Results of Prior GLOBEC NSF/NOAA Support

(Note: References cited are at beginning of Reference section)

Botsford, L.W. and **A. Hastings**, U.S.GLOBEC NEP Phase IIIb-CGOA: Environmental influences on growth and survival of Southeast Alaska coho salmon in contrast with other Northeast Pacific regions. OCE0535398, $1,152,732, April 1, 2006-March 31, 2009.

This collaborative research program is a comparative synthetic study of the responses of coho salmon to environmental change in the Gulf of Alaska and the California Current. Alex Wertheimer of NOAA is analyzing field data on marine juvenile habitat for 8 years in one location in Alaska and 4 years in another. Milo Adkison of the University of Alaska is extending his statistical analyses of coho spawning data from streams in Alaska. Botsford, Hastings and Teo are analyzing the past 23 years of coded wire tag data spanning the two regions. Thus far we have found that there is not inverse covariability between regions since 1980 (Teo et al. in review). We also find consistent inter-annual variability in age at spawning. Nick Bond of NOAA and University of Washington is developing environmental indicators for use in analyses of variability in survival along the coasts of B.C. and southeast Alaska. Hal Batchelder of Oregon State University is using an individual based model of juvenile salmon and a GLOBEC circulation model to test hypotheses developed in the statistical analysis. Broader impacts include co-authoring a publication (i.e., providing the oceanographic and population dynamics part) rebutting a publication claiming coho salmon south of San Francisco were not native, hence need not be protected under the endangered Species Act (Adams, et al. 2007).

D.J. Gifford, J.J. Bisagni,, J.S. Collie, E. G. Durbin1, **M.J.Fogarty**, J. Link, L. P. Madin, D.Mountain, D. L. Palka, M. E. Sieracki, J. Steele, and B.K. Sullivan. OCE-0217399. $507,383. April 1, 2002- March 31, 2006. GLOBEC-01: Patterns of Energy Flow and Utilization on Georges Bank.

We developed ecosystem network models for Georges Bank, for four decadal time periods characterized by different environmental forcing and anthropogenic disturbance regimes (Steele et al. 2007). The four decadal time stanzas examined encompassed: (1) the cold 1960s characterized by abundant groundfish stocks fished by distant water fleets; (2) the 1970s, characterized by average water temperatures, increased domestic fishing effort, and depletion of groundfish stocks; (3) the 1980s, characterized by average water temperatures, overfishing of groundfish stocks, and increases in elasmobranchs; and (4) the average temperature, lower salinity 1990s, characterized by reduced fishing mortality, rebuilding of groundfish stocks, and increases in elasmobranchs and pelagic fish. Comparisons of fish energetic requirements for plankton and benthos, in conjunction with inputs from the microbial web, indicate that we obtained reasonable agreement for the last three stanzas: 1973 to 2002.

F. Juanes: IOS 0104872: $5000; 5/01/01-5/01/03: Dissertation research for Rebecca Jordan: Visual factors affecting mate choice in Lake Malawi cichlids.

The cichlid fishes of Lake Malawi are one of the most salient examples of adaptive radiation in vertebrates. While some work has focused on population isolation along horizontal stretches of habitat, no work has considered population isolation with depth. We investigated the behavior, genetics, and morphology of two demes separated along a continuous habitat by 20m depth. In the laboratory we tested whether females would assortatively court with males from her depth strata. We found that females did not discriminate among males taken from different depths. We also extracted DNA from fin tissue and we assessed allelic variation in four microsatellite loci. At three of the four loci, we found significant genetic separation. To our knowledge, this is the smallest reported distance in which genetic structure has been found among African cichlids.

Introduction

We propose to compare and extend research results regarding salmon and cod populations in the Pacific through GLOBEC NEP (and other programs) and the Atlantic, through GLOBEC NWA/Georges Bank (and other research). Individual regional studies commonly describe environmental effects on populations simply as a change in abundance, while in other cases they are able to achieve an understanding of the specific mechanism (e.g., variation in survival at a specific age, variation in growth rate a specific age). From modern population dynamic theory, we know that this point of action of the mechanism makes a difference in terms of the magnitude and time scale of population response. For example, variability in salmon survival at the age of ocean entry has a different effect on population persistence than variability in salmon survival at the age of return from the ocean for spawning (Hill et al. 2003, Botsford et al. 2005). Our goal is to achieve a broader understanding of the general effects of climate change on populations by cataloguing the changes in mechanisms of environmental effects on populations of two GLOBEC focal taxa, cod and salmon, then explaining differences in population response due solely to population dynamics, and synthesizing these results across a broad geographic range These taxa include Pacific salmon (*Oncorhynchus*) in the eastern Pacific, and Atlantic salmon (*Salmo*) in the western and eastern Atlantic, and Pacific cod (Gadus) in the eastern Pacific and Atlantic cod (Gadus) in the western and eastern Atlantic.

