Introduction and Background

The U.S.GLOBEC program was initiated to develop a broader understanding of climate impacts on marine ecosystems. In this proposal we seek funds to synthesize knowledge of North Pacific krill through modeling and comparative studies across U.S.GLOBEC, Japan-GLOBEC, China-GLOBEC and related study regions. Within the GLOBEC Northeast Pacific program, our past research addressed three goals:

- Quantify how physical features in the NEP and variability related to climate change impact zooplankton biomass, production, distribution, and the retention and loss of zooplankton from coastal regions, and how these in turn influence the distributions of higher trophic levels such as forage fish, salmon and marine birds and mammals;
- Quantify the impacts of key coastal physical and biological processes on controlling juvenile salmon growth and survival in the coastal zone of the NEP;
- Compare the impacts of climate variability and change (such as ENSO cycles and PDO-related regime decadal variability) on similar marine animal populations (copepods, euphausiids and salmon) across the sub-regions of the northeast Pacific.

Within the goal of understanding climate impacts on euphausiids, we will follow two of the three research themes outlined in the U.S.GLOBEC Pan Regional Synthesis Program Solicitation:

- The response of krill populations at local and regional scales to basin- and global-scale change in climate forcing;
- Identify the processes controlling the population dynamics and recruitment of krill as a function of ecosystem type and ascertain how these processes would be affected by climate change, to be accomplished through comparing/contrasting population responses from a number of different North Pacific ecosystems.

The U.S. GLOBEC Northeast Pacific (NEP) program identified krill as target species because they are far less studied than copepods, yet they are among the most important links in coastal and oceanic food webs, transferring energy from primary and secondary producers to higher trophic level animals such as salmon, herring, sardines, mackerel, Pacific whiting, sablefish, many rockfish species, auklets, shearwaters and whales. Furthermore, GLOBEC identified the need for research that focused on krill because many aspects of their basic biology and ecology were not well understood. One species of euphausiid, *Euphausia pacifica*, is of special interest because of its broad distribution throughout most of the North Pacific Ocean (Figure 1). Across this range, it occupies a diversity of habitats, including cool upwelling regions off Baja Mexico, California, Oregon, Washington and British Columbia, the downwelling environment of the Gulf of Alaska, shelf-break waters of the Bering Sea, oceanic regions across the North Pacific Current and Sub-arctic Pacific in water north of ~ 40° N, and south through the western Pacific from Russia to China. In the western Pacific this species inhabits waters where temperatures range from sub-arctic (the Oyashio) to sub-tropical (the Kuroshio, the Japan/East Sea, and the East China and Yellow Seas). There are few invertebrate species that occupy such a wide variety of marine ecosystems and such a wide range of latitudes. Thus, we ask, what are the unique characteristics of the life history and ecology of this cosmopolitan euphausiid species that allows it not only to populate such a wide variety of ecosystems, but to become dominant among the plankton?"

Synthesis of Observations and Experiments

Because of our krill-centric U.S. GLOBEC-funded research, as well as research carried out by biological oceanographers in China, Korea, Japan, Russia, Canada and the U.S., a rapidly growing amount of information has become available on the phenology, seasonal cycles of abundance, feeding, reproduction, and growth rates of *Euphausia pacifica.* We propose to summarize much of this information into a series of multi-authored synthesis papers that focus on comparative life history and ecology of this cosmopolitan species. **Our aim is to determine unique aspects of its life history and adaptations that permit it not only to exist, but to prosper, in a wide variety of environments across the North Pacific.** Comparative studies are needed for analysis of the adaptations which allow this species to prosper in so many different regions. Armed with this basic information we will be in a better position to learn how climate change may affect their population dynamics.

The comparisons which we discuss in this proposal will also include synthesis of data on the less-well studied genus *Thysanoessa. T. spinifera* is the other dominant *Thysanoessa* species in the California Current, which, along with *Euphausia pacifica* makes up ~ 90% of the biomass of krill in the northern California Current (NCC) (Gómez-Gutiérrez et al. 2005). *T. spinifera* is a coastal species in the NCC but extends into offshore waters off northern and central California (Brinton 1962), likely because of extensive offshore transport of coastal waters in mesoscale upwelling jets, filaments and eddies. This species is the dominant euphausiid in the coastal Gulf of Alaska, however, in the Bering Sea; *T. spinifera* is largely replaced by *T. raschii* and *T. inermis. T. inermis* continues to be dominant in the western Pacific where it achieves phenomenal biomass in the Sea of Okhotsk.

We believe that our synthesis proposal to summarize the life history and ecology of these krill species has a high probability of success because we are personally acquainted with most of the krill researchers in the North Pacific. This has come about because of our 10-years of involvement in PICES, the North Pacific Marine Science Organization, an international scientific coordinating body similar to ICEDS in the North Atlantic. We have been active in the Climate Change programs of PICES (Batchelder has been co-chair of the Climate Change and Carrying Capacity program since 2001; Peterson chaired the Regional Experiments Working Group of CCCC from 1999-2006), has chaired both workshops and special sessions on comparative ecology of krill at PICES annual meetings, and now chairs the newly established Working Group 23 ("Comparative Life History of Krill around the Pacific rim" http://www.pices.int/members/working_groups/wg23.aspx). Also, a web document on the PICES webpage (http://www.pices.int/projects/Euphasiid/PICES%20Protocols%20COMPLETE.pdf) published in 2006 presents **Protocols for measuring molting rate and egg production of live euphausiids.**

Synthesis through Modeling

Another strength of PICES is the ecosystem modeling work carried out chiefly by Japanese and U.S. scientists. Many scientists within PICES have contributed to the development of NEMURO (North Pacific Ecosystem Model for Understanding Regional Oceanography) and NEMURO.FISH (NEMURO For Including Saury and Herring) and to the application of NEMURO, ECOSIM and ECOPATH models to the study of ecosystem dynamics in the North Pacific. PICES scientists would benefit greatly from a synthesis of the existing knowledge on *E. pacifica* and other euphausiids, including regional differences, so that the euphausiid component of these ecosystem models can be properly parameterized Improvements to the models will result in tools that will allow us to investigate quantitatively the role of euphausiids in food chain dynamics and the potential impacts of climate variability and change on their population dynamics.

