bering Sea ecosystem functions, and how North Pacific upper trophic level predators may respond to long-term climate change and global warming. In collaboration with other NPRB – BSIERP investigators and concurrent projects (National Marine Mammal Laboratory, Alaska Fisheries Science Center, Alaska Maritime National Wildlife Refuge, and NPUMMRC), we will integrate information on inter-annual changes in food availability, diet composition and population dynamics of fish, birds, and mammals, with changes in physical processes and zooplankton communities in the shelf ecosystems of the Bering Sea. Our coordinated research will contribute to developing an integrated perspective of concurrent responses of upper-trophic and lower-trophic ecosystem constituents, which is critical to evaluating the role of top-down and bottom-up forcing in structuring marine ecosystems (Hunt and Stabeno 2002; Hunt *et al.* 2002).

While this enhanced understanding has important intellectual implications for the fields of biological oceanography and community ecology, another important contribution of NPRB – BSIERP will be to advance the ability to manage fisheries in complex ecosystems forced by climatic variability. Our results will allow resource managers to better anticipate future changes in the functioning and structure of the Bering Sea marine ecosystems, and their ability to sustain commercial fisheries and subsistence harvests. By revealing how an ice-free Bering Sea may behave differently from the current seasonally ice-covered system, this proposed research program will lay the foundations for developing adaptive ecosystem management approaches to cope with the anticipated effects of global warming in sub-arctic seas (Overland and Stabeno 2004; Sarmiento *et al.* 2004).

The study will support graduate students at the University of Alaska, University of British Columbia, and Oregon State University. The research will yield graduate theses and many peer-reviewed scientific publications that will further our understanding of the mechanisms and factors that control the dynamics of the Bering Sea.

E. Program Management

Patch Dynamics Study Leader. Dr. Andrew Trites is a Professor at the University of British Columbia in the College of Interdisciplinary Studies, Director of the Marine Mammal Research Unit (UBC Fisheries Centre), and Director of the North Pacific Universities Marine Mammal Research Consortium. He works within a multidisciplinary framework and is experienced in overseeing research programs. As Program Leader, he accepts responsibility for completing the Patch Dynamics Study.

Marine Mammals. Team leader Andrew Trites will oversee fur seal foraging behavior (Task MM#1) by a Postdoctoral Fellow supported by a university based Researcher for field work and data analyses. A second field assistant will be hired from St. Paul Island. Phil Zavadil from the St. Paul Tribal Eco will collaborate with all fur seal field work. Walrus foraging behavior (MM#2) will be done by Dr. Chadwick Jay, Walrus Research Program Leader for USGS in Anchorage. Assistance in field work will be sought from a local village representative through collaboration with the Eskimo Walrus Commission. The retrospective analysis of fur seal data (MM #3) will be conducted by Dr. Trites in collaboration with Dr. Franz Mueller. Our research complements that supported by NMFS, USGS, and NPUMMRC and is expected to leverage additional funds to augment the Patch Dynamics Study.

Seabirds. Team leader Dr. Kathy Kuletz (USFWS) will oversee the at-sea component of the Patch Dynamics Study, and its integration with the BSIERP broad-scale at-sea surveys in the northern and southern Bering Sea. The broad-scale portion of the at-sea seabird surveys is supported through BSIERP, and includes at-sea observers plus one graduate student to assist with analysis and writing. An additional seabird observer will be required for one month of surveys for the PDS fine scale surveys and diet studies. The colony and telemetry work is also funded through BSIERP and USFWS. Dr. Vernon Byrd (AMNWR/USFWS) will oversee the colony studies on seabird diet, productivity, and population trends conducted by the Alaska Maritime National Wildlife Refuge and field crews. Dr. David Irons (USFWS) and Dr. Dan Roby (Oregon State University) will oversee the telemetry studies at the Pribilof Islands, and will support a graduate student through the analysis and publication phases of the project. Additional colony work will be funded by the PDS to support Dr. Alexander Kitaysky's (University of Alaska, Fairbanks) study of stress hormones, stable isotopes, and diving behavior. Dr. Kitaysky will support a post-doctoral research associate and/or a PhD graduate student, oversee laboratory analyses (conducted by E. Kitaiskaia, a research associate at IAB, UAF), and will coordinate analysis and integration of stress physiology research. He will also coordinate analyses and integration of earlier studies of seabird diet (direct and via stable isotope analyses) and stress physiology research (Project #320, 1999-2000, 2001, 2003-2005), and diving behavior of murres (2004-2006, PI-Prof. Y. Watanuki, University of Hokkaido, Japan) conducted at the Pribilof Islands with results obtained in the Patch Dynamics Study.