Our proposed study focuses on population dynamics, thus would lie within the second Research Theme identified in the Program Solicitation, Population Dynamics and Recruitment of Target Species. We will compare mechanisms of environmental action (i.e., life stage of change in growth or survival rate) across regions, and synthesize population responses in the framework of theoretical population dynamics. We anticipate this will, for example, provide explanations for differences in responses by various similar species. In addition, where mechanisms of environmental impact are not known our results will supply additional clues to mechanisms by describing population behaviors that would result from possible mechanisms. Our approach will involve mathematical models of the effects of the physical environment on biological populations hence would fall under Approach 2, Physical/biological modeling, though would be at upper trophic levels and would not involve circulation models. We note that the point of action is an indirect reflection of ecosystem structure (in the sense that an effect on growth rate is likely due to variability in prey and an effect on survival is likely due to variability in predator abundance). However, it would also be comparative across regions, examining species with similar and contrasting life histories (e.g., Pacific salmon are semelparous, while Atlantic salmon are iteroparous), falling under Approach 3, Comparative Regional Studies. Our work will also provide the type of guidance for monitoring described in Approach 4, in that one of the products of our study will be differences in frequency or time scales of population response, which influences the required sampling rate. We anticipate that our results will have other practical implications for resource management, as we will examine potential population responses to the environment across a range of fishing pressures, and the selective effects of fishing.

Most GLOBEC results for higher trophic level target species show varying responses over space and time. They rarely address the potential role of differences in population structure and dynamics in explaining those different responses. Given GLOBEC's mechanistic and population-oriented approach, there is a need to synthesize GLOBEC results in a population dynamics context, and determine the effects due to population dynamics, so that the effects of environmental change can be better understood.

Specific Questions

I. Based on population models and theory, how would we expect population structure (both life histories and point of environmental action) to determine the population response to a variable environment, varying over a range of time scales?
II. Based on all observations of the responses of **cod** populations to a varying environment across the north Atlantic and north Pacific semi-basins, how consistent are the differences in responses with those expected on the basis of population dynamic theory in sub-question 1?
III. Based on all observations of the responses of **salmon** populations to a varying environment across the north Atlantic and north Pacific semi-basins, how consistent are the differences in responses with those expected on the basis of population dynamic theory in sub-question 1?
IV. Based on the results from sub-questions I-III, what are the general implications for expected results when investigating any higher trophic level species, including cod, salmon and others, in the future?
V. How does the change in adult survival due to fishing influence a population's response to environmental variability?

Background

Population Dynamics

The role of population dynamics in climate change is often not discussed, but population dynamics is essential for understanding the form and time scale of responses of populations to external environmental change. In particular, for populations where age-structure is important, understanding population dynamics is essential for explaining differences in responses between closely related species, time scales of variability from specific mechanisms, and the effects of combinations of fishing and variable environment. Here we briefly summarize some of the different aspects of population dynamics that would be useful in extending our understanding of the effects of climate change on populations. We first begin with a discussion of the equilibrium level.

Because population changes due to climate change are often long term, it makes sense to examine factors determining the long-term "average" level of population abundance. These are included in the expressions for equilibrium, for a fixed point or for average population abundance. For age-structured models with density-dependent recruitment this is an expression involving lifetime reproduction and the stock-recruitment function (e.g., Botsford et al. 1997). As a first step one can focus on systems with only compensatory density dependence, or equivalently examine populations dynamics near the extinction point. For managed fish populations, fishery analysts have taken advantage of a graphical interpretation of this relationship by noting that the equilibrium recruitment can be determined as the intersection of the egg-recruit relationship with a line through the origin with slope 1/LEP, where LEP is the Lifetime Egg Production (Shepherd 1982, Sissenwine and Shepherd 1987). The fact that the equilibrium drops to zero when the LEP is reduced to the inverse of the slope of the egg-recruit function at the origin has been interpreted in terms of a lower limit on replacement, i.e., the minimum LEP required for each individual to replace themselves, thus for the population to persist (e.g., Mace and Sissenwine 1993, Botsford et al. 2004, Botsford and Parma 2005).