Modeling in this project will be multifaceted, including (1) local biophysically-coupled individual-based, Lagrangian models of krill to explore detailed interactions of life-history behavior and physiology with physical conditions and transports, and (2) Eulerian, coupled ecosystem-physical models based on NEMURO modified to include euphausiids and ROMS (or other physical models). The former type of modeling will continue synthesis begun by Batchelder under a NOAA funded GLOBEC NEP synthesis project. We developed particle tracking code that links an Individual-Based Model (IBM) of euphausiid bioenergetics and behavior to velocity and temperature fields derived from Regional Ocean Modeling System (ROMS) simulations. We use physical fields derived from 10 km (NEP) and 3 km (CCS) ROMS models, but the population dynamics and tracking code will interface with other ROMS results. We are initially focusing coupled population dynamics-physical simulations in the Northern California current on 2002, for which we have the best field observations for comparison. The model, named POPROMS, runs efficiently to advect individual organisms through the domain off Oregon and Northern California. We have explored the interaction of ontogenetically determined diel vertical migration and alongshore and zonal water circulation, and specifically, we used coupled Forward-in-Time-Trajectory (FITT) and Backward-in-Time-Trajectory (BITT) simulations (Batchelder, 2006) to examine processes potentially responsible for aggregations of euphausiids along the shelf break (Ressler et al., 2002). Simulations have been done for 90 day periods spanning June, July and August 2000. We focus on BITT simulations since what we know from plankton surveys are the regions where individuals were captured, and what we wish to know is where the individuals were at earlier points in time and what conditions they experienced. Simulations are completed for scenarios where individuals are fixed to certain depths (e.g., 5 m, 35 m, 95 m), and for simulations in which individuals undergo diel vertical migrations of various amplitudes (5->35m; 5->95m; 5-205m). These different amplitude migrations are representative of the observed amplitudes of different life history stages of *Euphausia pacifica*, the target organisms of this project. We have also done simulations where the amplitude of diel vertical migration is life-stage dependent and progression through the life history is temperature dependent. Results for three BITT

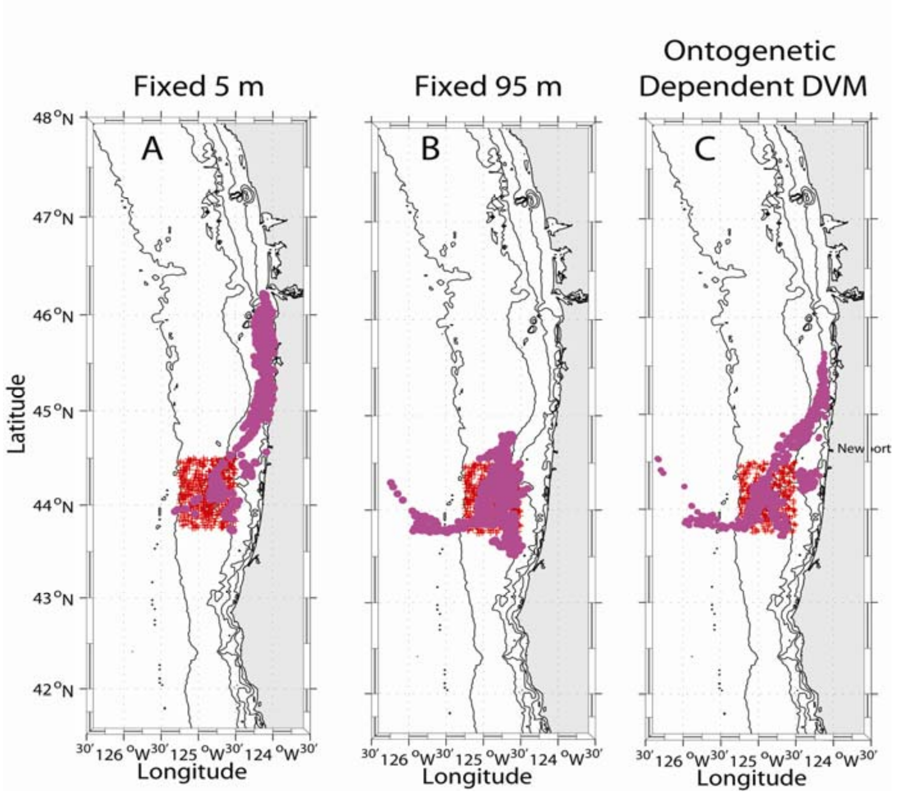

Figure 1. Backwards-in-Time-Trajectory (BITT) simulation result for the euphausiid, *Euphausia pacifica*. Purple dots show locations of particles 20 days prior to arriving at the locations near Heceta Bank identified by the red plus (+) symbols. Panel A shows the locations 20 days earlier for particles whose depths were fixed at 5 m for the duration of the simulation. Panel B shows the locations 20 days earlier for particles whose depths were fixed at 95 m for the duration of the simulation. Panel C shows the locations 20 days earlier for particles that began at the red (+) and had life-stage dependent vertical positions where the development of individuals was controlled by temperature. Youngest stages (eggs and nauplii) are nearsurface (10 m) only, whereas older furcilia life stages of *E. pacifica* undergo a DVM that spans from near-surface (10-20 m) at night to 100 m during the day. Since this was a BITT simulation, all individuals began the simulation at the red pluses (+) as furcilia 7 life-stage, and with time underwent reverse development (proceeding to ever-earlier stages).

simulation cases are shown in Figure 1. Aside from the behavioral dynamics, no population dynamics representative of euphausiids were included in these simulations. Results were shown at two scientific conferences:

> Batchelder, H. P., and E. Curchitser. Spatial patterns and processes of euphausiid aggregations in the Northern California Current: modeling interactions of flow, topography and behavior. AGU/ASLO Ocean Sciences 2006 Meeting, February 2006, Honolulu, HI
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> Batchelder, H. P., E. Curchitser, L. R. Feinberg, C. T. Shaw, and W. T. Peterson. Influence of currents, topography and behavior in controlling euphausiid distributions in the Northern California Current. PICES/GLOBEC Symposium on "Climate Variability and Ecosystem Impacts on the North Pacific: A Basin-scale Synthesis", April 2006, Honolulu, HI

