

## PROJECT DESCRIPTION

### RESULTS OF PRIOR NSF-SUPPORTED RESEARCH

**D.J. Gifford, J.S. Collie, B.K. Sullivan, E.G. Durbin.** OCE 0217399. *GLOBEC-01. Patterns of energy flow and utilization on Georges Bank.* \$507,382. 06/02-05/06. Co-investigators: **J.J. Bisagni, M.E. Sieracki, J.H. Steele, M.J. Fogarty, J.S. Link, D. Palka** This project synthesized data from the US-GLOBEC Georges Bank program and other sources into an end-to-end trophic web model of the Georges Bank ecosystem. Energy budgets for the upper and lower trophic webs were developed separately, recognizing their intrinsically different spatial and temporal scales. The lower web was driven from the bottom by NO<sub>3</sub>. Estimates of production by mesozooplankton, benthic suspension feeders and deposit feeders provided input to the upper web. Diets of commercial fish populations were used to calculate food requirements in three fish categories, planktivores, benthivores and piscivores, for four decades, 1963-2002, between which there were major changes in the fish communities. Consumption by fish of planktonic prey, relative to benthic prey, increased during this period. Comparisons of inputs from the lower web with fish energetic requirements for plankton and benthos, indicate that we obtained reasonable agreement for the last three decades, 1973 to 2002. However, for the first decade, 1963-1972, the fish food requirements were significantly less than the inputs. This decade corresponds to a period characterized by a strong Labrador Current and lower nitrate levels at the shelf edge, demonstrating that strong bottom-up physical forcing may determine overall fish yields. One post-doc and 2 graduate students were supported. Publications arising from the research are:

Steele, J.H., J.S. Collie, J.J. Bisagni, D.J. Gifford, M.J. Fogarty, J.S. Link, B.K. Sullivan, M.E. Sieracki, A.R. Beet, D.G. Mountain, E.G. Durbin, D. Palka, & W.T. Stockhausen 2007. Balancing end-to-end budgets of the Georges Bank ecosystem. *Progr. Oceanogr.* 74: 423-448.  
Bisagni, J.J. 2003. The seasonal cycles of nitrate supply and potential new production in the Gulf of Maine and Georges Bank regions. *J. Geophys. Res.* 108(C11), 8015, doi:10.1029/2001JC001136.  
Steele, J.H. & J.S. Collie 2005. Functional diversity and stability of coastal ecosystems. Chapter 20 in: A.R. Robinson & K. Brink (eds.). *The Sea*, Vol. 13. Harvard University PRESS, Cambridge.  
Steele, J.H., and A.R. Beet. Assessment of some linear food web methods. *J. Mar. Systems.*

**R.D. Brodeur.** *NEP-GLOBEC target species: Trophic relationships of juvenile salmon in coastal waters off Oregon and Washington: Bottom-up or top-down control?* \$ 1,161,064. 10/99-9/04. Collaborative: US-GLOBEC NEP phase II-CCS: Co-PIs Wainwright, Emmett, Jacobson. We characterized the temporal and spatial nature of trophic relationships within the pelagic fish community during the spring-summer transition (peak salmonid migration period) and related these dynamics to salmonid survival and trophic pathways using complementary techniques of direct stomach analysis, parasite communities, and stable isotope analysis. We developed an empirically-based description of food-web structure in the CCS and estimated trophic dynamics for seasons/years with GLOBEC sampling. We developed a multi-species population model of the CCS and applied it to testing hypothetical linkages between lower trophic and physical processes. The model was used to identify the relative importance of marine food web processes (food supply, predation, competition) in controlling salmonid population dynamics. To date, >25 presentations and 9 publications have arisen from the award. Two OSU graduate students were supported and the research contributed to the Ph.D. thesis of T. Miller.

Emmett, R.L., R.D. Brodeur, T.W. Miller, S.S. Pool, G.K. Krutzikowsky, P.J. Bentley, & J. McCrae 2005. Pacific sardines (*Sardinops sagax*) abundance, distribution, and ecological relationships in the Pacific Northwest. *CalCOFI Rep.* 46:122-143.

Brodeur, R.D., E.A. Daly, R.A. Schabetsberger, & K.L. Mier 2007. Interannual and interdecadal variability in juvenile coho salmon diets in relation to environmental changes in the Northern California Current. *Fish. Oceanogr.* 16:395-408.

Brodeur, R.D., E.A. Daly, M.V. Sturdevant, T. W. Miller, J.H. Moss, M. Thiess, M. Trudel, L.A. Weitkamp J. Armstrong, & E.C. Norton 2007. Regional comparisons of juvenile salmon (*Oncorhynchus* spp.) feeding in coastal marine waters off the West Coast of North America. *Amer. Fish. Soc. Symp.* 57:183-203.

Miller T.W. & R.D. Brodeur 2007. Diets of and trophic relationships among dominant marine nekton within the northern California Current ecosystem. *Fish. Bull.* 105:548-559.

Ruzicka, J.J., R.D. Brodeur, & T.C. Wainwright 2007. Seasonal food web models for the Oregon inner-shelf ecosystem: investigating the role of large jellyfish. *CalCOFI Rep.* 48:106-128.

Baldwin, R., T.W. Miller, R.D. Brodeur, & K.C. Jacobson In press. Expanding the foraging history of juvenile salmon: combining stomach content and macroparasite community analyses for studying marine diets. *J. Fish. Biol.*

Suchman, C.L., E.A. Daly, J.E. Kiester, W.T. Peterson, & R.D. Brodeur. In press. Prey selection and predation potential of scyphomedusae in a highly productive upwelling region. *Mar. Ecol. Prog. Ser.*

Miller T.W., R.D. Brodeur and G. Rau. Carbon isotopes reveal relative contribution of shelf-slope production to the Northern California Current pelagic community. *Limnol. Oceanogr.* In press.

- K.O. Coyle**, T. Weingartner. OCE-1019078; 3.5M, 10/00-2/28/06, *GLOBEC: Long Term Observations (LTOP): Gulf of Alaska*. The Coastal Gulf of Alaska GLOBEC program was tasked with collecting material to aid in developing a mechanistic understanding of climate-induced ecosystem variability on the Gulf of Alaska shelf. The LTOP component of the program collected data on physics, nutrients, zooplankton and fish along a cross-shelf transect off Seward Alaska during 6 cruises/yr, 2001-2004. Additional stations were sampled in Prince William Sound and Hinchinbrook Entrance. These data are being integrated with retrospective, modeling and process studies by the synthesis components of GLOBEC and NPRB research to quantify and explain shelf ecosystem variability. Papers authored by participants include: Childers, A.R., Whitlege, T.E. & Stockwell, D.A. 2005. Seasonal and interannual variability in the distribution of nutrients and chlorophyll a across the Gulf of Alaska shelf: 1998 – 2002. *Deep Sea Res. II* 52: 193-216.
- Coyle, K.O. & A.I. Pinchuk 2005. Seasonal cross-shelf distribution of major zooplankton taxa on the northern Gulf of Alaska shelf relative to water mass properties, species depth preferences and vertical migration behavior. *Deep Sea Res. II* 52: 193-216.
- Coyle, K.O. & A.I. Pinchuk 2003. Annual cycle of zooplankton abundance, biomass and production on the northern Gulf of Alaska shelf, October 1997 through October 2000. *Fish. Oceanogr.* 12: 327-338.
- Weingartner, T.J., S. Danielson & T.C. Royer 2005. Freshwater Variability and Predictability in the Alaska Coastal Current *Deep-Sea Res.*, 52: 169-192.
- Weingartner, T.J., K. Coyle, et al. 2002. The Northeast Pacific GLOBEC Program: Coastal Gulf of Alaska, *Oceanography*, 15: 48-63.
- K.L. Daly**. OPP-9910610, OPP-0196489 *WinDSSOck: Winter distribution and success of Southern Ocean Krill* \$300,000 (9/00-8/04). This project was designed to assess overwintering strategies for feeding, development, and growth of life history stages of *Euphausia superba* west of the Antarctic Peninsula. Acoustics and nets were used to assess krill abundance and distribution. The first target strength measurements of Antarctic fishes were acquired *in situ* and are being compared with that of krill and other potential targets. This award supported one MS and one PhD student and acknowledged 15 presentations. Publications are:
- Hofmann, E.E., D.P. Costa, K.L. Daly & J.M. Klinck, W.R. Fraser, and J.J. Torres. 2004. U.S. Southern Ocean Global Ocean Ecosystem Dynamics Program. *Oceanography* 15 (2): 64-74.
- Daly, K.L. 2004. Overwintering Growth and Development of Larval *Euphausia superba*: An Interannual Comparison Under Varying Environmental Conditions West of the Antarctic Peninsula. *Deep-Sea Res. II* 51: 2139-2168.
- Ju, S.-J., K. Scolaridi, K.L. Daly & H.R. Harvey 2004. Understanding the trophic role of ctenophore *Callianira antarctica* in an Antarctic ecosystem using lipid biomarkers. *Polar Biol.* 27: 782-792.
- Daly, K.L. & J. Zimmerman 2004. Comparisons of morphology and neritic distributions of *Euphausia crystallorophias* and *Euphausia superba* furcilia during autumn and winter west of the Antarctic Peninsula. *Polar Biol.* 28: 72-81.
- Scolaridi, K., K.L. Daly, E.A. Pakhomov, & J.J. Torres 2006. Feeding ecology and metabolism of the Antarctic Cydippid ctenophore *Callianira antarctica*. *Mar. Ecol. Progr. Ser.* 317: 111-126.
- Marrari, M., C. Hu & K.L. Daly 2006. Validation of SeaWiFS chlorophyll *a* concentrations in the Southern Ocean: A revisit. *Remote Sensing Environ.* 105: 367-375.
- Deibel, D. & K.L. Daly 2007. Zooplankton Processes. In, Smith, W.O., Jr. and D. Barber (eds), *Polynyas: Windows into Polar Oceans*. Elsevier Oceanography Series 74: 271-322.
- Marrari, M., K.L. Daly & C. Hu. Spatial and temporal variability of SeaWiFS derived chlorophyll distributions west of the Antarctic Peninsula: Implications for krill production. *Deep Sea Res. II*. (submitted).
- E.E. Hofmann**. OPP-0087690 (J. M. Klinck, **E.J. Murphy**), \$311,901, 02/15/01-01/31/06. *Variability in Transport and Recruitment of Antarctic Krill Across the Scotia Sea*. Hofmann has had NSF funding for ~25 years that has supported development of a range of coupled physical-biological models. The most recent NSF award, relevant to this proposal, was focused on development of circulation and Antarctic krill growth models for the Scotia Sea and development of bio-optical models for simulating primary production in Antarctic coastal waters. Results from the circulation-krill model show that: 1) Antarctic krill need multiple food sources to survive transport across the Scotia Sea; 2) overwintering in the Weddell Sea results in viable krill arriving at South Georgia the following spring; and 3) multiple source regions provide krill to South Georgia. The bio-optical model shows the importance of diatom-dominated communities in primary production of Antarctic coastal waters. This project resulted in training of two Ph.D. students - B. Fach and H.-C. Kim. Fourteen presentations at national and international meetings and 7 publications resulted:
- Fach, B.A., E.E. Hofmann, & E.J. Murphy. 2002. Modeling studies of Antarctic Krill (*Euphausia superba*) survival during transport across the Scotia Sea, *Mar. Ecol. Progr. Ser.* 213, 187-203.
- Fraser, W.R. & E.E. Hofmann 2003. A predator's perspective on causal links between climate change, physical forcing and ecosystem response, *Mar. Ecol. Progr. Ser.* 265, 1-15.