The corresponding equilibrium expression for a size-structured model with density-dependent recruitment adds the ability to evaluate the effects of changes in growth rate on equilibrium population level. As growth or development rate change, the age structure of spawners changes, thus changing the equilibrium. An example is the idea that populations that are reduced to low abundance by fishing can experience an increase in individual growth rate, which then causes a change in equilibrium that "locks" the population at the lower equilibrium level, even when fishing is reduced or removed (Botsford 1981). This behavior was considered a potential factor in the protracted decline of the cod stocks on Georges Bank.

The decline of populations that have experienced a change in equilibrium to an equilibrium level near zero can be described probabilistically through age-structured viability analysis. The population is typically assumed to be described by a linear model, presuming density-dependence is minimal at low abundance (e.g., Botsford and Brittnacher 1998). An example in a GLOBEC context is the case in which coho salmon populations in the California Current declined in response to the regime shift in the mid-1970s while populations of a congener, Chinook salmon did not. The difference in response was attributed by most researchers to a difference in spawning age structure, since female coho salmon in the California Current spawn at age 3 years while female Chinook salmon spawn at ages 3, 4 and 5 years. General ecological theory (e.g.,Murphy 1967, 1968, Stearns 1976, Philippi 1993) suggests that species distributing spawning over a larger number of age classes should be more persistent in a variable environment. However, calculation of probabilities of extinction (Hill et al. 2003) and cross-simulations (i.e., simulating Chinook salmon populations with estimated coho salmon survivals as input) (Botsford et al. 2005) both showed that the difference caused by age structure was very sensitive to small changes in the fraction not spawning at the primary age of spawning, an uncertain parameter in coho salmon (**Fig. 1**). This finding was valuable in guiding research, and directed the focus toward finding other difference between these congeners to explain the difference in response.

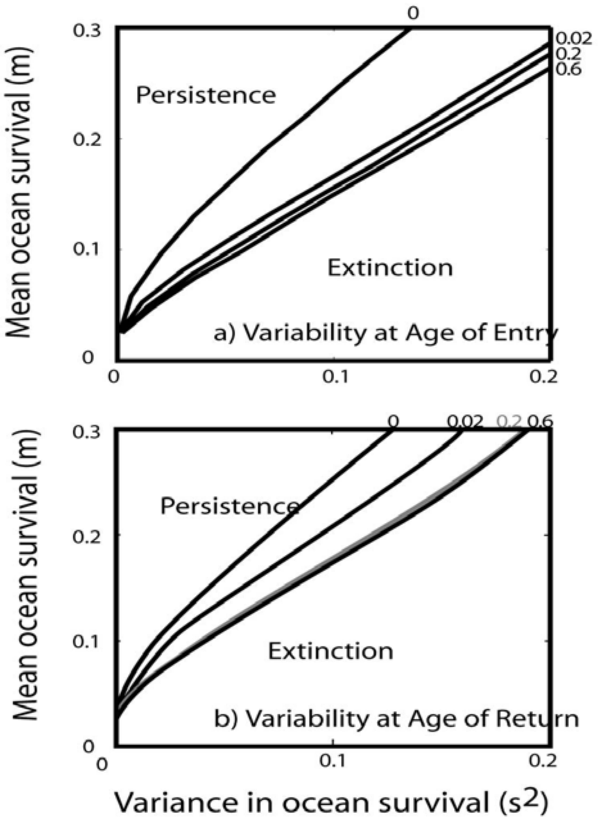


Fig. 1. The values of mean and variance in ocean survival at which salmon population goes from persistence to extinction, as a function of the fraction not spawning at the primary age of spawning for variability at two points of action.

A focus only on equilibrium levels or average population size is valuable in assessing slow changes in climate, but it misses much of the important information contained in population dynamics. Recent advances in understanding the interaction between external sources of variability and internal population dynamics hold great promise for unraveling the factors that regulate populations and predicting future population sizes (e.g., Bjornstad et al. 2004, Greenman and Benton 2005). In many cases, the variability in population abundance of environmentally influenced, age-structured populations with a non-zero equilibrium can be described and analyzed through various linearization procedures. These involve forming a linear model by approximating the model about both the equilibrium abundance and the mean level of environmental forcing. The analysis possible with this approximation gives useful insights into population behavior, which can then be verified with simulation. A useful byproduct of this kind of analysis is an understanding of the dominant modes of variability, and how each of those modes is influenced by variability at various life stages. An example in a GLOBEC context is our analysis of coho and chinook salmon in the California current. The dominant mode of variability in these populations was a decaying exponential returning to the equilibrium, while the second largest mode was cycles about the equilibrium with period equal to the mean age of reproduction (3 years for coho salmon and slightly greater for chinook salmon). Similar results have been demonstrated by (Myers et al. 1998) for sockeye salmon. The useful result was that variability in survival, either at the age of ocean entry or the age of spawning return tended to excite the dominant mode, while variability in development rate (hence in the spawning age structure) tended to excite the cyclic, second largest mode of variability (Worden et al. In prep).