Forage Fish. The forage base characterization component will provide partial support for two faculty members, two graduate research assistants, and one faculty research assistant/technician. Team leaders will be Dr. Kelly Benoit-Bird and Dr. Scott Heppell. Kelly Benoit-Bird is an Assistant Professor of Biological Oceanography at Oregon State University and has extensive experience applying acoustic sampling to predator-prey dynamics studies, including animals from zooplankton up to sperm whales. She was recently awarded the US Presidential Early Career Award for Scientists and Engineers for her work on the patch dynamics of spinner dolphins and myctophids. She will be responsible for directing the acoustic sampling at sea (FF#1) and analyzing the data (FF#2). She will work with the NMFS Alaska Fisheries Science Center teams to integrate this fine-scale study with their larger acoustic studies in the Bering Sea (FF#3). She will collaborate with Scott Heppell to integrate direct measurements of fish with the acoustics to measure patch characteristics and with members of the marine mammal and bird teams to identify key foraging areas and to synthesize data.

Scott Heppell is an Assistant Professor of Fisheries in the Department of Fisheries and Wildlife at Oregon State University. He has many years experience studying the physiological ecology of fish, and has three ongoing projects evaluating the health and condition of fish in both freshwater and marine ecosystems in Oregon and Alaska. He will be responsible for directing the targeted sampling during the forage surveys (FF#4), and will oversee the work investigating the bioenergetic aspects of forage patches (FF#5). He will work with the BSIERP bioenergetics group to incorporate the results of this work with the overall bioenergetics model being developed.

An Oceanographic Technician**,** Chad Waluk has been with the College of Oceanic and Atmospheric Sciences for 6 years and with Benoit-Bird's group for 2.5 years. He has extensive sea-going research experience. He is experienced in both the field deployment and data analysis for the acoustic echosounders as well as CTDs and fluorometers. He has recently become familiar with the operation of nets from research vessels and the use of flowmeters and the remote pressure sensing system. He will be responsible for the coordination of shipping of all OSU gear as well as borrowed net systems to and from the field operations, design and fabrication of the acoustic mount for the vessel, CTD operations at sea, supporting the acoustic and net tow operations at sea, preliminary analysis and quality control of CTD data, and initial data processing of echosounder data.

Two Graduate students will participate in the forage fish component. 1) **Physical-Biological Coupling Graduate Student.** An interdisciplinary Ph.D. student in the College of Oceanic and Atmospheric Sciences will be conducting thesis research under the direction of Kelly Benoit-Bird and R. Kipp Shearman, Assistant Professor of Physical Oceanography at COAS, OSU. This student will be integrating the physical data collected on the patch dynamics cruise with the biological samples collected to provide information on the responses of the target species to physical features. This focus on the interplay of physics and biology will be critical for interpreting the tag data provided from the CTDs on the fur seals and birds. **2) Bioenergetics Graduate Student.** A Ph.D. student in the Department of Fisheries and Wildlife will conduct thesis research under the direction of Scott Heppell, associated with the bioenergetics of forage patches in the eastern Bering Sea. The student will participate in the at-sea sampling in both years, will do the laboratory energetic analyses associated with directed sampling, and will model caloric distribution of forage organisms within the Pribilof prey field. The graduate student will integrate their work with that of the BSIERP bioenergetics group.