- Hofmann, E.E. & E.J. Murphy 2004. Advection, krill and Antarctic marine ecosystems, *Antarctic Sci.* 16, 487-499.
- Fach, B.A. & J.M. Klinck 2006. Transport of Antarctic krill (*Euphausia superba*) across the Scotia Sea Part I: Circulation and particle tracking simulations, *Deep-Sea Res. I*, doi:10.1016/j.dsr.2006.03.006.
- Fach, B.A., E.E. Hofmann & E.J. Murphy 2006. Transport of Antarctic krill (*Euphausia superba*) across the Scotia Sea Part II: Krill growth and survival, *Deep-Sea Res. I*, doi:10.1016/j.dsr.2006.03.007.
- Kim, H.-C., W.O. Smith, Jr., & E.E. Hofmann. A modeling study of primary production and carbon flux in west Antarctic Peninsula continental shelf waters, *J. Mar. Res.* (accepted pending revision).
- Kim, H.-C., B.B. Prézelin, & E.E. Hofmann, Model-derived estimates of primary production and carbon flux in the Ross Sea, *J. Mar. Res.* (accepted pending revision).

**W.O. Smith.** Smith has had NSF support for the past 20 years to conduct oceanographic research in the Arctic and Antarctic, and co-directed the Southern Ocean JGOFS program (AESOPS) that included 11 cruises to the Southern Ocean, and was the largest oceanographic project ever funded by OPP. More recently he has completed IVARS (*Interannual Variability in the Antarctic-Ross Sea*; NSF OPP-0087401; 4/1/01-3/31/06; \$595,000). The goal was to measure net community production of phytoplankton and diatoms by constructing nutrient budgets in the southern Ross Sea. Many of the results are being analyzed, as there were 5 full field seasons with 2 cruises/yr. Eighteen presentations were made at national and international meetings. Three PhD dissertations were supported fully or in part. The following publications were produced:

- Kim H.-C., W.O. Smith Jr. & E.E. Hofmann (accepted). Model-derived estimates of primary production and carbon flux in the Ross Sea. *J Mar. Res.*
- Smith, W.O. Jr., M. Dinniman, G.R. DiTullio, S. Tozzi, O. Mangoni, M. Modigh, & V. Saggiomo (accepted) Phytoplankton photosynthetic pigments in the Ross Sea: Patterns and relationships among functional groups. *J. Mar. Sys.*
- Peloquin, J.A. & W.O. Smith Jr. 2007. Phytoplankton blooms in the Ross Sea, Antarctica: interannual variability in magnitude, temporal patterns, and composition. *J. Geophys. Res.*112: C08013, doi: 10.1029/2006JC003816.
- Smith, W.O. Jr. & R.G. Barber 2007. Polynyas: Windows to the World's Oceans (eds). Elsevier, Amsterdam. 437 pp.
- Smith, W.O. Jr., D.G. Ainley, & R. Cattaneo-Vietti 2007. Marine ecosystems: the Ross Sea. *Phil. Trans. Roy. Soc. B* 362: 95-111.
- Tremblay J.-E. & W.O. Smith Jr. 2007. Phytoplankton processes in polynyas. In: *Polynyas: Windows to the World's Oceans* (Smith, W.O. Jr. & R.G. Barber, eds.), Elsevier, Amsterdam, pp. 239-270.
- Smith W.O. Jr., A.R. Shields, J.A. Peloquin, G. Catalano, S. Tozzi, M.S. Dinniman & V.A. Asper 2006. Biogeochemical budgets in the Ross Sea: variations among years. *Deep-Sea Res. II* 53: 815-833.
- Smith W.O. Jr., S. Tozzi & V.A. Asper. (submitted). Continuous fluorescence measurements in the Ross Sea, Antarctica: scales of variability. *Deep-Sea Res.*
- Shields, A.R. & W.O. Smith Jr. (submitted). Photosynthesis/irradiance relationships of solitary and colonial forms of *Phaeocystis antarctica* from the Ross Sea, Antarctica. *Mar. Ecol. Prog. Ser.*

**S.L. Strom.** OCE 0101397 *GLOBEC 2000: Responses of the Neocalanus spp. – microplankton community to physical forcing in the coastal Gulf of Alaska.* 1/01-12/05. \$654,757. We conducted 5 cruises to the coastal Gulf of Alaska in 2001-2003, investigating lower trophic level processes in Prince William Sound and across the shelf near Seward. Major findings were: 1) There was cross-shelf zonation in nearly every aspect of phyto- and microzooplankton community structure and function, consistent with a gradient in dissolved Fe availability. 2) Microzooplankton consumed nearly all production by small phytoplankton, and a substantial amount of diatom production. However, most diatom production was not consumed by any major zooplankton group on the shelf and must have been exported from the euphotic zone. 3) (with M. Dagg) Consumption of large heterotrophic protists by *Neocalanus* spp. copepods in spring could strongly influence planktonic community structure through trophic cascades. To date, 13 presentations and 7 publications have been supported by this grant. Seven WWU students participated in the cruises, including 2 undergraduates and 6 women. Grant funds provided assistantship support for 6 different WWU graduate students; research in the CGOA constituted a substantial portion of the M.S. thesis of K. Frederickson.

- Strom, S.L. & E.L. Macri. Summer primary production in the coastal Gulf of Alaska and its sensitivity to environmental variation, assessed from photosynthesis – irradiance relationships. *Mar. Ecol. Prog. Ser.* Submitted.
- Frederickson, K.A. & S. L. Strom. The algal osmolyte DMSP as a microzooplankton grazing deterrent in field and laboratory studies. *J. Plankton Res.* Submitted,
- Strom, S.L., E.L. Macri & M.B. Olson 2007. Microzooplankton grazing in the coastal Gulf of Alaska: variations in top-down control of phytoplankton. *Limnol. Oceanogr.* 52: 1480-1494.

- Strom, S.L., M.B. Olson, E.L. Macri & C.W. Mordy 2006. Cross-shelf gradients in phytoplankton community structure, nutrient utilization, and growth rate in the northern coastal Gulf of Alaska. *Mar. Ecol. Prog. Ser.* 328: 75-92.
- Liu, H., M.J. Dagg & S. Strom 2005. Grazing by the calanoid copepod *Neocalanus cristatus* on the microbial foodweb in the coastal Gulf of Alaska. *J. Plankton Res.* 27: 647-662.
- Bingham, B.L., S.D. Sulkin, S.L. Strom & G. Muller-Parker 2003. Increasing diversity in the marine sciences through the Minorities in Marine Science Undergraduate Program. *J. Geosci. Ed.* 51: 474-480
- Weingartner, T. J. & 18 others, incl. S. Strom 2002. The northeast Pacific GLOBEC program: coastal Gulf of Alaska. *Oceanography* 15(2): 48-63.

**A.C Thomas:** OCE-0531289. *Large-scale Influences on Mesoscale Structure in the California Current System: A Synthesis of Climate-forced Variability in Coastal Ecosystems.* \$289,486. 5-1-05 to 4-30-08. Collaborative proposal with F.Schwing and S.Bograd (both NOAA NMFS) and P.T.Strub (OSU.) We focused on quantification of time/space variability of chlorophyll in the California Current System (CCS) and the Coastal Gulf of Alaska (CGOA), its relationship to local and non-local forcing and circulation, and its influence on mesoscale variability in the 2 regions. The dominant timescales of chlorophyll variability in the CCS were associated with interannual variability and the PDO. Spring chlorophyll development was associated with upwelling at lower latitudes and with light and mixing at higher latitudes. Strong negative chlorophyll anomalies in the CCS in spring of 2005 were related to wind anomalies, a late spring transition and spatial mismatches between chlorophyll anomalies and components of the higher trophic-level ecosystem. Chlorophyll variability along the shelf break in the CGOA was dominated by offshore eddies. Spatial patterns of the Columbia River plume were strongly related to wind forcing. Two research associates, 2 post-doctoral fellows and one high school summer student were supported. We processed and made available the entire SeaWiFS 4-km time series, along with climatologies and weekly and monthly averages, as standard remapped products over the CCS and the CGOA, supplemented with 1km and 9km versions of the CCS data and served through the GLOBEC NEP data server. Publications are: Henson, S.A. & A.C. Thomas 2007. A census of oceanic anticyclonic eddies in the Gulf of Alaska. *Deep Sea Res.* In Press

- Venegas, R., et al. 2007. Satellite-derived variability in chlorophyll, wind stress, sea surface height, and temperature in the northern California Current System. *J. Geophys. Res.*, In Press.
- Henson, S.A. & A.C. Thomas 2007. Interannual variability in timing of seasonal chlorophyll increases in the California Current. *J. Geophys. Res.*, 112, doi:10.1029/2006JC003960.
- Legaard, K. & A.C. Thomas. 2007. Spatial patterns of intraseasonal variability of chlorophyll and sea surface temperature in the California Current. *J. Geophys. Res.*, 112, doi:10.1029/2007JC004097.
- Crawford, W.R., P.J. Brickley & A.C. Thomas 2007. Eddy Transport into a Cyclonic Gyre: An Example in the Gulf of Alaska, *Prog. Oceanogr.* 75: 287-303.
- Henson, S.A. & A.C. Thomas. 2007. Phytoplankton scales of variability in the California Current system: Interannual and cross-shelf variability. *J. Geophys. Res.* 112, C07017, doi:10.1029/2006JC004039
- Henson, S.A. & A.C. Thomas 2007. Phytoplankton scales of variability in the California Current system: Latitudinal variability. *J. Geophys. Res.*, 112, C07018, doi:10.1029/2006JC004040.
- Thomas, A.C. & P. Brickley 2006. Satellite measurements of chlorophyll distribution during spring 2005 in the California Current. *Geophys. Res. Lett.* 33, doi:10.1029/2006GL026588.
- Legaard, K. & A.C. Thomas 2006. Spatial patterns of seasonal and interannual variability in chlorophyll and surface temperature in the California Current. *J. Geophys. Res.* 111, C06032, doi:10.1029/2005JC003282.
- Thomas, A.C. & R. Weatherbee 2006. Satellite-measured temporal variability of the Columbia River plume. *Rem. Sensing Env.* 100: 167-178.
- Dagg, M.J., H. Liu & A.C. Thomas 2006. Effects of mesoscale phytoplankton variability on the copepods *Neocalanus flemingeri* and *N. plumchrus* in the coastal Gulf of Alaska. *Deep-Sea Res.* 53: 321-332.
- Mackas, D., P.T. Strub, A.C. Thomas & V. Montecino 2006. Eastern Ocean Boundaries Pan-Regional View, In: *The Sea*. A.R. Robinson and K.H. Brink, Eds.. Harvard Press Ltd.. In Press.
- Montecino, V., P.T. Strub, J. Tarazona, F. Chavez, A.C. Thomas & T. Baumgartner 2006. Bio-physical interactions off western South America, In: *The Sea*. A.R. Robinson & K.H. Brink, Eds. Harvard Press Ltd. In Press.