A further useful consequence of this type of analysis is the sensitivity of salmon population abundance to variability at different frequencies (time scales). The ENSO time scale (5-7 years) fell on the shoulder of the unimodal frequency response of time to extinction for California salmon, indicating that a change in ENSO frequency, as seen in proxies for past ENSOs (e.g., corals) would have an effect on salmon populations. The results are similar to our analysis of the differences in time scales of variability of California Current crabs and salmon (McCann et al. 2003).

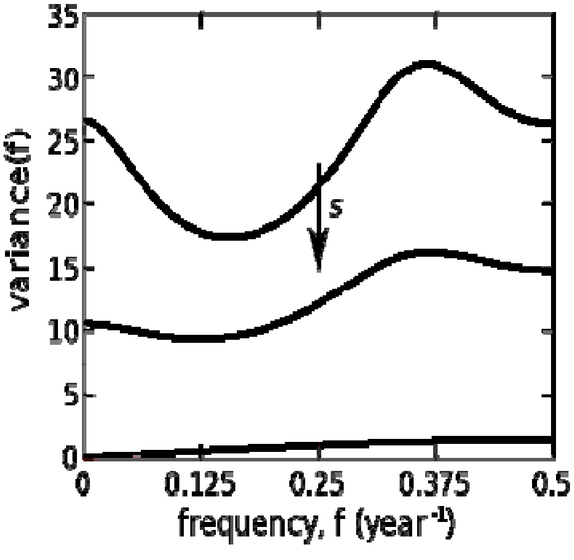


Fig. 2. Sensitivity of coho salmon model with density-dependent recruitment to frequency of environmental fluctuations. As mean adult survival declines, density-dependence becomes less important and cycles of period ~3 appear, as does sensitivity to frequencies near zero.

Similar analytical methods have been employed in the study of Atlantic cod populations, in particular the Norwegian Skagerrak cod (Fromentin et al. 2000, Chen et al. 2005). Bjornstad et al. (1999, 2004) fit a stochastic, age-structured model to data from these cod stocks that included intra-cohort and inter-cohort density dependence in the two youngest age classes. The model explained cycles of period 3+ that appear in the data, but more important from a GLOBEC point of view was that Bjornstad et al. (2004) also noted that this "cohort resonance" led to increased variance at low frequencies (i.e., long-term, slow changes in abundance and recruitment). They noted with concern that these low-frequency fluctuations, which could arise from just random white noise, would confound efforts to detect slowly changing climate forcing.

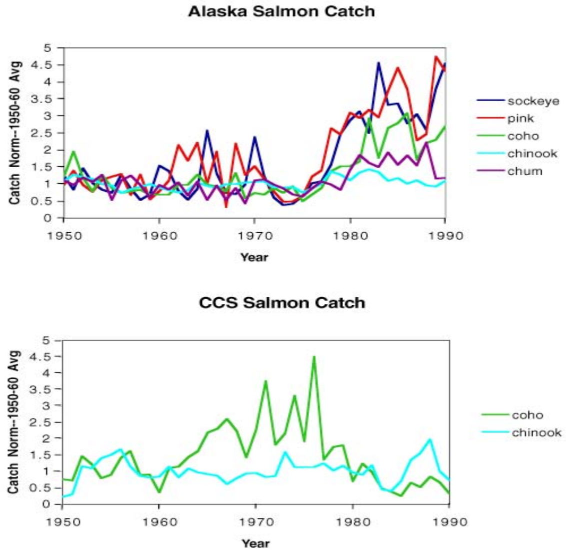
Similar effects arose in our salmon modeling (Worden et al. In prep). The resonant mechanism differs, being an echo effect rather than due to density-dependence, but the increase in low frequency fluctuations is similar. In the salmon model, as marine survival declines, the cohort resonance increases because the slope of the Beverton-Holt spawner-smolt relationship increases. With the increase in resonance, we see an increase in the frequency response at low frequency (**Fig. 2**). In both systems there is a need to understand further the problems this creates for GLOBEC research, and to develop solutions.