More recently, the IBM has focused on including reasonably realistic biological dynamics into the POPROMS coupled model. To couple biological models with physical models we described the vital rate processes of the euphausiid, *Euphausia pacifica*. Specifically, we need to parameterize the processes of respiration, growth, and development. To complete model closure, we need to parameterize survival and reproduction; however, for the simulations we have done to date, we are considering the dynamics from egg to first juvenile (e.g., the larval stages of *E. pacifica*), thus, we can ignore reproduction. Moreover, since survival rates are quite variable and difficult to estimate from observations, we ignore mortality effects. Respiration is parameterized as an allometric (individual weight dependent) function that includes a fixed cost and a variable cost related to consumption. Growth is allometric and depends primarily on food consumption, but also secondarily on environmental temperature. Development rate is stage based and dependent on a nonlinear Belehradek function between temperature and stage duration (using data reported in Ross, 1982 and Feinberg et al., 2006). Since the earliest life stages—egg, nauplius and metanauplius stages are non-feeding—we focus on only the feeding larval stages (Calyptopis-1 to Furcilia-7). We assume a Calyptopis-1 of *E. pacifica* has an initial biomass of 3 μg C. Since, both respiration and growth are food dependent, we need to specify the spatial distribution and concentration of food resources throughout the model domain, and through time. The physical simulation is not coupled with a lower trophic level ecosystem model, so instead we use the spatially mapped fields of chlorophyll estimated from the spring and summer GLOBEC SeaSoar surveys in 2002. We obtained the irregularly spaced SeaSoar chl-a data from the US GLOBEC data server and regridded the June and August surveys to a regular rectangular grid. We developed routines to interpolate chl-a to an individuals location in space from the gridded fields. We assumed a linear interpolation in time between the two temporal 3D maps of chlorophyll.

Individuals initialized to specific starting locations were examined for several specific cases: (1) fixed location, but dynamically evolving temperature and prey fields, (2) horizontal advection, with dynamically evolving temperature and prey fields, but individuals fixed to specific depth horizons (e.g., 5m, 35m, 85m, etc.), and (3) horizontal advection, with dynamically evolving temperature and prey fields, and vertical position controlled by stage (e.g., temperature) dependent diel vertical migration. Simulations were run from June 1 to August 30. Since development and growth are primarily dependent on temperature and food concentration, respectively, we expected to find that there would be locations where growth was fast, but development was slow and vice versa. In upwelling regions, like the Oregon region studied here, nearshore, cold water regions have high food (slow development, fast growth), while offshore warm water regions have low food (fast development, slow growth). Realistically, the only places where *E. pacifica* are likely to survive are locations where a balance of growth and development is achieved. Case 1 (fixed location) simulations show that growth is best in nearshore regions and poorest in offshore regions. In Case 2 (horizontal, fixed depth) simulations, larval euphausiids that start on the shelf on June 1 are mostly advected off the shelf within 30 days, with the duration of shelf residence also partially controlled by the depth at which the individuals are fixed. When individuals are advected off the shelf and into generally low-food environments, weight of the individual begins to decrease as respiratory losses at high temperatures offshore exceed consumptive gains. In general, DVM (Case 3) moves animals between shallow depths during the night and deeper depths during the day, but this vertical movement alone was not sufficient to retain individuals on the shelf for more than about 30 days—eventually, most individuals ended up offshore, perhaps because of the influence of two large eddies off the shelf in the domain. Results of this research were shown at several scientific conferences or workshops:

Batchelder, H. P., and B. J. Lindsey. Modeling interannual variation of spring-summer transport of plankton and juvenile salmon in coastal regions of the Northeast Pacific. PICES 15th Annual Science Conference, Yokohama, Japan. October 2006.

Batchelder, H. P. An Ecosystem Modeler's Expectations of Ocean Physics Models. Workshop on "Climate Impacts on the Gulf of Alaska Large Marine Ecosystem", Juneau, AK, February 2007.

Batchelder, H. P., B. Lindsey, E. Curchitser, and W. T. Peterson. Modelled growth and development of *Euphausia pacifica* in the Northern California Current. 4th International Zooplankton Production Symposium, Human and Climate Forcing of Zooplankton Populations. Hiroshima, Japan. June 2007.

Lindsey, B. J., and H. P. Batchelder. A *Euphausia pacifica* bioenergetic model for the California Current system. PICES 16th Annual Science Conference, Victoria, BC, Canada, Oct-Nov 2007.

The NEMURO model has become a de facto standard ecosystem model for pan-regional comparisons in the North Pacific (Batchelder and Kashiwai, 2007; Werner et al., 2007). The base lower trophic level NEMURO model has 11 state variables: dissolved nitrate, ammonia, and silicate; small and large phytoplankton; small, large and predatory zooplankton; particulate silica and organic nitrogen; and dissolved organic nitrogen (Kishi et al., 2007). The base NEMURO model has been extended in various ways, depending on the specific application and scientific interests, including extension to include carbon biochemistry (Fujii et al., 2007) and higher trophic levels, in particular to describe growth and population dynamics of saury and herring (Megrey et al., 2007b; Rose et al., 2007; Mukai, et al., 2007; Ito et al., 2007). NEMURO has been used to examine interdecadal variability (Aita et al., 2007) and regional differences (Megrey et al., 2007a). It has not been extended to model the dynamics and energetics of krill. That is a goal that this synthesis project will pursue, esp. as a collaboration of Batchelder and Professor Michio Kishi (Tokyo University). Dr. Kishi is one of the originators of the NEMURO project and has expressed great interest in working with us to develop a model that can represent krill. This is especially important given the recent emphasis on linking NEMURO to various fish species, as none of the three zooplankton state variables in the present version of NEMURO is parameterized in any way like krill would need to be. Addition of a krill state variable to NEMURO would not only enable prediction of krill dynamics in multiple Pacific regions, but would also significantly improve representation of processes linking plankton production to fish.

Synthesis of U.S.GLOBEC Observations: Copepod and Krill Observations off Oregon

Because of funding from U.S. GLOBEC, NOAA, and the Bonneville Power Administration, we have accumulated and compiled an extensive long-term data set on observations of ocean conditions in coastal waters of the Pacific Northwest (Figure 2), and on the nutrients, phytoplankton, copepods, krill, ichthyoplankton, sardines, anchovies and juvenile salmon that live within these waters. The data have come from three time series.