**C. T. Tynan & D.A. Ainley:** NEP-GLOBEC target species: *Interactions with top trophic levels*" \$290,738 (10/99-9/04NSF-OCE-0534609 Collaborative: US-GLOBEC NEP phase IIIA-CCS: *Scale-dependent dynamics of top-trophic predators and prey – Toward predicting predator response to climate change.* \$393,885 (07/05-06/08) co-PIs Brodeur, Dugger, Ford, Pierce. We described occurrence patterns of top-trophic species (cetaceans, pinnipeds, birds) as predators and/or competitors of Pacific salmon on 4 cruises in 2 years. We edited and merged data sets with other investigators, and are well underway with publications. One set-back was the death, a year ago, of the biostatistician with a major role in the bird-mammal data, and the need to bring a new collaborator up to speed. Results have been presented at 14 conferences and we have given 7 invited seminars. Now in the modeling phase, we are working on 4 papers to be submitted in

2008: occurrence patterns of seabirds and whales relative to estimates of prey biomass; a regional carbon model; and a comparison of carbon transport in whales versus cross-shelf processes. Publications are: Ainley, D.G., D.N. Nettleship, H.C. Carter & A. Storey. 2002. Common Murre (*Uria aalge*). In: *The Birds of North America* (A. Poole & F. Gill, Eds.). The American Ornithologists' Union, Washington, D.C.

Ainley, D.G., L.B. Spear, C.T. Tynan, J.A. Barth, T.J. Cowles & S.D. Pierce. 2005. Factors affecting occurrence patterns of seabirds in the northern California Current, spring and summer 2000. *Deep-Sea Res. II*, 52: 123–143.

Batchelder, H., J.A. Barth, P.M. Kosro, P.T. Strub, R.D. Brodeur, W.T. Peterson, C.T. Tynan, M.D. Ohman, L.W. Botsford, T.M. Powell, F.B. Schwing, D.G. Ainley, D.L. Mackas, B.M. Hickey & S.R. Ramp 2002. *The GLOBEC Northeast Pacific California Current Program. Oceanography* 15: 36-47.

Karnovsky, N.J., L.B. Spear, D.G. Ainley, H.R. Carter, K.D. Amey, L.T. Ballance, K.T. Briggs, R.G. Ford, G.L. Hunt Jr., C.A. Keiper, J.W. Mason, K.H. Morgan, R.L. Pitman & C.T. Tynan 2005 (publ in 2007). At-sea distribution, abundance and behavior of Xantus's Murrelet. *Mar. Ornithol.*, 33: 89-104.

Spear, L.B. & D.G. Ainley 2007. Storm-petrels of the eastern Pacific Ocean: species assembly and diversity along marine habitat gradients. AOU Monograph No 62.

Spear, L.B. & D.G. Ainley 2007. The seabird community of the Peru Current, 1980-1995, with comparisons to other eastern boundary currents. *Mar. Ornithol.* 35 in press.

Tynan, C.T., D.G. Ainley, J.A. Barth, T.J. Cowles, S.D. Pierce & L.B. Spear 2005. Cetacean association with hydrographic features in the northern California Current System. *Deep-Sea Res. II* 52: 145–167.

Ribic, C.A., E. Chapman, W.R. Fraser, G.L. Lawson & P.H. Wiebe 2007. Top predators in relation to bathymetry, ice, and krill during austral winter in Marguerite Bay, Antarctica. *Deep-sea Res. II*, in press.

**OBJECTIVES OF THE RESEARCH.** *Two overarching questions are addressed by this project: are marine food webs leading to fisheries controlled from the top-down, the bottom up, or a combination of the two? And what is the role of environmental disturbance on top-down and bottom-up forcing?* To address these questions we will (1) compare end-to-end energy budgets of the 4 US-GLOBEC study regions to identify attributes of these systems that influence their sensitivity to top-down v. bottom-up forcing, (2) assess the skills of the regional models in capturing basic material fluxes, (3) extract diagnostics from the regional models that will be used to evaluate the effects of climate change and fishing pressure across GLOBEC regions and (4) develop quantitative methods to compare the diagnostics.

## SCIENTIFIC BACKGROUND

**Rationale.** Our inability to conduct controlled experiments is a major impediment to the scientific study of open sea ecosystems. An alternative is to compare studies of different ecosystems as a proxy for manipulations of the same system, particularly when climatic change and over-fishing provide perturbations at the bottom and top of trophic webs. This approach is especially appropriate for end-to-end analysis of marine trophic webs with their complicated structure and complex dynamics. Such analyses depend on the comparability of the available data and the compatibility of the analytical methods. Ideally, such comparisons are based on identical methods for data collection and analysis. The 4 US GLOBEC programs provide one of the closest approximations to this ideal situation.

**Species-centric and trophic-centric approaches.** Existing ecosystem model approaches generally fall into two distinct types. One focuses on the dynamics of individual species (species-centric) and the other on food web processes (trophic-centric). Both acknowledge the importance of physical drivers of the system, but these can operate in two complementary ways. The species-centric approach emphasizes the direct effects of currents and mixing on important components of the life cycle, especially larval transport and feeding. Trophic budgets of food webs usually start from physical fluxes of nutrients into the euphotic zone. The species-centric “horizontal” approach benefits from advances in modeling the physical dynamics of shelf regions with complex hydrography. The trophic-centric “vertical” method can utilize complicated optimizations with large matrix inversions to resolve fluxes in linear steady state systems. At issue is how far these methods, jointly, can illuminate some of the central problems in marine ecosystems, especially those on the continental shelf that involve both pelagic and benthic components of the food webs that determine fishery resources. Each approach involves trade-offs. The species-centric approach combines complex physical processes and relatively simple population dynamics; the trophic-centric approach analyzes complicated food webs using linear steady state descriptions of energy transfer processes. *We argue that there are no contradictions between these two approaches: they are complementary. The trophic-centric approach provides a wider system view; the species-centric approach allows transfer of details of individual species to the more general trophic structure.* One challenge for GLOBEC synthesis is whether, together, the two approaches can encompass the major issues and problems in biological oceanography in the context of potential management strategies. *Specifically, can we combine our understanding of factors determining the interannual variability of recruitment, with measures of overall productivity and its response to decadal climatic change?*

The US-GLOBEC program is species-centric, focused on target species selected for their ecological or economic importance in their regional ecosystem. This program has been very successful in providing detailed illustrations of the spatial dynamics of plankton and fish larvae (e.g., Werner et al. 2001). Historically, these detailed simulations of spatial and temporal processes have focused on zooplanktonic or early pelagic life stages of fisheries species over relatively short time scales (< 1 yr) and have largely ignored the benthic components of the ecosystem. This approach is consistent with deYoung et al.'s (2004) recommendation: "rather than model the entire ecosystem we should focus on key target species and develop species-centric models". The power of this approach is also apparent in recent publications dealing with physically complex basin and shelf ecosystems (e.g., Wiebe et al. 2001) where questions concerning dispersal, retention and connectivity are addressed. More recently, these models have been extended to include older life history stages, providing a method for forecasting climate and fishery impacts over the entire life cycle of the target species (Megrey et al. 2007). Species-centric approaches have been used to evaluate processes underlying fish movement including ideal free distribution, random walk, directional movement, and gradient tracking (Humston et al. 2004). Stock assessments provide an additional species-centric approach to forecasting ecosystem changes on future fish production. Historically, these projections were used to assess the short-term future of fish stocks in order to evaluate whether a stock was overfished or likely to become overfished. Such projection models are currently being adapted to evaluate the performance of different management strategies under different environmental conditions (De la Mare 1996).

Here, we take a trophic-centric approach, which draws upon data and understanding obtained from species-centric studies in the 4 US-GLOBEC regions. The overall productivity of marine populations results from physical processes that determine nutrient fluxes and primary production. In turn these influence higher trophic level yields that depend on benthic as well as pelagic sources of food. The problems in adopting the vertical end-to-end trophic-centric approach lie with the large range of time scales involved in the dynamics of different trophic levels as well as in complicated food web interactions. Usually the upper and lower trophic levels are treated separately. For example, the microbial web in the open ocean was studied intensively in the JGOFS program (e.g., Laws et al. 2000; Buesseler 2001) where export was defined as downward transport out of the euphotic zone or trophic transport upward. More recent studies have attempted to link upper and lower trophic level models (e.g., Aydin et al. 2005). For the upper trophic levels, emphasis is on predatory interactions (Polovina 1984; Christensen & Pauly 1993; Heath 2005). To encompass these complicated interactions, linear steady state web models have been used (Vezina & Platt, 1988; Richardson et al. 2004; Steele et al. 2007). *We argue that a trophic-centric perspective is critical to understanding production processes of the US-GLOBEC target ecosystems.* Comparative study of the basic processes determining productivity at all trophic levels is essential for increased insight into the dynamics of individual species in each ecosystem. Further, in the absence of a resource-based, trophic-centered approach, individual species and climate forcing cannot be linked.

**US-GLOBEC regions.** We will compare energy budgets and structure of the 4 US-GLOBEC ecosystems—Georges Bank, Northern California Current, Coastal Gulf of Alaska and the Southern Ocean. Specifically we ask whether the energy budget or structure of the 4 ecosystems makes them more or less vulnerable to environmental variability or commercial fishing. Although the AO for US-GLOBEC Pan Regional Synthesis treats the 2 North Pacific regions as a single entity, we consider them separately because of their striking differences in physical forcing, hydrography and trophic structure. All four systems have been subject to large amplitude trends or perturbations, including both climate change and overfishing. Extensive data sets are available for each region, covering most trophic components from nutrient input to top predators. Recent assessments of fluxes have been done for the first three systems (Aydin et al. 2005; Ruzicka et al. 2007; Steele et al. 2007). For the Southern Ocean, we have earlier investigations of the entire trophic web (Everson 1977; Hempel 1985; Hopkins 1985; Hopkins & Torres 1989; Hopkins et al. 1993; Atkinson 1998; Deibel & Daly 2007; Everson 1984; Schnack 1985; Kawaguichi et al. 1998; Pakhomov et al. 2002; Lancraft et al. 2004; review in Knox 2007, chapt. 15) and modeling studies focused on details of specific components (Murphy 1995; Hofmann & Lascara 2000; Hofmann & Husrevoglu 2003; Salihoglu et al. 2002, Daniels et al. 2006, and Murphy et al. 2007).