Responses to Environmental Variability - Salmon

Here we describe the state of knowledge of the influence of the marine environment on populations of salmon. We include the five predominant species of Pacific salmon, pink (*Oncorhynchus gorbuscha*), sockeye (*O. nerka*), chum (*O. keta*), coho (*O. kisutch*) and Chinook (*O. tshawytscha*), as well as Atlantic salmon (*Salmo salar*). The five Pacific species are found from the western Pacific across to the Gulf of Alaska, but only coho and Chinook are found in the California Current. *Salmo salar* is found in both the western (from the Connecticut River north) and the western Atlantic (from northern Spain north). While much is known about the influence of the environment, the mechanisms of influence on populations (e.g., changes in upwelling led to changes in prey level which led to changes in juvenile growth rate) still need to be worked out. All salmon are anadromous, returning to rivers to spawn, with Pacific salmon being semelparous (with the exception of steelhead, *O. mykiss*), and Atlantic salmon being iteroparous. The suspected point of action (life history phase) of dominant environmental influence is the early ocean phase (Pearcy 1992), and that was one of the three major hypotheses to be tested in the GLOBEC NorthEast Pacific program. We anticipate that our analysis will result in a wide range of population behavior since salmonids exhibit tremendous variability in life history traits compared to most other vertebrates (Mills 1989, Groot and Margolis 1991).

Pacific Salmon

The dramatic change in catch of some species of Pacific salmon associated with the regime shift in atmospheric and oceanographic conditions as reflected in a change in the Pacific Decadal Oscillation (PDO) in the mid-1970s is well known, and was a focus of the GLOBEC Northeast Pacific program (**Fig. 3**) (Mantua et al. 1997, Hare et al. 1999, Botsford and Lawrence 2002). At that time catch and survival of pink, sockeye, coho, and to a lesser degree chum salmon in Alaska increased dramatically, while Chinook remained the same. At the same time catch of coho salmon declined dramatically in the California Current (Weitkamp et al. 1995, Weitkamp 2004), while catch of Chinook salmon did not.


Alaska Salmon Catch

CCS Salmon Catch

Fig. 3. Differences in responses of Pacific salmon species to regime shift in the mid-1970s. Note inverse covariability in coho salmon, but not chinook.

Fluctuations in salmon abundance north of the latitude of Vancouver Island need to be considered in the context of the increase in hatchery releases in the 1970s and 1980s (Mahnken et al. 1998). In particular pink salmon hatchery releases by Alaska increased dramatically in the 1980s, and chum salmon hatchery releases by Japan increased in the 1970s. These releases change population dynamics by adding recruits in addition to natural production, and they would affect catches and possibly limit available food to other species. The earlier hatchery increases in the contiguous U.S. were to replace reproduction as mitigation for the loss of spawning habitat, whereas since spawning habitat in Alaska has not been affected nearly as much, hatcheries add to natural recruitment.

A growing body of literature indicates that local environmental conditions such as local SST are better predictors of recruitment than basin wide indicators such as the PDO (Mueter et al. 2002, Mueter et al. 2005). This is consistent with the finding that the scales of spatial covariability of salmon populations tend to be shorter than associated scales of physical variability, which may indicate an effect of population dynamics, beyond simply following physical variability. A number of studies have found that within-species correlations between survivals of pink, sockeye and chum salmon indicate high covariability is confined to local or regional scales (Peterman et al. 1998, Pyper et al. 2001, 2002, Pyper et al. 2005). We have extended these results to coho salmon, based on coded wire tag data from California to Southeast Alaska, finding similar scales of spatial variability (Teo et al. in review). These findings indicate that salmon populations differ in their response to the environment. Part of those differences in response could be due to differences in population structure and dynamics.

Mechanisms of environmental action

Initial conditions. Freshwater conditions determine the initial conditions for the marine phase of life in that they set the abundance, size of entry and time of entry of wild stocks (**Fig. 4**). These are determined by conditions in freshwater, which may covary with ocean conditions (Kope and Botsford 1990). Lawson et al. (2004) have recently shown that smolt abundance in several Oregon coho salmon streams are related to stream flow, and that favorable conditions in freshwater are associated with favorable conditions in the marine environment.