F. Program Timeline and Milestones

There will be two field seasons (2008 and 2009) with a third year to complete data analysis and reports. All researchers will be expected to provide preliminary findings to other Patch Dynamic Study participants within 10 months of completing each year of field work. Researchers will also be expected to give an oral presentation and discuss their findings at an annual Patch Dynamics Study meeting to be held in January 2009 and 2010 in conjunction with the annual Marine Science in Alaska Symposium. Success of the two year field program may result in a request being made to NPRB to support a third year of field work (2010).

Each of the components of the Patch Dynamics study is expected to result in one or more publications that will be led by an individual from within their respective components. Investigators from other Patch Dynamic components may be included as co-authors at the discretion of the lead author.

One publication is expected to synthesize the overall Patch Dynamics study and findings and will be led by A.W. Trites (with co-authors included from all patch-dynamics components).

Marine Mammals. 2008 and 2009: field studies on fur seal and walrus foraging behavior (MM#1 and MM#2). 2008-2011: all other tasks (MM#1, MM#2, MM#3). Annually: reports, presentations on findings. All tasks will lead to one or more peer reviewed publication per task. PIs have a strong record of publishing their findings and disseminating them to a wide audience.

Seabirds. 2008 and 2009: field studies on seabird distribution and diet within both PDS sites, and intensive colony work (foraging behavior, chick diet, productivity parameters), on thick-billed murres and black-legged kittiwakes at St. Paul and St. George islands. Annually data will be prepared and submitted to the appropriate repository: North Pacific Pelagic Seabird Database, Seabird Diet Database, Seabird Monitoring Database. 2008-2011: PIs and their graduate students will prepare progress reports and will make presentations at scientific meetings, and will publish findings and disseminate them to a wide audience, including web postings on the USFWS, OSU, and UAF web sites.

Benthics. 2008 and 2009: Field studies for benthic infaunal and sediment tracer collections, under NSF-support, with annual spring cruises in the Bering Sea using the USCGC Healy. Annually: PI presentations and progress reports at BSIERP and BEST PI meetings as well as at other scientific meetings. Graduate students theses and associated papers will result. PIs have a strong record of publishing their findings and disseminating them to a wide audience, including local communities in the Bering Sea region.

Forage Fish. 2008 and 2009: One, 30-day research cruise around the Pribilof Islands will occur in late July, early August of each of the two field years. Beginning immediately following each sampling period and continuing through 2009 and into 2010, the team will focus on sample analysis for lipid content of the prey base and data analysis of the oceanographic and acoustic information as well as synthesis with other data sets including those from the marine mammal and seabird teams. PIs and their graduate students will prepare progress reports, will make presentations at annual NPRB and BSIERP conferences and other scientific meetings, and will publish findings and disseminate them to a wide audience, including web postings on OSU websites.

G. Data Management Plan

Copies of data collected will be archived in accordance with those proposed for all BSIERP investigations.

Benthic data submission to the National Center for Atmospheric Research/Earth Observing Laboratory (NCAR/EOL) is required under NSF BEST grant requirements (J. Moore-lead for BEST data management). Pertinent data sets for the walrus-prey patch dynamics study and modeling effort will be provided on collaborative basis.

H. Outreach, Education & Coordination Plan.

The Patch Dynamics Study team will meet in Anchorage for half a day in January 2008 to finalize upcoming field plans. In subsequent years (2009 and 2010), the Patch meeting will occur over 2.5 days. All meetings will be held in conjunction with the Marine Science in Alaska Symposium sponsored by NPRB. The Patch Dynamics Study team leader will ensure the research is coordinated with BEST and BSIERP (and that findings are made available to others) through participation on the BSIERP Executive and Science Committees

Input and guidance from experts with oceanography and ocean climate would enhance the Patch Dynamic Study, as would an individual knowledgeable about zooplankton. Such expertise will be sought from the BSIERP team, with an invitation to participate in our team discussions.

Researchers will provide materials as requested by those responsible for outreach and will attempt to involve media and local people in field research where possible.

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