Although similarities exist among the four US-GLOBEC regions, there are striking differences in bottom depth and topography, circulation and stratification, annual cycles and trophic components, especially top predators (**Table 1**). These differences have prompted collection of different data sets and use of different food web models, making direct end-to-end comparisons of the four ecosystems challenging, although we argue not impossible. Nevertheless, we propose to make these comparisons. Discussion and development of different methods will form a major component of the first year's work, involving modelers and data analysts. One approach will use existing models for the four regions as the input to directly comparable mass-balance budgets of the end-to-end fluxes. These budgets will be used (a) to compare diagnostics for the 4 regions, (b) to investigate the sensitivity of specific ecosystem components to uncertainties in the data and (c) to consider the effects of changes in the drivers and in the ecosystem

structure. These perturbations can be expressed as different mass-balance scenarios, or as initial conditions for dynamic simulations. *These will provide comparisons of systems and of methods.*

**Georges Bank (GB).** This relatively small (42,000 km<sup>2</sup>) shallow bank located off-shore of Cape Cod, MA (Fig. 1) has been studied intensively (Backus and Bourne 1987; DSR II, 1996, 2001, 2006). Currents over the Bank are dominated by strong semidiurnal tidal components and a mean clockwise gyre that

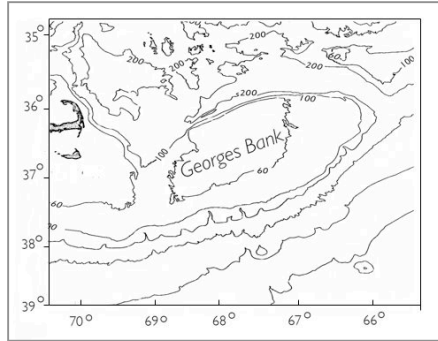


Fig. 1. GLOBEC GB region.

intensifies with increasing stratification in the summer. During the summer period, the gyre becomes partially closed with water parcels recirculating around the Bank with an approximate period of 50 days (Flagg et al. 1982). Bank waters exhibit a large seasonal temperature variation, typically increasing from 5 °C in late winter to 15 °C in late summer (Flagg 1987). A permanent hydrographic front along the southern edge of the Bank separates shelf water over the Bank from more saline Slope Water offshore (Flagg 1987). Water movements on the Bank are dominated by strong tidal forcing and wind events associated with storms. Water properties exhibit characteristic seasonal cycles. Over the shallow, central region of the Bank, turbulent tidal mixing is sufficiently strong to keep the water column well mixed year round. Tidally mixed fronts develop near the 60-m isobath, separating the central Bank from stratified waters to the north in the Gulf of Maine and to the south on the Bank's flank. Bank

biology is characterized by high plankton and fish biomass, and high primary and secondary production. Strong interactions occur between benthic and pelagic components at several trophic levels, which complicate end-to-end analysis. Previous (Cohen et al. 1982; Sissenwine et al. 1984) and recent (Steele et al. 2007) energy budgets rely on steady state linear analyses.

**Northeast Pacific.** The US-GLOBEC Northeast Pacific program includes two separate ecosystems, the Northern California Coastal Current and the Coastal Gulf of Alaska. Similar end-to-end models have been applied to both systems (Aydin et al. 2005; Field et al. 2006). These use NEMURO, a bottom-up NPZ protocol (Fujii et al. 2002), for the lower web and ECOPATH, a top-down linear program (Christensen & Pauly, 1992) for the upper web, linked by ECOSIM (Walters et al. 1997). Because of their marked differences in bathymetry, hydrography, biology and climatic drivers, we treat the 2 regions separately.

**Northern California Current (NCC).** The NCC extends from roughly northern Vancouver Island to Cape Mendocino in the south (Fig. 2). It is a zoogeographic transition zone; the pelagic community is a mix of subarctic and subtropical species with few endemic species (Brodeur et al. 2003). Seasonally, it is highly productive. Upwelling favorable winds predominate following the spring transition in March-April and continue through October-November, when downwelling begins (Strub et al. 1987). During the upwelling season, the NCC is home to a diverse pelagic fish community that includes both year-round resident species (anchovies, smelts, herring) and transient species migrating from the south (sardines, hake, mackerels) (Brodeur et al. 2005). Ecosystem productivity and pelagic community structure vary on inter-annual to inter-decadal time scales due to the timing and strength of upwelling-favorable winds, variability in the size and location of the Columbia River plume, and forcing by basin-scale physical processes (e.g., ENSO, PDO) (Batchelder et al. 2002, Keister and Peterson 2003, Emmett et al. 2006).

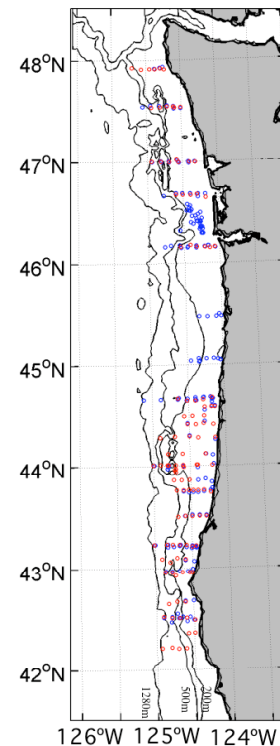


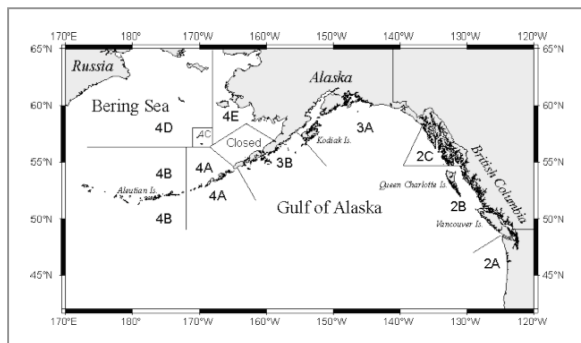
Fig.2. NCC model domain Blue circles (spring), red circles (summer) GLOBEC & BPA pelagic trawl coverage, 2000.

Lower trophic level dynamics in the NCC are strongly coupled to the strength and duration of seasonal upwelling (Thomas and Strub, 2001, Thomas & Brickley 2006), and are additionally influenced by Fe supply from rivers and shelf sediments (Chase et al. 2007). In comparison with the CGOA, phyto- and zooplankton production are more strongly influenced by ENSO events (interannual variability) and climate regime shifts associated with the PDO (Bane et al. 2007). Weak or delayed upwelling greatly reduces spring and summer primary production, reduces the importance of diatom production, reduces zooplankton biomass and abundance, and shifts the shelf zooplankton community composition toward smaller-bodied, subtropical crustacean species

(Keister & Peterson 2003; Kudela et al. 2006, Thomas & Brickley 2006). Benthic invertebrate production is also reduced (Barth et al. 2007). These shifts directly affect yields of pelagic fish species including Chinook and coho salmon (Brodeur & Pearcy, 1992). The community of top predators is well known (e.g. Ainley et al. 2005; Tynan et al. 2005) and it, too, strongly responds to the above two states (e.g., Ainley & Boekelheide 1990; Keiper et al. 2005).

During upwelling periods the region can be modeled as a series of cross-shelf zones in analogy to the Steele et al.'s (2007) approach for GB. In this approach the nearshore zone (~0-15 km from shore) represents recently upwelled water (coldest, high nutrient, low chlorophyll and zooplankton), a region further offshore (but still primarily shelf-associated) corresponds to the upwelling-induced diatom bloom (warmer, lower nutrient, very high chlorophyll, high dependence of production on  $\text{NO}_3$ , dominance by boreal copepod species), and further offshore the system transitions to the oceanic condition (low nutrient, low chlorophyll, high dependence of production on regenerated nutrients, dominance by subtropical copepod species) (Kokkinakis & Wheeler 1987; Landry et al. 1989; Keister & Peterson 2003; Sherr et al. 2005). During winter or non-upwelling periods (such as El Niño) the shelf is occupied by a more uniform coastal community without pronounced zonation other than the coastal – oceanic transition. The upwelling-related zonation can be closely linked to bottom topography (i.e. the upwelling front following the shelf break) (Venegas et al. 2008), but this is not always the case (Barth et al. 2005). It is possible that zonation in the NCC is less closely associated with bottom topography (i.e. location of shelf, shelf break, slope) than in either the GB case (where bottom depth strongly influences production regime) or in the CGOA case (where the coast-hugging ACC and slope eddies both influence production). Considerably more is known about alongshore variation in lower trophic level processes, including the role of river plumes, headlands and seamounts, than in the CGOA (Anderson 1964; Barth et al. 2005; Huyer et al. 2005). Because the NCC is in its 3<sup>rd</sup> or 4<sup>th</sup> major iteration of biological oceanographic study, while the CGOA is just emerging from its 1<sup>st</sup>. Pelagic fish production is generally higher in the CCS than in the CGOA (Ware & Thompson 2005, Orsi et al. 2007)

**Coastal Gulf of Alaska (CGOA).** The Gulf of Alaska is an arm of the northeast Pacific Ocean bounded by the south coast of Alaska to the east (Fig. 3). The CGOA marine ecosystem is a highly productive ( $300 \text{ gCm}^{-2}\text{y}^{-1}$ ) downwelling system. It is the largest ( $291,840 \text{ km}^2$ ) and, historically, the least-studied of the US GLOBEC regions, particularly with regard to lower trophic levels. Circulation on the CGOA continental shelf is driven by large-scale ocean gyres, seasonally variable local winds, and freshwater runoff interacting with complex bathymetry (Reed & Shumacher 1986, Reed & Stabeno 1989). Mesoscale eddies strongly modulate hydrographic and phytoplankton patterns, especially over the outer shelf and shelfbreak (Ladd et al. 2005, Crawford et al. 2007). CGOA continental shelf physics is highly variable at local scales, and the time series of coastal SST and SLP do not display the obvious decadal shifts associated with the PDO in the North Pacific (Stabeno et al. 2004). However, fish and marine mammal populations have changed dramatically over last 40 years, with some species



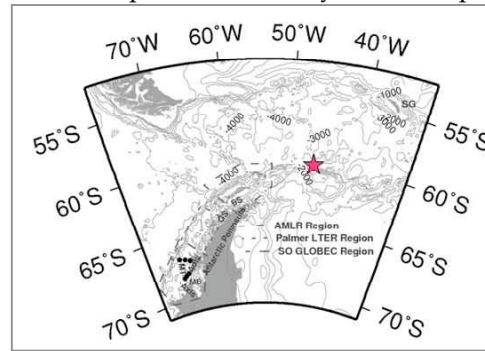
**Fig. 3.** Management areas included in the ecosystem models for the Eastern Bering Sea (EBS), (GOA) and Aleutian Islands (AI).

(Stabeno et al. 2004; Royer 1998, 2005; Weingartner et al. 2004), nutrients (Childers et al. 2005), phytoplankton distributions, growth and production (Thomas & Brickley 2006; Strom et al. 2006; Strom & Macri 2008), and zooplankton (Coyle and Pinchuk 2003, 2005; Strom et al. 2007). Pinniped, fish and invertebrate diet and monitoring data are available from NMFS surveys and other studies (e.g., Fritz & Stinchcomb 2005, Yang et al. 2006).

**Southern Ocean (SO).** Marguerite Bay on the western Antarctic Peninsula (WAP) is the focus of the US-GLOBEC SO program (DSR II, 2004; in press) (Fig. 4). The continental shelf of the WAP is deep (>400 m) and is strongly influenced by onshelf intrusions of oceanic Circumpolar Deep Water (CDW) derived from the ACC (Klinck 1998; Smith et al. 1999; Prézelin et al. 2000, 2004; Klinck et al. 2004), and seasonal changes in sea ice extent and concentration (Stammerjohn et al. 2001; 2003). Connections between the inner and outer shelf region occur via at least one circulation gyre (Klinck et al. 2004; Beardsley et al. 2004). There is no assessment, as yet, of overall ecosystem fluxes on the WAP. However, estimates have been made of fluxes of nutrients (Serebrennikova & Fanning, 2004; Serebrennikova et al. in press) and phytoplankton biomass (Marrari et al. in press) and carbon (Kim et al. submitted), as well as seasonal changes in mesozooplankton distribution and abundance (Asjian et al. 2004; Lawson et al., in press),

zooplankton feeding behavior (Scolardi et al. 2006), krill (Daly 2004; Lawson et al. in press) and higher trophic levels (Chapman et al. 2004; Thiele et al. 2004; Burns et al. 2004). The relative composition of zooplankton taxa, krill and top predators varies across the WAP (Ashjian et al. 2004; Chapman et al. 2004; Thiele et al. 2004), potentially allowing different trophic pathways and fluxes.