The Newport Time Series. The Newport time series was established in 1996 and is based on biweekly cruises off Newport OR (44°40'N). Seven stations are currently sampled across the continental shelf and slope, at distances of 1, 3, 5, 10, 15, 20 and 25 nautical miles from shore in water depths ranging from 20 m to 300 m. Sampling includes a CTD profile (Seabird 19+ with WetStar fluorometer and Seabird 43 oxygen sensor), secchi disc depth, a surface sample for nutrients, phytoplankton species and chlorophyll, a vertical plankton net tow from 100 m to the surface (or from 5 m off the bottom to the surface in shallower waters) with a ½ m diameter 200 µm mesh net, and an oblique Bongo tow of the upper 20 m (60 cm diameter, 333 µm mesh net). Since 2001, most of these cruises have been at night so as to collect adult euphausiids. During the night-time cruises, euphausiids from one side of the bongo tow are used for live animal experiments -- we incubate individual krill in 500 ml or 1 L jars, 30-60 individuals for molting rates and up to 20 females for brood size measurements. Animals are also returned to the shore laboratory as needed for other experiments on developmental rates, long-term variations in brood size and inter-brood periods, and grazing rates. Data on distribution and abundance of copepods, euphausiid eggs, larvae, juveniles and adults from these cruises is supplemented by a wealth of historical data on hydrography, copepods and euphausiids from samples collected in 1969-1973, 1983, 1990-1992 (copepods and euphausiid eggs and larvae) and 1963-1967 (Smiles and Pearcy, 1971) and 1971-1972 (Gomez-Gutierrez et al. 2005) for juveniles and adults.

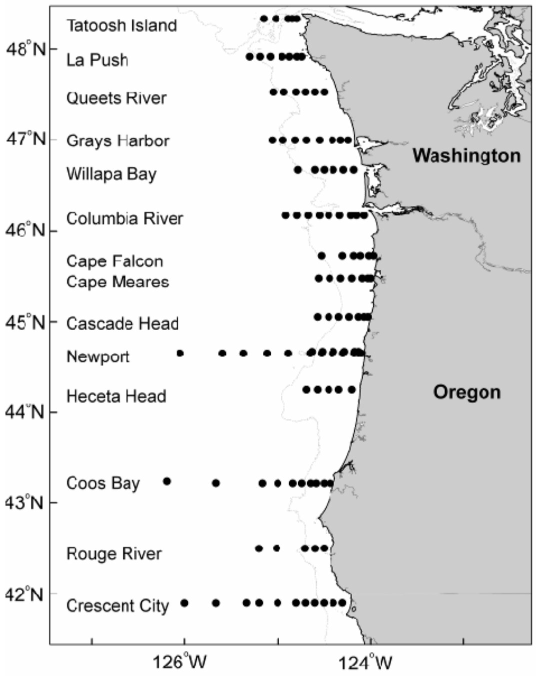

Figure 2. A chart showing station locations sampled by three different programs. The **Newport Line** hydrographic and plankton time series includes biweekly sampling at seven stations located from nearshore (water depth 20 m) to beyond the shelf break (water depth 300 m), since 1996. That program enters its 13th year in 2008. **GLOBEC-LTOP** sampled from Newport south to Crescent City, in April, July and September, for hydrography and zooplankton from 1998 to 2003, and sampled Newport only out to 85 miles in February and November. We continue to sample these transects when NOAA shiptime becomes available. **Bonneville Power Administration (BPA)** Hydrography-plankton-pelagic fish-salmon surveys sample 50 stations along nine transects from Newport north to LaPush, in May, June and September, since 1998. An additional **BPA** survey provides high-frequency data on hydrography, plankton and pelagic fish collected biweekly along the Columbia River and Willapa Transects, from late April through August, 1998-present.

The GLOBEC LTOP Time Series. We also sampled zooplankton and euphausiids at ~ 40 stations, ranging from 1-85 nautical miles from shore and water depths to ~4000 m along five transects from Newport south, in February, April, July, September and November as part of the GLOBEC Long Term Observation Program (LTOP) cruises. Physical, chemical and chlorophyll data are available on line for each station (http://ltop.oce.orst.edu/~ctd/index.html). We also sampled zooplankton at ~100 stations during each of four GLOBEC "mesoscale" cruises (MESO) in June and August 2000 and 2002, and mapped oceanographic features and zooplankton from Newport south to Crescent City, to resolve finer-scale and feature-specific copepod and krill distribution and abundance associated with eddies, meanders, the upwelling jet and upwelling filaments. For both the LTOP and MESO cruises, zooplankton was sampled with a ½ m diameter (200 µm) net towed vertically from 100 m to the surface, and a 1 m^2 MOCNESS (333 µm) in depth-stratified tows from 500 m to the surface.

The Bonneville Time Series. The relevant feature of the Bonneville time series is that it includes zooplankton sampling as described above, thus (as with GLOBEC-LTOP time series), we are able to place the Newport time series within a spatial context.

Synthesis of Krill Ecology in Coastal Waters off Oregon and Washington

The Newport time series is now of sufficient length (13 contiguous years) that when coupled with the historical data sets from the 1960s and 1970s, the potential impacts of climate change on lower trophic level organisms (copepods and euphausiids) can be investigated. Moreover, we can compare our seasonal cycles of temperature-chlorophyll-copepods-euphausiids to cycles associated with the PDO, NPGO and ENSO. The observation that the PDO has cycled at a much higher frequency lately has provided us with a natural experiment that will allow us to infer mechanisms by which the ecosystem change might be related to PDO cycles; some of these are discussed for copepods in Hooff and Peterson (2006). Global warming appears to be accelerating (IPCC 4th AR), and to investigate how warming will impact ecosystems, we will need "baselines", which we now have, based both on recent data (1996-present) and on data from the late 1960s and 1970s. From our recent work on north Pacific krill, we accomplished the following:

1. **Krill biomass** peaks in autumn, as juvenile stages that were born during the July-August phytoplankton blooms that result from summer upwelling. These juveniles become the adults that may spawn as early as the following winter (if a February phytoplankton bloom occurs), spring and summer.

2. **Stage-specific development times** and **developmental pathways** were worked out in laboratory experiments in which individuals were raised from eggs and maintained in the laboratory for more than two years. Detailed information on developmental rates and progression through instars resulted from daily examination of larvae from egg to juvenile (Feinberg et al. 2006). These known-age animals were also used to **calibrate the lipofuscin technique** for *Euphausia pacifica* which was subsequently used to age wild populations and specifically reproductive females (Harvey et al. submitted).