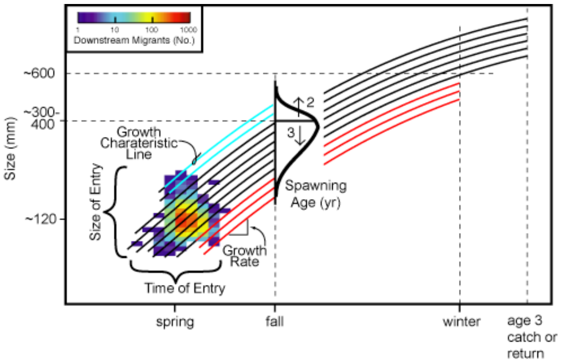


Fig. 4. A schematic view of the dynamics of individual size in coho salmon. The size and time of ocean entry (or hatchery release) and the ensuing growth rate determine the size distribution at the beginning of the Fall. The largest fish (blue growth lines) will spawn precociously in the first fall, the medium size fish (black growth lines) will survive to be caught in the fishery or spawn in the following year, while the smallest fish (red growth lines) will die during the first ocean winter (Beamish, et al. 2003). The axes are not to scale.

Survival. It is clear that biological and physical conditions during the period following ocean entry have a substantial effect on the fraction of salmon surviving to adulthood (e.g., Pearcy 1992, Mueter et al. 2005). The mechanism underlying this effect is not known, but potential mechanisms can be divided into: (1) an effect of variable mortality rate and (2) an effect of variable growth rate. The latter is a mechanism well known to meroplankton and ichthyoplankton ecologists in which variable development rate through a stage involving high, size-dependent mortality rate leads to variable survival through the stage (e.g., Moloney et al. 1994). Early examples of the varying results regarding growth and mortality rates of coho salmon include a study off Oregon in which varying upwelling determined cohort survival, but did not act through varying growth rate (Fisher and Pearcy 1988), and a study off Vancouver Island in which early marine growth rate did covary with adult survival (Holtby et al. 1990). The direct effect of mortality can be due to variability in abundance or type of predators, caused by inter-annual variability in predator distribution or the distribution of juvenile salmon, or by the abundance and distribution of non-coho alternate prey for predators. The indirect effect of growth rate can be determined by variability in temperature and primary and secondary productivity.

Size, growth and spawning age. The mechanism(s) by which size and growth rate affect survival in salmon are portrayed schematically in **Fig. 4** for coho salmon as an example. Growth rate during the first summer, and size in the fall were shown to determine mortality during the winter for the 2000 brood year in Georgia Strait (Beamish et al. 2004). This result is consistent with those in Beamish and Mahnken (2001) who demonstrated physiological limitations in slower growing juvenile salmon. Variable growth rate also obviously influences size at the end of the first summer, which in turn (along with genetic identity) determines spawning age distribution (Young 1999, Vollestad et al. 2004, Quinn 2005). The dominant effect of this variability in coho salmon growth is on the fraction of males spawning precociously after the first summer. Size at the end of the first summer, and hence the likelihood of an individual spawning, also then depends on the size of entry (Vollestad et al. 2004). In early U.S. GLOBEC research, Mangel (1994) analyzed the response to climate change of a similar dynamic life history model using a behavioral ecology approach.

Points of action

The empirical evidence presented here indicates that the life history phase at which the environment influences Pacific salmon, i.e., the point of action, is likely to be shortly after their entry into the marine environment, but there are known influences on the age of return for spawning (e.g., Young 1999). The environment appears to influence both growth and survival rates, both as long-term slow change and inter-annual variability.

A general trend in the north Pacific, which could be related to hatchery increases, is the existence of primarily downward trends in growth rates of virtually all five species (Bigler et al. 1996). These include declining trends in Asian chum salmon, Alaskan chum salmon, and pink and sockeye salmon in Alaska and British Columbia (Ricker 1997, Holt and Peterman 2004). In most cases these declines are associated with a decrease in the ages of maturity.

Attempts to determine the physical and biological conditions in the coastal ocean that determine salmon survival typically involve statistical analyses of the covariability between time series of salmon population data and environmental data. In the CCS, results for **coho** salmon from the past several decades (Nickelson 1986, review in Botsford et al. 1989, Cole 2000, Hobday and Boehlert 2001, Botsford and Lawrence 2002, Koslow et al. 2002, Logerwell et al. 2003) have generally shown better survival during years when higher biological productivity would be expected (i.e., La Nina: cooler temperatures, higher upwelling, lower sea level, shallower mixed layer depth). However, the phases of the ENSO cycle also promote shifts in the distributions of predators or alternate prey.