The WAP also forms the southern most region of a much larger system, which extends northeastward to the Scotia Sea (Fig. 4). The whole region is connected physically by the eastward flowing Antarctic Circumpolar Current (ACC) (Hofmann et al. 1998; Murphy et al. 1998). This system is an important component of the SO, maintaining about half of the overall Antarctic krill population (Atkinson et al. 2004). It also supports some of the largest populations of zooplankton and vertebrate predators in the SO (Everson 1977, 1984). However, there is marked spatial variation in the operation of the system (Murphy et al. 2007a). For example, krill populations in northern regions, such as around South Georgia, rely on advection of recruits from further south along the Scotia Arc and the Antarctic Peninsula (Marr 1962; Murphy et al. 2004; Fach et al. 2006; Tarling et al. 2006; Thorpe 2007). Satellite tracking studies have also shown that breeding populations of vertebrates within the Scotia Sea are highly mobile, with some species foraging across and beyond the Scotia Sea (Clarke 1985a; Croxall 1992) and as far south as the Antarctic Peninsula (Cstry et al. 2004; Phillips et al. 2004; Croxall et al. 2005; Phillips et al. 2005; Biuw et al. 2007). Thus, trophic structure and pathways within the Scotia Sea ecosystem are potentially strongly influenced by variability in upstream sources as well as by local processes.



**Figure 4.** SO study region. LTER is Palmer Long-term Ecological Research (LTER) site. AMLR is US Antarctic Marine Living Resources (AMLR) region. These regions provide a continuum of data sets along the western Antarctic Peninsula. Filled circles are locations of current meter moorings for US SO GLOBEC field studies. Star is the intermediate ice edge study region. MB is Marguerite Bay, BS is Bransfield Strait, GS is Gerlache Strait, and SG is South Georgia in the Scotia Sea.

The Scotia Sea ecosystem in general, and South Georgia in particular, is the long-term continuing focus for the British Antarctic Survey (BAS) (Murphy et al. 2007a). Changes in solar irradiance and sea ice cover from the WAP and across the Scotia Sea result in strong seasonal variation, which impacts the physiology and ecology of many of its species (Laws 1983; Clarke 1985b; Hempel 1985; Longhurst 1998; Peck et al. 2004; Peck 2005; Peck et al. 2005). Extensive spring phytoplankton blooms characterize the region and the enhanced production supports large populations of land and water based predators. The physical nature of the Scotia Sea, coupled with the large foraging range of its vertebrate predators, means that the Scotia Sea ecosystem is an *open system* that is trophically linked to surrounding regions. Fluxes between specific ecosystem components (krill to top predators) have been estimated for South Georgia (Murphy 1998; Atkinson et al. 2004; Murphy et al. 2007a), but an overall Scotia Sea ecosystem flux assessment remains to be done. Long-term studies reveal variations in the diet, distribution and abundance of zooplankton, including krill, and higher trophic level predators in the Scotia Sea ecosystem (Murphy et al. 2007b). Some of these variations have also been linked to SO and southern hemisphere scale variations (e.g. Forcada et al. 2005; Murphy et al. 2007b).

The WAP and Scotia Sea ecosystems were historically exploited by commercial harvesting (Kock 2007; Croxell & Nicol 2004; Smetacek & Nicol 2005; Balance et al. 2006), the consequences of which are ongoing. Commercial fisheries for Antarctic krill still exist in the Scotia Sea region, albeit at a reduced level. These two ecosystems are further impacted by recent climate variability and change at a range of temporal and spatial scales (Stammerjohn et al. 2001; Reid & Croxall 2001; Fraser & Hofmann 2003; Atkinson et al. 2004; Ainley et al. 2005; Murphy et al. 2007a,b). The spatially variable but highly connected nature of these systems means that for comparative trophic analyses of food web operation two scales of data syntheses and analyses are required, (i) at the WAP scale and (ii) at the regional WAP-Scotia Sea scale.

Similarities and differences among the regions. As the above synopsis demonstrates, among-region comparisons are complex, especially in terms of physical forcing, hydrography, bathymetry, and trophic structure of the 4 regions (Table 1). Major factors include:

(1) Lateral fluxes. Trophic models of the two Northeast Pacific programs use vertical (1-D) NPZ-style models to describe lower trophic dynamics in oceanic waters. However, both Pacific regions cover continental shelf areas, and cross-shelf fluxes between oceanic and shelf environments influence resource availability and production, a factor that will be considered in this synthesis effort. Simple, 1-D horizontal

plankton models have been developed for the NCC shelf ecosystem that are driven by only upwelling intensity and cross-shelf Ekman transport but capture the same basic dynamics of the system (seasonality, cross-shore distributions, and biomass) as models coupled to sophisticated 2-dimensional circulation models (Newberger et al. 2003, Wainwright et al. 2003). A 1-D vertical approach is appropriate for WAP because this shelf area can be sub-divided into regions that are characterized by specific hydrographic, sea ice and biological characteristics (Smith et al. 1999; Prézelin et al. 2004; Kim et al. submitted). Lateral fluxes between the WAP shelf regions can be specified via direct or simulated current observations (Moffat et al. in press; Dinniman & Klinck 2004). A similar approach is feasible for South Georgia. Lateral physical fluxes and benthic biology are important on Georges Bank (Steele et al. 2007).

(2) Upper trophic levels. The components of the upper trophic levels of the 4 systems have similarities and differences. There are a number of resident fish species on GB, comparable groundfish species, salmon and herring in the CGOA and krill in the NCC, WAP and South Georgia. For the Antarctic there are unresolved, interesting, questions about the role of species other than krill in transferring energy between primary producers and higher trophic level predators (e.g. squid, myctophid fish and salps), and squid appear to play a significant role in pink salmon energetics in the CGOA (Aydin et al. 2005). Upper trophic levels in the CGOA have been particularly dynamic. During the 1960's, CGOA fish biomass was dominated by a zooplanktivorous rockfish, Pacific ocean perch, that declined after heavy fishing in the mid-1960s. Intensive whaling during the mid-1960s removed another  $10^6$  metric tons of plankton-feeders. Lucrative CGOA crab and shrimp fisheries collapsed in the 1980s (Orensanz et al. 1998), and groundfish catch increased. Groundfish biomass was dominated by walleye pollock (also a zooplankton feeder) in the 1980's which subsequently declined as its predators (arrowtooth flounder, halibut, and Pacific cod) increased in total biomass. Pinniped populations declined over the same period. At present, the CGOA food web appears dominated by piscivorous groundfish predators, many of which still feed on the forage species (shrimp and capelin) that apparently declined after the 1976-77 regime shift (Aydin et al. 2007; Yang et al. 2005; Anderson & Piatt 1999). A similar dynamism in the species composition of harvested fish on GB during the past ~40 years is reviewed by Steele et al. (2007). The top predator community in the NCC was affected by the same PDO shift (Ainley & Divoky 2001). The SO GLOBEC regions also include important upper trophic level components, such as seabirds, penguins, seals and cetaceans, which are integral components of the trophic structure and account for significant ecosystem fluxes (e.g. Murphy et al. 2007a). It, too, was affected by a regime shift, in this case that of the Southern Annular Mode (Ainley et al. 2005; Jenouvrier et al. 2005; Stammerjohn et al. 2007).

(3) Lower trophic levels. GB primary production is driven by  $\text{NO}_3$  input (lateral flux) and mixing. Primary production in the NCC is driven by upwelling supply of macronutrients, light and mixing, depending on location and season. CGOA primary production processes are driven by Fe and light, and in the SO light, Fe, sea ice cover and hydrographic structure are the major drivers depending on season and location. All regions support variable, but typical, assemblages of bacteria, and heterotrophic nano- and micro-zooplankton. The dominant mesozooplankton taxa are copepods on GB and the CGOA, and copepods and krill in the NCC and SO.

(4) Temporal changes. In all 4 regions there are important and controversial issues concerning major temporal changes—regime shifts in the North Pacific and Antarctic, trophic cascades in all areas, and the effects of variable sea ice cover in the Antarctic. Explanations of underlying processes require quantitative end-to-end pictures for each system.

## RESEARCH PLAN

**Personnel.** The project includes 23 scientific investigators, 12 from academia, 6 from the US NMFS, 3 from BAS, and 2 from private industry (Table 2). This is a well-integrated interdisciplinary team, most with direct GLOBEC experience, but investigators new to GLOBEC are included. In assembling the team, we have endeavored to minimize the number of investigators to produce the most parsimonious budget and management plan. Toward this end, the GB team is small because the end-to-end budget for this region is reasonably complete (Steele et al. 2007), although it will be modified and upgraded in this project. The SO team is larger because there is as yet no trophic model for this region, and more work needs to be done. Also, inclusion of the wider Scotia Sea region involves researchers from BAS. The two North Pacific teams have overlapping personnel covering several components (e.g., Thomas, Bograd, Strom). In addition, investigators from specific regional teams will contribute to the overall effort in all of the regions (Gifford and Strom on microzooplankton, Bisagni and Thomas on primary production fields, Ainley and Tynan on seabirds and mammals). The project consists of 3 interdependent and tightly linked streams of activity: modeling, data assembly, and analysis. Particular attention will be given to data assembly to insure that calculations of standing stocks and transfer functions are consistent among the 4 regions. This is necessary for legitimate among-region comparison of diagnostics (Task 3 below).

Because integration of the streams is so critical for the success of synthesis, we have designed a research program centered on excellent communication among these elements (**Table 2**).

**Table 1.** Major characteristics of the US-GLOBEC regions.

Characteristic	GB	NCC	CGOA	SO
Bathymetry	Shelf bank	Shelf to deep water	Shelf to slope	Shelf to deep water
Area	42,000 km <sup>2</sup>	34,000 km <sup>2</sup>	291,840 km <sup>2</sup>	89,000 km <sup>2</sup>
Hydrographic drivers	Retention	Advection Seasonal upwelling	Downwelling, slope eddies, winds, freshwater inputs, coastal current	Advection, wind, sea ice, freshwater inputs
Major climatic indicators	NAO	ENSO PDO	ENSO PDO	ENSO, Southern Annular Mode
Major primary production drivers	Vertical & lateral flux of macronutrients	Light, upwelling-derived macronutrients, Fe	Light, macronutrients, Fe	Light, Fe, sea ice, hydrographic structure
Characteristic mesozooplankton	Copepods	Copepods Krill	Copepods	Krill, Salps Copepods
Invertebrate predators	Carnivorous copepods, medusae	Medusae	Squid	Salps Squid
Characteristic fish	Groundfish, pelagics, elasmobranchs	Salmonids, groundfish, pelagics	Salmonids, groundfish, pelagics	Demersal spp. On shelves
Benthos (non-fish infauna & epifauna)	Important	Important on shelf	Important on shelf	Myctophids Not important (deep shelf)
Top predators	Mammals, birds <i>Minor importance</i>	Mammals, birds <i>Medium - Major importance</i>	Mammals, birds <i>Unknown importance</i>	Mammals, birds <i>Major importance</i>

**Workplan.** We have designed a 4-part workplan in which we will sequentially assemble end-to-end models for each region, assess the skills of each model, extract diagnostics that will be used to evaluate the effects of changing climate and changing trophic structure in each of the GLOBEC study regions, and develop quantitative methods to compare the metrics. The four tasks are described below.