3. **Egg production** was further investigated by measuring brood size of females collected and incubated during cruises (Gomez-Gutierrez et al. 2006; Gomez-Gutierrez et al. 2007). Potential differences in brood sizes and interbrood period (IBP) were investigated for two populations of *E. pacifica* (Oregon and Santa Barbara, CA) and we found the brood size was the same but IBP was one day shorter for the Santa Barbara females, 4 vs.5 days (Feinberg et al. 2007). We also compared the brood size of *E. pacifica* females from Japan, Puget Sound and Oregon and found that brood sizes were the same after correcting for female body length (Gomez-Gutierrez et al. 2006).

4. **Growth**. Euphausiids have a strong cohort age structure (Smiles and Pearcy 1971; Brinton 1976; our own unpublished data). We have shown from cohort data that growth rates estimated from cohort analysis are similar to growth rates estimated from incubations of animals collected during our cruises (Shaw et al., in preparation).

5. **Molting**. Intermolt periods, measured from molting rate incubations, range from 2-20 days with a median of 8-10 days (Shaw et al., submitted). We have also staged animals in the molt cycle by examining development of setae in the uropods (following Dexter 1981). We refined her work and have shown that one can estimate molting rates from preserved samples by staging animals and then using the proportion of individuals in pre-molt stage as an indicator of the animals that should molt within 48 hours (Jarvis et al. in prep).

6. **Feeding**. *E. pacifica* feeding rates on suspensions of *Rhodomonas salina* were determined at concentrations ranging from 50 to 800 μg L^{-1} (Sremba and Peterson, in prep). Animals could consume up to 30% of their body weight per day. Trials with foods of others sizes showed that they could feed on cells as small as 4.5μm diameter (*Isochrysis galbana*). Perhaps this is one adaptation that allows them to prosper not only in coastal waters but in open ocean waters where cells are typically of this size. Analysis

of the lipids in wild *E. pacifica* indicated the importance of diatoms in their diet, but a comparison to the lipids found in the seston also suggested a degree of selective feeding (Ju et al. 2004, 2006).

7. **Cross shelf distributions**. *Thysanoessa spinifera* is usually found only in shelf waters except in one year, 2002 – during this summer females were consistently found offshore. *E. pacifica* are most abundant at and beyond the shelf break, however they are carried into the nearshore upwelling zone with the deep upwelled water in the same manner as described by Peterson et al. (1979) for *Calanus marshallae*. Shoreward transport of adults during the July-August peak period of upwelling and phytoplankton blooms often results in spawning and may lead to egg concentrations in excess of 1000 eggs m^{-3}. Larvae are subsequently found at greater distances from shore with ontogeny (Feinberg and Peterson 2003 and unpublished data). Predation by large scyphomedusae may result in high mortality of euphausiid eggs in this nearshore zone (Suchman et al. in press).

8. **Diel Vertical Migration**. DVM was investigated from analysis of more than 300 samples from 40 MOCNESS tows. In shelf waters, eggs are found only near the surface whereas in deep off-shelf waters, eggs are usually found at depths > 200 m. The first developmental stage to perform diel vertical migrations is Furcilia III (Vance et al. in prep). This is also the stage where all swimming appendages first become well developed. In oceanic waters, adults migrate from depths of 200-300 m; in shelf waters it would appear that adults reside on or very near the sea floor during the day (Ressler et al. 2005) but migrate to the surface at night.

9. **Ciliate-Euphausiid interactions**. We discovered that a ciliate, *Gymnodinioides pacifica*, can invade the bodies of *E. pacifica* and *T. spinifera*, consume the internal organs and, through rapid cell division, cause the adults to rupture (Gómez-Gutiérrez et al. 2003). Other species of ciliates consume the organic matter that remains inside euphausiid molts (Landers et al. 2006, 2007) suggesting that the idea of Jerde and Lasker (1966) that euphausiid molts are an important source of organic matter to the deep sea is unlikely.

Synthesis and Resource Assessment and Management

A final aspect of krill ecology that needs investigation is the degree to which euphausiids can be harvested commercially. Nicol and Endo (1999) provide a fascinating review of this issue. *Euphausia pacifica* is currently harvested off the northeast coast of Honshu (Japan) and in the Strait of Georgia (Canada). Presently, harvest of *E. pacifica* in the California Current is prohibited (Anon, 2005, and website for PFMC) however that ban has now been challenged. Given the cap on harvesting *Euphausia superba* in the Antarctic, we can expect continued pressure from commercial fishers to increase harvest of North Pacific krill populations. Our synthesis activities will provide the information needed to conduct a formal stock assessment, as required for nearly all managed fisheries.

Proposed Research

Through synthesis of our own data as described above, and through synthesis activities carried out in collaboration with our PICES colleagues (described on page 11, "State of our Knowledge of *Euphausia pacifica* Ecology"), we propose to evaluate and publish on a set of basic research questions, which include:

- What are the seasonal variations in distribution, abundance, growth rates and brood sizes in krill populations, and how do they vary regionally around the Pacific Rim?
- Are growth rates and brood sizes related to seasonal cycles of primary production?
- How do populations in the eastern and western Pacific respond to ENSO and PDO cycles?
- How are individuals of the same species (*Euphausia pacifica*) adapted to survive year-around in

the very warm water regions of the Yellow Sea, East China Sea and Japan/East Sea; what mechanisms enable individuals to survive the long winters in northern regions, e.g., the Gulf of Alaska, Sea of Okhotsk and northern California Current?

- What interactions between physical transport and life-stage dependent dynamics control the local scale distributions of krill and are similar interactions important at regional and basin-scales around the Pacific?

Synthesis which focus' on a single species, *Euphausia pacifica,* provides a common starting point for international exchanges and partnerships, largely because of these species broad distributions. Scientists from the PICES nations have information and experience to share, and all would benefit from an increased understanding of this species. Moreover, synthesis work proposed here will further foster the exchange of ideas and will promote long-term collaborations among a culturally diverse set of established research scientists as well as graduate students and young investigators from the PICES nations. *Thysanoessa* spp. will also be investigated, however the biology and ecology of this genus is at present far less well known than for *E. pacifica* thus we focus our efforts on the latter species.