In the CGOA there are fewer studies of the covariability between **coho** salmon and environmental time series. The GLOBEC-funded study of the time series of wild coho salmon survival from Auke Creek in southeast Alaska revealed marginal covariability with ocean temperature, but a strong positive dependence on local hatchery releases of pink and chum salmon. This relationship is under investigation in our current coho salmon project.

Investigations of interannual relationships between **chinook** salmon and the physical environment at various specific locations include both marine and freshwater variables (e.g., van Hyning 1973, Barton 1980). Kope and Botsford (1990) found a negative influence of ENSO conditions on central California chinook salmon in the year in which they returned to spawn or were caught in the fishery. Regarding decadal-scale variability, Beamish et al. (1995) noted that chinook salmon catches in the Strait of Georgia have declined since the mid 1970s. On the Columbia River, analyses of covariability separate the Chinook populations into 3 units with different responses (Botsford and Paulsen 2000, Levin 2003). Scheuerell and Williams (2005) showed that survival in one of those depended on upwelling during the previous April, September and October. Analyses of returning coded wire tagged fish showed that growth in Washington, Oregon and California was negatively correlated with ENSO, while growth in British Columbia/Puget Sound was positively correlated (Wells et al. 2006). Analysis of scales from spawners in a northern California stream showed that Chinook growth in all ages was negatively related to ENSO conditions, and that the age of maturation and fork length was related to the environment in the year prior to return (Wells et al. 2007).

Marine survival rates of **sockeye** salmon vary in stocks from British Columbia to Bristol Bay, with little covariability between those regions (Peterman et al. 1998). Growth rate also varies, affecting body length and age of spawning, and there is greater coherence across space between Alaskan and Canadian stocks than in survival (Pyper et al. 1999). Body length covaried substantially with both sockeye abundance and sea surface temperature, in a way that was not just due to the common linear trends (Pyper and Peterman 1999). In one instance, sockeye salmon in the Fraser River, the consequences of warming were tied to a circulation model, via a model of sockeye salmon bioenergetics (Hinch et al. 1995). Quinn et al. (2007) pointed out the potential that for seasonal variation in exploitation rates to select for changes in run timing of sockeye in two Bristol Bay systems.

For these species in more northern waters, survival during the early ocean stage seems to be the most important. Survivals of **pink**, **sockeye**, and **chum** salmon all covaried with ocean temperature near the time of entry into the ocean, but none of them covaried with upwelling (Mueter et al. 2005). The sign of this covariability differs between British Columbia and Washington.

Atlantic Salmon

Atlantic salmon (*Salmo salar*) are distributed throughout the North Atlantic, with southern limits ranging from the Connecticut River (New England, USA) on the American side to northern Spain on the European side. Populations are in decline range-wide but populations at the southern extremes are suffering the most serious declines mainly due to anthropogenic stresses (Parrish et al. 1998, Kellogg 1999). Population conservation status (a proxy of population size) declines with increasing latitude although genetic variability does not covary with population abundance as would be expected (Valiente et al. 2005). The high genetic variability of southern, smaller populations may be an effect of the diverse life histories exhibited by these populations leading to large mixtures of cohorts on the spawning grounds (Garcia-Vazquez et al. 2001, Juanes et al. 2007).

We expect to see a broad range of population responses by Atlantic salmon since they perhaps show the greatest extent of life history variation of the salmonids (Willson 1997, Hutchings and Jones 1998). For example, age at maturity can range from less than one year to 10 years (Power 1969, Letcher and Terrick 1998); size at maturity varies from less than 7 cm to more than 100 cm (Huitfeldt-Kaas 1946, Hutchings 1986, Gibson et al. 1996). Marine migrations are extensive, with anadromous adults spending 2-4 years at sea. Generally populations at the southern extremes of the distribution are furthest from marine feeding grounds and thus believed to be most susceptible to changes in the marine environment (Parrish et al. 1998).