**Task 1: Assembly of end-to-end models for each study region.** We recognize that the 4 regions differ in hydrography, trophic structure and physical forcing. Thus, the initial requirement is for transportable data sets and end-to-end models for each region. In developing these models we will draw upon the species-centric data and models for each region to develop trophic-centric models (e.g. Steele et al. 2007). We expect that initial protocols for these will be available for each region at the start of the work. The following summaries indicate the general nature of data and models for each region.

*Georges Bank.* The existing mass-balance model of GB treats the upper and lower food webs separately because they operate a fundamentally different space and time scales (Steele et al. 2007). The lower food web is partitioned into 3 seasons: spring, summer and autumn/winter and 3 regions with different water column vertical structure, for a total of 9 combinations. The lower web is driven from the bottom by physical influx of nutrient rich deeper water, with concomitant export off the Bank of near surface water and associated plankton. The input of NO<sub>3</sub> determines “new” production. This, together with estimates of “net” production (new + recycled), provide constraints on the calculation of fluxes in the lower web. The outputs from the 9 component webs are combined to give yearly average fluxes in carbon units for mesozooplankton, suspension-feeding macrobenthos and for fecal material that fuels the meiobenthos and deposit feeding macrobenthos. The upper web operates on an annual time scale over the entire bank and is driven by known consumption rates and diet composition of fish. Two key parameters of the upper web were estimated: the proportions of fish consumption consisting of benthic and pelagic invertebrate carnivores. The output of the upper web is the total consumption of zooplankton and benthos, which is matched with the output of the lower web. The upper web was fit to 4 decadal periods (1963-2002) for which detailed fish abundance and diet data are available (Smith 2004). Fish are classed as piscivores, planktivores and benthivores based on diet (Garrison & Link 2000). We assume that the fish eaten by other fish are juvenile pre-recruits that eat predominantly mesozooplankton. These data and assumptions allow the food requirements of the fish communities on GB to be expressed in terms of 2 fluxes, consumption of plankton and benthos by fish, that are defined by function, rather than species groups. Fluxes

through the planktonic and benthic invertebrate carnivores are used to match the fish requirement for plankton and benthos with output from the lower web.

**Table 2.** Scientific investigators and institutional affiliations.

Investigator	Institution
Dian J. Gifford	University of Rhode Island
Jeremy S. Collie	University of Rhode Island
John H. Steele	Woods Hole Oceanographic Institution
James J. Bisagni	University of Massachusetts, Dartmouth
Eileen E. Hofmann	Old Dominion University
Kendra L. Daly	University of South Florida
Eugene Murphy	British Antarctic Survey
Nadine Johnson	British Antarctic Survey
Martin Collins	British Antarctic Survey
Walker O. Smith	Virginia Institute of Marine Science
David G. Ainley	H.T. Harvey & Associates
Cynthia T. Tynan	Associated Scientists of Woods Hole
Christine A. Ribic	University of Wisconsin
Andrew C. Thomas	University of Maine
Richard D. Brodeur	Northwest Fisheries Science Center
Steven Bograd	Southwest Fisheries Science Center
Suzanne L. Strom	University of Western Washington
Anne Hollowed	Alaska Fisheries Science Center
Kenneth O. Coyle	University of Alaska, Fairbanks
Kerim Aydin	Alaska Fisheries Science Center
Sarah K. Gaichas	Alaska Fisheries Science Center
James Ruzicka	Oregon State University
Robert J. Foy	Alaska Fisheries Science Center

In this iteration of GLOBEC synthesis, we will: (1) Compile a centralized database of observations for the different trophic levels. The database will be in a standardized format that can be shared among the PIs and used as input to different modeling approaches. (2) Update the database and model with additional data, including new mesozooplankton data that are now available from the GB GLOBEC program. (3) Add marine mammals and seabirds to the upper web. (4) Improve the methodology for fitting the model to the data. An objective function will be used to minimize the differences between model predictions and the measured trophic fluxes and biomasses. With the incorporation of more data, we will attempt to fit more of the unknown parameters, which were assumed fixed in the Steele et al. (2007) end-to-end model. (5) Construct dynamic models of the

decadal changes in the food web. The dynamic models will concentrate on the fish community, for which the best time series data exist. We will adapt the multispecies biomass dynamics models that were successfully applied to the Georges Bank fish community by Collie & DeLong (1999). The fish community will be divided into benthivores, piscivores, and planktivores as was done in the food-web model. The parameters of these coupled difference-equation models will be estimated with AD Model Builder, a software program that is commonly used for complex parameter estimation problems

*Northern California Current.* Two trophic models have recently been developed for the NCC ecosystem (Field et al. 2006, Ruzicka et al. 2007). Both are mass-balance models developed on the ECOPATH platform (Christensen & Walters 2004). The Field et al. (2006) model is annualized for the full NCC region along the Washington, Oregon, and northern California coasts to Cape Mendocino and seaward to the 1280 m isobath, the extent of available groundfish survey information collected by NOAA Alaskan and Northwest Fisheries Science Centers. It has 63 functional groups and 7 fisheries with most detail given to commercially important fish species, especially groundfish. The Ruzicka et al. (2007) model, which we will use in this project, incorporates data from pelagic trawl surveys sponsored by GLOBEC and the Bonneville Power Administration (BPA) off the Oregon and Washington coasts (Brodeur et al. 2005; Emmett et al. 2005). It is a full food web model with 54 functional groups and 2 fisheries that include both benthic and pelagic environments, but it gives greatest detail to the pelagic community. The timing of the BPA and GLOBEC surveys allows resolution of seasonal change in the community structure and food web as species migrate into the region during the productive upwelling season, resulting in spring and summer versions of the Ruzicka et al. (2007) model.

The model domain is covered by the combined GLOBEC and BPA pelagic trawl surveys, the Oregon and Washington coasts out to the upper continental slope (34,000 km<sup>2</sup>). Incorporation of data from the full trawl survey region, will provides an expanded model domain from the original Ruzicka et al. (2007) model, which was restricted to the Oregon shelf. Our modeling efforts will focus on improving the model's accuracy with respect to pelagic trophic interactions. Some of the aggregated functional groups will be divided into individual species, as allowed by available data. A microzooplankton group will be added to include the substantial grazing impact upon primary production by heterotrophic protists and their importance as prey for copepods in the NCC upwelling ecosystem (Landry & Hassett 1982; Fessenden & Cowles 1994; Neuer & Cowles 1994). More recent data on composition, productivity, and migration patterns of the seabird and mammal community will be incorporated (Ainley et al. 2005; Tynan et al. 2005). Finally, trophic linkages will be better informed by recent local diet studies (Miller & Brodeur 2007).

Data necessary to construct a food web model must be gathered together from many sources that have been collected at different frequencies or over different periods of time. For comparison with the other GLOBEC regions, we will produce a composite model representing the 'mean' community structure and trophic interactions of the period for which the most recent available data are pooled. However, we will also consider information implied about interannual variability of food web structure from data collected at relatively high frequency (e.g., seasonal pelagic trawl surveys).

*Coastal Gulf of Alaska.* In the CGOA, access to impressive fishery independent and fishery dependent datasets made it possible to model trophically explicit age structured groups of major groundfish and pinnipeds, and substantial taxonomic detail in benthos, pelagics, birds, and marine mammals within an independent implementation of ECOPATH (Polovina 1984; Christensen & Pauly 1992; Pauly et al. 2000; Christensen & Walters 2004; Aydin et al. 2007). The current CGOA model includes 113 consumer groups and 14 fishing fleets, with an additional 4 producer groups (large and small phytoplankton, macroalgae, and external production), 5 detritus groups (benthic and pelagic detritus, fishery discards, fishery offal, and external detritus) and 2 microbial loop groups (benthic and pelagic) (Aydin et al. 2007). The model was constructed to represent the state of the ecosystem during the early 1990's based primarily on groundfish biomass and diet data from averages of 1990 and 1993 bottom trawl surveys. Information on primary production, zooplankton, benthos, and marine mammals was not always available for the early 1990's time period, so the nearest available information was substituted.

The current mass balance model of the CGOA continental shelf system is defined laterally by the North Pacific Fishery Management Council (NPFMC) management areas 610, 620, 630, and 640, which coincide roughly with International Pacific Halibut Commission (IPHC) management areas 3A and 3B. The continental shelf and slope to approximately 1000 m are included in the model following AFSC bottom trawl surveys; nearshore areas < 50 m depth are not included. Within the NPFMC management areas, the area of the CGOA shelf/slope covered by NMFS trawl surveys is 291,840 km<sup>2</sup> (Table 1). This total shelf area was used to calculate biomass and production per unit area as model inputs. There are 9 spatial strata in the CGOA model, representing 3 general habitat types in each of 3 geographic sections: "shelf" habitats 50-200 m depth, "gully" habitats 100-200+ m depth, and "slope" habitats 200-1,000 m depth. In general, gully habitats are deep areas within the continental shelf surrounded by shallower shelf areas, whereas slope habitats are found at the seaward margin of the continental shelf.

The existing model will be updated to include recent spatially and seasonally detailed information on primary production and lower trophic levels collected by US-GLOBEC projects in the northern CGOA, as well as more detailed information on benthos and key groundfish predators for years concurrent with the US-GLOBEC work. Hollowed and Foy will review these new data sets to inform modelers on approaches for downscaling the scope of the current model from the entire CGOA to focus on processes at intermediate spatial scales within the area currently modeled as the central CGOA (Fig. 3) where long time series of hydrography and climate data exist, and to include seasonal effects where data allow. In parallel with recent end-to-end modeling of the GB ecosystem, the CGOA shelf will be considered as 3 zones. Compelling evidence for broad cross-shelf zonation in hydrography, resource availability, and species distribution has recently been presented (e.g. Weingartner et al. 2005; Strom et al. 2006, 2007; Dagg et al. 2006).

*Southern Ocean.* The SO is a new region for implementing the food web-trophic level approach. Models equivalent to those for GB, NCC and CGOA are not available for the SO system. Our first task will therefore be to develop models for the study sites guided by the existing models for the other GLOBEC study sites. We have as starting points existing models for specific components of the trophic web, e.g., phytoplankton carbon production (Kim et al. submitted), Antarctic krill growth (Hofmann & Lascara 2000), Adélie penguin chick growth energetics (Salihoglu et al. 2002; Chapman et al. submitted), and predator-prey linkages (Murphy 1995; Murphy & Reid 2001) as starting points models for specific components of the trophic web. The food web-trophic pathway models will be designed to address specific research questions directed at understanding food web regulation by bottom-up and top-down controls as follows:

(1) Regulation of food web dynamics by bottom-up controls.