Objectives

1. Data and Metadata. We have already begun to obtain copies of all published research papers on *Euphausia pacifica*, and the three *Thysanoessa* species, as an activity under PICES WG-23. For papers, monographs, and theses written in languages other than English, the abstracts, figure captions and table legends will be translated by M. Kishi (Japanese), H. Bi (Chinese), and Y.-S. Kang (Korean). We are working now to identify Russian translators of similar documents. Research results that are deemed critical but which are unavailable in peer-reviewed journals (theses, tech reports, cruise reports) will be translated fully then scanned so that an electronic file is created. All papers will reside on our server as well as on the PICES server to assure broad availability to all PICES and krill scientists worldwide. This activity will constitute one of our legacy products.

2. State of our Knowledge. One of our key synthesis activities will be to devote considerable effort towards distinguishing what is known from what is not known. Thus, once all published and unpublished work (e.g., theses, tech reports, etc.) have been identified, they will be reviewed to identify gaps in our understanding of krill ecology and population dynamics. Subsequently, members of the PICES WG 23 will summarize these gaps into a "Research Needs" document that outlines ideas for future research to be conducted by students within their respective countries. We will further refine knowledge gaps by asking each WG member to summarize what they *believe* to be known on "key attributes of krill life history and ecology" that pertain to *E. pacifica* and *Thysanoessa* spp. in their local/regional waters. Once we know "everything" that is known, we will determine what kinds of overview and synthesis papers can be written.

3. Collaborative Papers. This activity will include papers written by members of our team. Where possible, within national constraints, the data discussed in each paper will become part of our database, and thus a legacy product. In some cases, scientists from several nations would collaborate on joint papers whereby each author would analyze their own data following the same techniques and using a common set of illustrations to facilitate comparisons. Our target journal would be Progress in Oceanography with the recent paper by Heath et al. (2007) as a good example of a collaborative paper. A list of potential topics is discussed below.

4. Monographs. A number of classic krill publications which are frequently referenced need to be updated, based on knowledge accumulated with GLOBEC funding as part of the Northeast Pacific program, as well as research around the Pacific Rim that has been published in the peer reviewed literature. Some examples include the distribution charts in Brinton (1962), general biology and ecology in Ponomareva (1963), Mauchline and Fisher (1969) and Mauchline (1980), growth, reproduction, survivorship in field studies (Brinton 1976), Special Section on krill that appeared in the Can. J. Fish Aquat. Sci (2000), and the book edited by Everson (2000) on krill biology, ecology and fisheries. The monograph which we will produce will follow the format of the book by Everson (2000), and will serve as a GLOBEC legacy product.

Topics which will be covered in our Collaborative Papers and Monographs include the following:

- Biomass and seasonal cycles where possible of abundance of eggs, larvae, juveniles and adults of *E. pacifica* and *T. spinifera* within the GLOBEC-Northeast Pacific Region: the California Current (CalCOFI region, Monterey Bay and northern California Current off Washington and Oregon), coast of Vancouver Island, Inland waters (Puget Sound, Strait of Georgia, Dabob Bay and Barkeley Sound), Gulf of Alaska/Prince William Sound, and shelf-break waters of the eastern Bering Sea.

- The same exercise, by our colleagues in the western Pacific (Yellow Sea, Japan/East Sea, Oyashio and Kuroshio Currents, Sea of Okhotsk, and western Bering Sea).

- Parameters of population dynamics and variations along latitudinal gradients, pan Pacific:
    - Spawning and recruitment
    - Age structure, sex ratios
    - Eggs and larval abundances; survivorship and mortality schedules where possible.
    - Growth estimated from cohorts vs. growth estimated from direct measurements of growth from molting rate determinations
    - Brood size and interbrood periods

- Comparative life history of *E. pacifica* in coastal waters around the Pacific Rim. Here we discuss differences in life history strategies, such as over-summering in Yellow Sea (where surface temperatures exceed 25°C); over-wintering off Oregon and in the Gulf of Alaska (when there is no primary production for at least three months); shrinking as a strategy for reducing metabolic rates; spawning seasons in relation to seasonal cycles of phytoplankton biomass and production; developmental pathways/instars; seasonal cycles of abundance, biomass and age structure in relation to seasonal cycles of temperature and phytoplankton production.

- Cross shelf distributions of eggs/larvae/juveniles/adults to look at population maintenance strategies, cross-shelf transport, hot spots. Data are available from Oregon, Canada and Alaska GLOBEC regions, and from monitoring programs off Hokkaido (A-Line) and Honshu, Japan (PM Line).

- Vertical distribution and diel vertical migrations of developmental stages.

- Models. Use one model in several places (NEMURO). Use different models in different places (IBMs). Use ECOPATH for California Current developed by T. Wainwright (NOAA/Fisheries Newport).

- How will climate change affect krill populations around the Pacific Rim? We have a number of thoughts on this for euphausiids in the California Current, and discuss them later in this proposal. This topic will also be treated by the PICES WG 23 since it is likely that large-scale climate forcing will express itself regionally in fundamentally different ways.

Our strategy to produce a monograph on krill ecology is to first communicate with krill scientists about our vision for this book, then enlist their assistance in developing an outline of chapters, form collaborative writing teams, produce the team-written chapters, revise and complete publication. Our goal is to begin this process at the inaugural workshop of the PICES Working Group 23 "Comparative Life History of Krill around the Pacific Rim" that will be held at PICES 17 in Dalian, China in October 2008. Informal, iterative discussions about the monograph structure will occur via email between then and spring 2009, when a krill symposium will occur in Paris (see the next numbered item). At that meeting, the chapter structure will be determined and lead authors determined. First complete drafts of the chapters will be submitted to the monograph editors (Peterson, senior editor) by 1 February 2010. Several chapters might even be the basis for presentations at the final US GLOBEC symposium (Washington, DC, spring 2010). After reviews and revisions are complete, we expect publication of the krill monograph by summer 2011, perhaps with PICES co-sponsorship (PICES not approached yet about this).