H1. The large abundances of zooplankton/krill in WAP and larger Scotia Sea study sites result from a suite of favorable environmental conditions. *Physical forcing (e.g. seasonal light levels, circulation, retention gyres, ice cover, glacial meltwater, water-column stability, and intrusions of warmer, nutrient-rich CDW) govern the seasonal availability of microplankton (i.e. sea-ice biota, phytoplankton, microzooplankton) to intermediate trophic levels.*

H2: The dominant trophic pathways on the WAP and the larger Scotia Sea study sites vary seasonally, shifting from the mid to outer shelf during spring/summer to the inner shelf during fall/winter. Adult krill migrate from the outer to inner shelf in response to a seasonal change in the cross-shelf gradient of phytoplankton biomass, thereby extending the seasonal availability of food resources to krill. *The change in krill distribution influences the seasonal distribution of predators.*

H2a. *The change in krill distribution has no influence on the seasonal distribution of predators, as in winter predators in the outer WAP feed extensively on myctophid fish.*

(2) Regulation of food web dynamics by top-down controls

H1. At a range of temporal scales, from decadal to interannual, the extent and intensity of phytoplankton blooms in the WAP are influenced by sea ice distribution, bathymetry, and oceanographic processes (e.g. glacial melt water, water column stability, macro/micronutrient availability, intrusions of CDW), which in turn are influenced by atmospheric forcing (e.g., Southern Annular Mode). *Grazing losses (top down control) vary spatially and temporally depending on the abundance and species composition of zooplankton.*

H2. In WAP and around South Georgia, decimation of seals, whales and demersal fish by commercial fishing for two centuries prior to about 1985 led to an increase in krill abundance as a compensatory response. It also has led to krill now being the primary forage for colony-bound top predators during summer. Since, the 1970s krill abundance has been negatively influenced by climate warming, reduced sea ice extent, increased predator consumption, commercial fishing, and competition. *With no longer a viable option for prey switching, predator populations tied to shore-based colonies in summer have become much more unstable, responding sensitively to krill abundance. In fact, there is no longer any top-down pressure.*

Two sites on the WAP shelf will be used for model development; one inside Marguerite Bay, and one located on the central shelf. Additional model development sites will be in the Scotia Sea and at South Georgia. As part of the model development we will construct a centralized database for each trophic level, similar to what will be done for GB. Development of these complementary models will entail a broader-scale analysis of the biological connections within the WAP-Scotia Sea system. This will be achieved by drawing upon work undertaken by BAS on the Scotia Sea ecosystem and historical data sets for the Scotia Sea.

Task 2: Skill assessment of each end-to-end model. Many approaches exist for using discrete observations, such as those obtained during the GLOBEC studies, to evaluate the skill of a model. These range from simple model-data comparisons to more formal data assimilation methodologies such as constrained parameter optimization (Friedrichs et al. 2007). Quantitative model skill assessment will be a significant activity in which all components of this project will be engaged. Model skill assessment will be done by comparison with *in situ* data using a suite of statistical approaches of escalating rigor, including comparisons of spatial distributions, means, variance, two-dimensional histograms and other skill assessment methods, such as Target (Joliff et al. 2007) and Taylor (Taylor 2001) diagrams. These approaches will reveal spatial and/or seasonal timing/phase relationships for the different regions and provide a measure of model bias relative to observations. For example, means computed from the models should match those from *in situ* data with little bias; the models should capture the dynamic range over seasonal time scales, and timing of minima, e.g., plankton blooms, should match observations. *Also, the skill of each model will be assessed by evaluating how well each model captures the basic fluxes of, e.g., primary production, secondary production and export production, for example.* This diversity of model skill assessment methods will provide guidance on when and where model improvements are required and will provide a quantitative basis for evaluating models from the four regions. Rigorous assessment of model skill for the 4 regions is critical before comparisons can be made between systems. Quantitative skill assessment has not been done for the types of models proposed for the four GLOBEC regions, and as such, this project will set a new standard for cross-system model skill assessment.

Task 3: Determination of diagnostics. *This effort will provide the primary end results of the entire project and permit comparison among regions.* Once model skill has been assessed for each region, we will extract from the regional models a set of diagnostics that can be used to evaluate the effects of top-down (fishing pressure) and bottom-up (climate change) across the 4 regions. We will choose diagnostics that are common to all 4 regions. What these will be is not known at this time. However, we do know that comparisons that are based on concentration or biomass are unlikely to be useful. Rather, obvious candidate diagnostics are material fluxes, which avoid issues of species and biomass differences among the regions. Such an approach is used to compare across the varied and disparate sites included in the Long-term Ecological Research program (Hobbie et al. 2003). Potential candidate fluxes are primary production, mesozooplankton production, benthos production, and nutrient fluxes. However, we do not expect that every diagnostic will necessarily be applicable to all regions, e.g., macronutrient fluxes are less important for primary production in the SO than for GB. The identification of the diagnostics for cross-system comparisons will be a major focus of our first science investigator meeting (**Table 4**).

Task 4: Methods for among-model comparison of diagnostics. The diagnostics for the models in the different regions will be compared using quantitative methods that will be developed as part of this project. Descriptive comparisons of trophic structure across the 4 regions are the 0-order activity for this task. This can include statistical methods of comparison and quantitative measures of trophic or size structure. Linear mass-balance and inverse methods will be used as beginning 1<sup>st</sup>-order comparisons while we investigate the use of approaches such as parameter optimization via variation adjoint methods

in the four regions (e.g., Friedrichs et al. 2007). The linear and mass balance analyses can be based on existing top-down (ECOPATH), bottom-up (Inverse) or combined (Steele et al. 2007) approaches. Potential 2<sup>nd</sup> order methods involve dynamic simulation either as direct representation of parts of the web or perturbation analyses of the mass balance solutions. The development of these methods will be the primary focus of the postdoctoral researcher supported by this project (see Hofmann budget). Development of a consensus on the methods to be used for across-model comparisons will be closely linked to the definition of the diagnostics and form another major focus of the first meeting.

The comparison approaches chosen rely upon estimation of similar processes in the 4 regions. One example of such a process that goes across all regions is potential new production (PNP) which can be defined as the difference between the rate of change of NO<sub>3</sub> “storage”, vertically-integrated between the surface and the depth of the euphotic zone and “nitrate vertical flux” into the euphotic zone (Bisagni 2003; Steele et al. 2007). The rate of change of vertically integrated NO<sub>3</sub> contained in the euphotic zone is determined from the mean annual cycle, while the vertical NO<sub>3</sub> flux is computed using the mean annual cycle of nitrate change with depth in the euphotic zone and corresponding vertical diffusion values. PNP is determined as the difference between the two. Vertically integrated NO<sub>3</sub> will be computed for the euphotic zone for each study region. Euphotic zone depth for each station is computed prior to integration, providing an additional diagnostic for comparison between the regions. It is anticipated that this particular diagnostic will be more relevant for some regions (GB) than others (SO), but this type of calculation will allow us to quantify these differences. Data sets adequate for the calculation of PNP exist for each study region from historical data sources and GLOBEC program observations (see next section).

#### Data Sources.

*Nutrients.* Steele et al. (2007) used a large nutrient database compiled by Fisheries and Oceans Canada merged with data collected by the US-GLOBEC GB program. This provided a comprehensive nutrient dataset available for the GB study region, archived by Bisagni. Nutrient data for the SO, NCC and CGOA GLOBEC study areas, although less extensive in time and space than the GB dataset, will be acquired and organized for parallel analyses. These data, available within the GLOBEC program, include survey stations from LTOP surveys and WAP surveys, and additional stations from process cruises in the 4 study areas. Nutrient data at South Georgia are available from 1995-2005. Published CGOA nutrient data include Childers et al. (2005) and Strom et al. (2007). Coyle will provide long-term (1988-2004) nutrient data from the northern GOA. Available data will be merged with regional data from the World Oceanographic Data atlas as needed. Data on Antarctic nutrient fluxes are cited in Serebrennikova and Fanning (2004).

*Lower trophic levels.* Data sources for the lower trophic levels of the GB end-to-end web are cited in Steele et al. (2007). Data on phytoplankton and microzooplankton standing stocks and rates in the NCC and CGOA are available and will be assembled by Strom, including data on phytoplankton growth and production (Strom et al. 2006; Strom & Macri 2008). Data on phytoplankton standing stocks and production in the SO study region are available from AMLR (~1995-2003), Palmer LTER (1991-2002) and SO GLOBEC (2001-2002) and BAS (1995-2005). Data on SO microzooplankton will be compiled from the literature by Gifford and Strom.

*Mesozooplankton.* Sources of GB mesozooplankton data are cited by Steele et al. (2007). Additional data on mesozooplankton from the GB GLOBEC program are now available through the program's database. Mesozooplankton data for the NCC region are available from the BPA Ocean Salmon Survey (1998-2007) and from the NCC GLOBEC program (2000 and 2002) (Reese et al. 2005; Ressler et al. 2005; Pool & Brodeur 2006). For the CGOA, mesozooplankton abundance and biomass data are archived by K. Coyle in conjunction with a larger database and time series for the region (1988-2004). Published mesozooplankton data include GLOBEC studies by Coyle and Pinchuk (2003; 2004). Data on krill and other zooplankton abundance in the SO study region are available from AMLR (1995-2003), Palmer LTER (1991-2002), SO GLOBEC (2001-2002), BAS (1995-2005) and the literature (e.g., Ashjian et al. 2004; Daly 2004).

*Invertebrate predators.* Data sources for invertebrate predators on GB are cited in Steele et al. (2007). Data on large invertebrate predators (mainly jellyfish) in the NCC GLOBEC program are available from Suchman et al. (2005; in press) and Brodeur, in the CGOA from K. Coyle, and in the SO from Daly.

*Benthos.* Data sources for invertebrate macrobenthos on GB are cited in Steele et al. (2007). Benthic data for the NCC will be compiled from the literature. For the CGOA we will use data collected from the biennial bottom trawl survey conducted by the Alaska Fisheries Science Center since 1984 and Alaska Department of Fish and Game crab and groundfish surveys in 1976-1977 (Blackburn 1979) and then annually after 1984. The SO study sites are deep, with an effectively pelagic trophic web, so benthic data

will not be compiled for this region.

*Fish standing stock and diet.* Data sources on fish standing stocks for GB are cited in Steele et al. (2007) and are available from published NMFS stock assessments. Abundance data for pelagic fish in the NCC are available from a combination of BPA Ocean Survey data (1998-2007) (Brodeur et al. 2003; 2005) and GLOBEC (2000 & 2002) (Brodeur et al. 2003; 2004). Data on demersal fish in the same region are available from federal, state and academic trawl surveys (Shaw et al. 2000; Weinberg et al. 2002) and NMFS stock assessment reports (Schirripa 2007). In the CGOA, we will use fish abundance data compiled by Aydin et al. (2007) and other sources. Data on fish standing stocks and fishery catches are available from various NMFS AFSC databases, state fish ticket databases and from the International Pacific Halibut Commission survey database. Data on fish in the SO are available from the literature (e.g. Kellerman, 1996; Chapter 7, Knox, 2007; Donnelly & Torres, in press). Sources for GB fish diet data are cited in Steele et al. (2007). Pelagic fish diet data collected during NCC-GLOBEC are contained in Miller (2006) and Brodeur et al. (unpubl.). Other pelagic fish diet data are reported by Brodeur et al. (1987; 2007). Demersal fish diet data for the NCC will be compiled from the literature. Data on fish physiological parameters are contained in Ruzicka et al. (2007). Diet data for CGOA fish are available from federal, academic and state groundfish and crab trawl surveys. Fish diet data for the SO will be compiled from the literature (e.g., Chapter 7, Knox 2007).