5. Convene Symposia. So Kawaguchi (CSIRO, Tasmania) and Bill Peterson (NMFS, U.S.) convened a Krill Symposium at the 4th International Zooplankton Production Symposium in Hiroshima Japan in May 2007. This Symposium accommodated 42 contributions (18 oral presentations and 24 posters) and hosted > 100 scientists. The Symposium resulted in the preparation of a Special Issue of Deep-Sea Research, expected in July 2008. The overwhelming success of this venture led to recommendations by attendees that we convene another Krill Symposium, which is now planned to coincide with the final GLOBEC Open Science Meeting in Paris in May 2009. We also plan another Krill Symposium for the PICES-20 meeting in October 2011. Both symposia will include a special journal issue.

State of our Knowledge of *Euphausia pacifica* Ecology*

1. Seasonal cycles of biomass/abundance, spawning and recruitment

California. Brinton (1976, and many publications in CalCOFI Reports), Marinovic et al. (2002), Brinton and Townsend (2003), Abraham and Sydeman (2004), Croll (2005), Dorman et al. (2005)

Oregon/Washington. Hebard (1966), Laurs (1967), Smiles and Pearcy (1971), Pearcy (1976), Feinberg and Peterson (2003), Gómez-Gutiérrez et al. (2005, 2007)

Vancouver Island. Mackas et al. (1997), Tanasichuk (1998, 1999 and 2002)

Inland waters of Washington and British Columbia. Heath (1977), Hulsizer (1971), Cooney (1971), Ross et al. (1982), Bollens et al. (1992), Kunze et al. (2006)

Gulf of Alaska. Coyle-GLOBEC LTOP data; Cooney et al. (2001), Pinchuk and Hopcroft (2005)

Japanese Coastal Waters. Taki (2004) Iguchi et al. (1993, in Japanese), Taki and Ogishima (1997, in Japanese), Taki et al. (1996, in Japanese)

Korean Coastal Waters. Hong (1969), Rebstock and Kang (2003)

Yellow Sea. Cai (1986, in Chinese), Suh et al. (1993), Yoon et al. (2000), Wang et al. (2003, in Chinese), Liu et al. (submitted)

2. Distribution

Brinton (1962), Pearcy (1976), Simard and Mackas (1989), Nishikawa et al. (1995), Taki et al. (1996, in Japanese), Brinton and Townsend (2003), Ressler et al. (2005)

3. Developmental rates, developmental pathways (stages, instars)

Boden (1950), Ross (1981), Suh (1993), Iguchi and Ikeda (1994), Rumsey and Franks (1999), Pinchuk and Hopcroft (2005), Feinberg et al. (2006)

4. Egg production, brood sizes, interbrood period

Ross et al. (1982), Iguchi and Ikeda (1994), Tanasichuk (1998), Liu and Song (2002, in Chinese), Gómez-Gutiérrez (2002), Pinchuk and Hopcroft (2005), Gómez-Gutiérrez et al. (2006 and 2007), Feinberg et al. (2007),

5. Growth and age structure of cohorts

Lasker (1966), Smiles and Pearcy (1971), Brinton (1976), Bollens et al. (1992), Iguchi et al. (1993, in Japanese), Taki and Ogishima (1997, in Japanese), Tanasichuk (1998), Taki (2004), Liu et al. (submitted), Shaw et al. (in prep)

6. Molting rates/growth rates in incubations

Jerde and Lasker (1966), Dexter (1981), Bollens (1992), Iguchi and Ikeda (1995), Marinovic and Mangel (1999), Pinchuk and Hopcroft (2006), Shaw et al. (submitted)

7. Feeding rates and role as grazers

Lasker (1966), Parsons et al. 1967, Ohman (1984), Dilling et al. (1998), Passow and Alldredge 1999, Nakagawa et al. (2001, 2003, 2004) Bargu et al. 2006, Sremba and Peterson (in prep.)

8. Cross shelf differences in larval abundance

Feinberg and Peterson (2003), Lu et al. (2003), Gómez-Gutiérrez et al. (2005)

9. Diel Vertical Migration

Brinton (1962, 1967), Youngbluth (1976), Bollens et al. (1992), Iguchi et al. (1993, in Japanese), Iguchi (1995, in Japanese), Taki et al. (1996, in Japanese), Rumsey and Franks (1999), Nakagawa et al. (2003), Kunze et al. (2006), Liu et al. (submitted)

10. Swarming

Terazaki (1980), Endo (1984), Odate (1991, in Japanese), Kotori (1995), Nishikawa et al. (1995)

* Similar, but fewer in number, references could be compiled for *Thysanoessa spp*.

Ongoing Research Relevant to this Proposal

A large number of research programs are in place around the Pacific Rim that continue to sample krill on a routine basis and/or experiments on living krill. These are summarized briefly below so that referees can become somewhat familiar with the breadth of ongoing research on North Pacific krill. PICES scientists, and especially members of WG 23, are uniquely capable of increasing our understanding of euphausiids because many oceanographic stations and monitoring lines have been and continue to be, routinely sampled for hydrography and zooplankton. Using our published sampling and experimental protocols (op. cit), PICES scientists have learned how to collect living animals (easily done at night) and to make measurements of reproduction, molting and growth rates following protocols we published on the PICES website.

a. IMECOCAL, since 1997, off Baja Mexico, since (Lavaniegos and others, Mexico)
b. CalCOFI, since 1950 (Ohman and others, Scripps)
c. Monterey Bay and CalCOFI Line 67 (Marinovic)
d. Gulf of the Farallones; field sampling of krill using nets and acoustics, plus sampling of krill in seabird stomachs (Sydeman)
e. Newport Line; since 1996 for eggs and larvae; since 2000, all stages, eggs through adults, at night (Peterson)
f. Spatial surveys of eggs and larvae (Newport north to the tip of Washington state), June and September (Peterson)
g. Canada. Quarterly surveys off Vancouver Island Shelf (Mackas)
h. Canada. Barkley Sound. Monthly surveys since 1992 (Tanasichuk)
i. Gulf of Alaska. GLOBEC LTOP data along Seward Line since 1998. Continuing with North Pacific Research Board funding (Hopcroft)
j. Bering Sea. Multi-year surveys by NOAA (Napp) and others (Coyle). Three year study recently funded by NSF/BEST program (Lessard).
k. Russia. Routine sampling in Sea of Okhotsk, some in collaboration with Japan
l. Japan. A-Line and PH Line off Hokkaido and Honshu (Hokkaido Univ and Japanese National Fisheries Research Institute; Okazaki)

m. Korea. Bimonthly CTD and plankton sampling around all sides of the Korean peninsula (Kang and others)
n. China. Monitoring of ocean conditions in the Yellow Sea and East China Sea (Sun Song and others from institutions in Qingdao).