*Top predators.* Data on marine birds and mammals for the GB region are available from NOAA. NCC seabird and mammal data from GLOBEC studies are available in Ainley et al. (2005) and Tynan et al. (2005). Other NCC data are available from the BPA Ocean Salmon Survey and from Zamm and Roby of Oregon State University. For the CGOA, pinniped, fish and invertebrate diet and monitoring data are available from NMFS surveys and other studies (e.g., Fritz & Stinchcomb 2005, Yang et al. 2006, Britt and Martin 2001). For the SO study area, data on cetaceans are available from the IWC (1999-2001), GLOBEC (2001-2003), Palmer LTER (1993-2003), Tynan and Ainley, SO GLOBEC synthesis, in progress and Ribic et al. (in press). SO seabird and pinniped data are available from a combination of SO GLOBEC, Palmer LTER, and BAS data sets.

*Hydrographic and climate data.* Hydrographic and climate data for the GB region are cited in Steele et al. (2007). Hydrographic data from the CGOA LTOP program are available on the program's web page (<http://www.ims.uaf.edu/GLOBEC/results/index.html>) for the years 1997-2005. For the NCC, other hydrographic data from the Newport Line (1961-1971; 1997-2004) and OSU archives (~1972-1993) are also available. For the 2 Northeast Pacific regions, retrospective data for hydrography, nutrients, winds, surface fluxes, SST, climatic indices (PDO, NPGO, PNA, AO, NAO, MEI) and upwelling indices are available from the World Ocean Database (pre-1900-2005), NCEP Reanalyses (1948-present), ECMWF (1979-present) and other sources. Hydrographic data are also available from GLOBEC research in the northern CGOA (Stabeno et al. 2004; Royer 1998, 2005; Weingartner et al. 2004). Hydrographic data for the SO are available from a combination of AMLR (1995-2003), Palmer LTER (1992-2002), SO GLOBEC (2001-2002) and BAS (1985-2005) data sets. Meteorology data for the SO are available from Palmer LTER (1989-1999), SO GLOBEC (200-12002) and BAS (1946-1991). Remotely sensed ocean color and SST data for all 4 regions are available from SeaWiFS, /MODIS, PATHFINDER, AVISO and Quikscat for various time periods.

**Management Plan.** Overall project management will be coordinated by lead PI Gifford, who provided this service in the GB synthesis project that culminated in the Steele et al. (2007) end-to-end model. She will organize meetings (**Table 3**) of the science team, facilitate communication among investigators, and track progress of the project. A critical feature of the work is the need to integrate the 3 research "streams" (models, data assembly and analysis) so that there is continual interaction. The range of expertise and skills needed to undertake a pan-regional food web synthesis results in a large research team (**Table 2, Table 3**), which makes coordinated communication the key to success of the project.

Many of the project investigators have worked together on previous or ongoing projects, have a history of successful collaboration and timely publication, and have extensive experience with the type of research outlined for this project. Thus, we are starting with a team that understands coordinated interdisciplinary research. To ensure integration and communication, an executive committee (Steele, Gifford, Hofmann, plus one person from each regional group) will be responsible for overall project management. This group will meet by conference call at least monthly. Our project communications plan (**Table 4**) includes frequent meetings, which involve all project science investigators, or subsets of investigators focused on specific GLOBEC ecosystems, models, data sets, and / or processes. The latter meetings will occur at ~ 3-month intervals for 2-3 days at one of the team institutions. The meetings will maintain communication between investigators, ensure that the different project components remain coordinated, and ensure timely submission of abstracts for meetings and timely publication of project results. At monthly

intervals, we will have project conference calls that will incorporate web-based video capability (e.g., Skype). Our experiences in other large programs show that monthly phone/web conferences are an effective means of maintaining excellent communication between team members. Additional team coordination will be done via a team web site hosted by CCPO. Project data, models and results will be posted on the web site, allowing us to simultaneously access and analyze simulations. This will facilitate model evaluation and skill assessment, within-region comparisons, and inter-region comparisons. The web site will also provide project meeting results, publications, and other project information. Manuscript preparation and publication will continue throughout the project, but meetings explicitly devoted to this activity will take place in year 3.

**Table 3.** Responsibilities of scientific investigators.

REGION	GB	SO	NCC	CGOA
<b>Team Leaders</b>	Steele Gifford	Hofmann Daly	Thomas Brodeur	Strom Hallowed
<b>Physical oceanography</b>	Bisagni	Hofmann	Bograd	Bograd
<b>Retrospective</b>	Bisagni	Hofmann Murphy	Bograd Thomas Brodeur	Bograd Thomas Strom
<b>Foodweb modeling</b>	Steele Collie	Murphy Hofmann Johnson Collins	Ruzicka Brodeur	Gaichas Aydin
<b>Nutrients, 1° production</b>	Bisagni	Smith	Strom	Strom
<b>PNP fields</b>	Bisagni	Bisagni Smith	Thomas Bisagni	Thomas Bisagni
<b>Microzooplankton, lower web</b>	Gifford	Collins	Strom	Strom
<b>Mesozooplankton (incl. jellies)</b>	Gifford	Daly Smith Collins	Brodeur	Coyle
<b>Fish (+squid) abundance</b>	Collie	Daly Murphy	Brodeur Ruzicka	Hollowed
<b>Fish (+squid) diet</b>	Collie	Daly Murphy	Brodeur Ruzicka	Aydin Hollowed
<b>Benthos</b>	Collie	Not needed-- deep-- pelagic	Brodeur	Foy
<b>Top predators</b>	Ainley Tynan Ribic	Ainley Tynan Ribic	Ainley Tynan Ribic	Ainley Tynan Ribic

Comparisons across regions via models and data analyses (e.g. retrospective analysis in Steele et al. 2007) will provide the integrating synthesis for this project. This effort will be done by a postdoctoral researcher located with E. Hofmann at ODU, who will work with science investigators in the individual regions. This project will be the sole focus of the postdoctoral researcher.

**Intellectual Merit.** The major successes of GLOBEC have been in elucidating the processes underlying the dynamics of middle trophic levels in diverse physical settings. The “global” perspective has proved more elusive. At the same time there is an increasing demand for an ecosystem approach to management of marine resources subject to fishing pressure and climatic change.

Both of these challenges require an end-to-end approach that can provide the framework for detailed studies of particular species that are economically or environmentally significant. The path to such general protocols needs to begin with specific case studies. The US-GLOBEC sites provide sufficient diversity to test a range of methods as prologue to the larger global challenges. This modeling and synthesis project is a logical extension of studies initiated under the GLOBEC program that will advance the understanding of energy flow and trophic dynamics of marine food webs. Analyses of the response of marine ecosystems to climate change and their role in biogeochemical cycles have highlighted the importance of understanding trophic interactions. This point has been emphasized in the synthesis phase of GLOBEC and in the implementation phase of the Integrated Marine Biogeochemistry and Ecosystem Research (IMBER) program. Improving the understanding of trophic links in oceanic food webs is integral to the ability to understand and predict ecosystem responses to climate change and anthropogenic forcings. There is therefore a pressing need to compare the spatial coverage, trophic resolution, and dynamics of a suite of food webs, such as those present within GLOBEC. The research is directly relevant to the goals of the US GLOBEC synthesis and integration effort in that it synthesizes a range of *in situ* data sets by modeling. Our models will allow us to quantify and compare the spatial and

temporal variability of food web pathways that represent shelf regions in high (CGOA, SO) and middle latitudes (GB, CCS), including the obvious ‘hotspots’ associated with banks (NCC, SG) and other bathymetric features (SO). These represent characterizations of some of the most productive and economically and sociologically important shelf ecosystems in the global ocean. A strong aspect of the proposed study is the integration by modeling of extensive biological data sets to evaluate processes, from primary producers to top predators, controlling energy flow, trophic transfers, carbon cycling, flux and export dynamics. The complementary and divergent aspects of the study areas provide a basis for developing a framework that allows extension and comparison to systems elsewhere.

**Table 4.** Project timeline and schedule of interactive activities.

DATE	ACTIVITY	OBJECTIVE
<b>Year 1</b> Sept 2008 Fall 2008	Start Date PRS Workshop, organized by US-GLOBEC national office. Project PIs meet 2-3 days before or after workshop.	Refine scope of work for all PIs, plan meetings and workshops for the remainder of the project.
Fall 2008	Project PI meeting at one of the PI institutions, 2 days. Data group and modelers meet concurrently and jointly for 1-2 days before project meeting.	Continue to refine scope of work for entire project. Data managers and modelers meet separately, together and with all PIs to define modeling needs, data needs and standardization.
Spring 2009	Regional groups meet separately (locally) 2-3 days.	Construct detailed workplan for each region using input from fall meetings.
Spring 2009	Modelers meet separately. 2-3 days.	Define food web models for the different regions.
Summer 2009	Subgroup meeting w specific focus (e.g., Southern Ocean). Open to all PIs. 2-3 days.	Review results and refine workplan for the specific focus.
<b>Year 2</b> Fall 2009	PRS Workshop, organized by US-GLOBEC national office. Project PIs meet 2-3 days before or after workshop.	Update national program and PIs on project progress. Update progress of all regional components. Plan further work for all regional components. Begin among-region synthesis. Plan meetings and workshops for the remainder of the project.
Winter 2010	Subgroup meeting w specific focus (e.g., NCC). Open to all PIs. 2-3 days.	Review progress and refine workplan for the specific focus.
Spring 2010	Subgroup meeting w specific focus (e.g., CGOA). 2-3 days. Open to all PIs.	Review progress and refine workplan for the focus
Summer 2010	Subgroup meeting w specific focus (e.g., Georges Bank). 2-3 days. Open to all PIs.	Review progress and refine workplan for the specific focus
<b>Year 3</b> Fall/Winter 2010 Spring 2011 Summer 2011 Aug 2011	Whole PI meeting, 5 days, Sub-group meeting. 3-5 days. Sub-group meeting. 3-5 days. End project	Focus on publication products and writing. Writing. Writing.

**Broader Impacts.** The use of state-of-the-art modeling approaches coupled to data assembly and analyses provides opportunities to train graduate students (3 included in project) in a variety of disciplines (food web modeling, data analyses, data assimilation, marine ecology) that are needed to address the important scientific and societal problems facing marine systems. The project includes 2 postdoctoral scientists, many women (9 of 22 investigators) including several in lead roles, several talented young scientists new to GLOBEC, other scientists new to GLOBEC, and an outstanding team of international collaborators (see Letter of Support from BAS). The cooperative effort among academic, and government, scientists from private industry is beneficial to all groups. The scientific investigators from diverse professional backgrounds bring a synergistic perspective to the proposed research. The management plan centered on intensive, frequent communication via in-person, digital and electronic meetings is a unique and potentially transformative aspect of the project.

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