Climate Change and Krill in the California Current

Climate change is likely to affect krill populations in different ways when the eastern, northern and western North Pacific krill populations are compared. The main thrust of our pan-Pacific krill-and-climate change synthesis activities will be directed at comparing the response of local krill populations to basin-scale forcing: PDO, NPGO and ENSO. Below we suggest ways that California Current krill may be impacted.

Several key factors affect ocean conditions and living marine resources of the northern California Current. Climate change will affect each of these factors in uncertain ways:

1. Source waters which feed the northern California Current. Different source waters feed the northern California Current as a function of the strength and phase of the PDO, NPGO and ENSO. Negative phase of the PDO results in the transport of cold waters (and the zooplankton which they contain) from the subarctic whereas water types that characterize the positive phase of the PDO have an offshore or southern subtropical origin (Hooff and Peterson 2006). The results of alternating signs of the PDO are food chains that are anchored by large, lipid-rich cold water copepods when the PDO is negative, but small lipid-poor warm copepods when the PDO is positive. This has implications for salmon; their survival is poor when PDO is positive but high when PDO is negative (Peterson and Schwing 2003; Logerwell et al. 2003). The PDO is primarily a temperature signal, and is the dominant source of temperature variability in waters north of about 40°N, whereas the NPGO signals are in salinity, nutrients and chlorophyll and are primarily seen south of 40°N. Both the PDO and NPGO signals are clearly seen in the western Pacific, their role in controlling source waters is still under investigation (and is a theme of a proposal submitted by DiLorenzo and others to this announcement). It is not known if the PDO cycles in the future will be decadal as observed in the 20th century, if they will continue on their present 4-year cycle, or if the PDO will disappear altogether. According to model output shown in the IPCC AR4, the PDO may become overwhelmed by a warming ocean by 2030, suggesting that the California Current may shift to an ecosystem that is primarily subtropical in nature, with a loss of salmon populations but an increase in warm-water fishes such as tunas. This change is likely to have a negative impact on *Thysanoessa spinifera* as they showed a marked decline on the Oregon shelf during the 1997-1998 El Niño event, but it is unclear what the impact would be on *Euphausia pacifica*, a species that has successfully adapted to such a wide range in ocean conditions around the north Pacific.

2. Strength of coastal upwelling. Upwelling may become stronger (Bakun 1990) with a warmer planet, due to more intense gradients in atmospheric pressure between the land (over western North America) and the sea (the North Pacific High). However, the IPCC climate models do not yet have sufficient spatial resolution to simulate coastal processes. Another scenario is if the ocean warms and becomes more stratified, regardless of the strength of upwelling winds, they will become less effective at bringing cold, nutrient rich water to the sea surface. Seasonal upwelling is critical to euphausiids because spawning does not tend to start until upwelling does and the most intense spawning is in July/August, at the height of the upwelling season. Irregularities in the onset of upwelling may greatly impact euphausiid egg production. For instance, in summer 2005, the upwelling season was delayed by several months and no spawning was observed until upwelling began in late July.

3. Spring transition and seasonal reversal of coastal currents: Coastal waters flow southward in summer, and northward in winter (Peterson and Miller 1977), with the reversals occurring at the beginning and end of the upwelling season. If the transition to the upwelling season in spring is earlier, southward flows begin earlier, a situation which has a positive impact on the major marine fisheries in the northern California Current (whiting, sablefish, rockfish, and salmon). Thus, phenological changes in circulation and plankton production will be a theme of our comparative collaborative work. An example of the importance of phenological events are the late-winter phytoplankton blooms observed in February, since 2003 that have stimulated February spawning by *Thysanoessa spinifera*.

Synergistic Research Activities

As discussed above, a great deal of research on krill is ongoing around the Pacific Rim. Here we point out that we were recently funded by the NSF/BEST program (Evelyn Lessard) to work on krill during extensive cruises in the Bering Sea. On each cruise some work will be done at the shelf break where we know *E. pacifica* to live (Alexei Pinchuk, personal communication) thus we will be producing new data on *E. pacifica* brood size and molting rates in very cold, northerly populations.

It is also noteworthy that the North Pacific Research Board, in a recent call for proposals, specifically requested proposals for work on euphausiids in the Gulf of Alaska and Bering Sea. We submitted a proposal (see Current and Pending) to estimate krill brood sizes for comparison with similar brood size research we have done previously off Oregon and Santa Barbara, CA.

We are also collaborating on studies of population genetics of *Euphausia pacifica* that are being carried out at the Hatfield Marine Science Center by Dave Jacobson and Michael Banks. Once markers have been identified, the work will expand to include populations around the Pacific Rim. We expect to carry out this work with Japanese colleagues as part of the PICES Working Group 23.

Communications

Because of the PICES organization and annual PICES meetings, we already communicate efficiently through our long-standing friendships and through the annual PICES meetings where we will discuss the status of this collaborative krill research in formal 2-day workshops convened at forthcoming PICES meetings.

Broader Impacts

Broader Impacts. This collaborative proposal has a high-probability of success because the PIs are actively involved with PICES, the North Pacific Marine Science Organization, which coordinates scientific meetings, and exchanges of scientists from the U.S., Canada, Russia, Japan, Korea and China. Batchelder and Peterson have chaired committees, working groups, and special sessions, co-convened PICES Scientific Symposia and have co-edited special journal issues. Peterson chairs PICES Working Group 23, “Comparative ecology of krill in coastal and oceanic waters around the Pacific Rim”. This synthesis project will support one graduate student and involve three young scientists in China and Japan. Peterson has mentored six undergraduate REU students, four of whom did projects on krill ecology. Furthermore, krill are harvested in Japan and Canada, and pressure will soon mount to allow harvest elsewhere. Results of this synthesis will contribute to an assessment of krill resources and vulnerability in coastal ecosystems around the Pacific Rim. A tangible product of this research is a monograph of the population ecology, life history strategies, and interactions of krill with their environment in multiple regions of the North Pacific. Our work will also result in a better understanding of *E. pacifica* in (a) ecosystem models and (b) integrated ecosystem assessments because we will supply the latest information on biomass and vital rates, thus as such, our work will contribute to ecosystem management in the California Current.

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