Warm water conditions appear to be critical for European stocks during their first months at sea (Friedland et al. 1998), whereas for North American stocks the strongest relationship is for winter thermal habitat of fish with two sea winters (2SW) and spring thermal conditions correlate with longerm trends in recruitment (Friedland et al. 2003). Condron et al. (2005), using a 90-yr record of salmon catches in the northwest Atlantic showed a strong correlation between historical catches and values of a the Atlantic Multidecadal Oscilllation (AMO), a basin-wide low frequency climate mode producing variability in sea-surface temperatures over the last century. During the warm phases of the AMO, salmon abundance is generally lower and vice versa. Further, the relationship between AMO and SSTs are strongest during the winter season near the Grand Banks of Newfoundland, a known overwintering area for salmon and at a time critical for survival. The authors conclude that although the change in SSTs is likely too small to affect salmon directly, changes in currents and food resources driven by climatic change ultimately affect salmon survival. Because the AMO has shifted to a warmer phase since the early 1990s, salmon stocks are predicted to continue to decline even with the implementation of a fisheries moratorium.

In Europe, the North Atlantic Oscillation winter index (wNAOI) correlates with the abundance of returning salmon to the Foyle River, Ireland over the last 125 years. However, the wNAOI failed to predict abundance in 8 out of the last 10 years of the study when the index has been high, suggesting that population sizes may have become uncoupled from broad scale climatic effects. As the wNAOI is predicted to continue to exhibit high values, its use as a predictor of salmon abundances will be limited and population sizes are likely to continue to decline (Boylan and Adams 2006).

Recent work ha also examined long-term changes in run timing, age structure (primarily in the proportion of returning multi-seawinter fish, MSW) and size of returning adults. In North American stocks, body sizes have remained constant, but return timing has consistently shifted to earlier dates over the last 23-40 years across the range of the species. These changes correlate with environmental factors such as river temperature, flow and SSTs (Juanes et al. 2004), and are likely to affect spawning age structure. In contrast, for Irish populations, run timing has been delayed, and proportion of MSW fish and average sizes have declined over the last 40-70 years (Quinn et al. 2006). These authors also note the potential for genetic selection for run timing from season variability in fishing. Similarly, in Spanish populations, found at the southern edge of the European distribution, run timing has been delayed and average weight has declined. These shifts are strongly correlated with the wNAOI (Valiente et al., unpublished) and may be a consequence of changing ocean conditions including temperature and fluctuations in prey abundances leading to diminished energetic reserves, slower migration and declining condition.

Responses to Environmental Variability - Cod

Atlantic cod (*Gadus morhua*) populations are distributed throughout the North Atlantic from Labrador to Southern New England in the west and from the Barents Sea off Norway and Russia to the Celtic Sea off southwest Britain in the east. The Pacific cod (*Gadus macrocephalus*) is a close relative of the Atlantic cod (G*adus morhua*) and has similar life history and ecological patterns (Ketchen 1961). The Pacific cod is widely distributed among the shelf regions of the North Pacific Ocean. Major stocks are distributed along an arc ranging from the Oregon coast in Northeast Pacific to the Gulf of Alaska and the Bering Sea in the north and the Sea of Japan in the Northwest Pacific.

Atlantic Cod

Cod inhabit coastal and continental shelf waters with seasonal bottom temperature regimes ranging from less than -1^{o}C to over 20^{o}C and annual mean temperatures from 2-12^{o}C (Dutil and Brander 2003, Drinkwater 2005). Temperature has been shown to affect distribution (Dutil and Brander 2003, Drinkwater 2005, Perry et al. 2005, Rose 2005), recruitment success (Planque and Fredou 1999, Brander 2000, Drinkwater 2005), feeding (McKenzie 1934, 1938, Rose 2005) and individual growth rates (Brander 1995, Ratz and Lloret 2003) of Atlantic cod. Thus there is great potential for differences in population responses over space.

Strong latitudinal gradients in age-at maturation are observed, with median ages of maturity ranging from approximately 2 years in the southernmost populations in the both the eastern and western Atlantic to over 7 years in arcto-boreal populations. Growth rates are also strongly temperature-dependent (Brander 1994, 1995). Rätz and Lloret (2003) further reported a close relationship between cod condition factors and average bottom temperature. These differences in growth and reproduction hold potentially important implications for reproductive dynamics of the stock and the overall resilience of the population to external stressors, including exploitation.

Inter-annual variability also depends on temperature. Increases in temperature have a positive effect on cod recruitment in arcto-boreal regions off Greenland, Iceland, and Norway where temperatures are close to the lower thermal tolerance limit of cod and negative effects in stocks inhabiting areas at the upper end of the temperature range, notably in the Irish and Celtic Seas (Planque and Fredou 1999, Drinkwater 2005). Stocks inhabiting regions characterized by intermediate temperature regimes (e.g. Faroe Islands and Georges Bank) showed no detectable effect of temperature on recruitment (Planque and Fredou 1999, Drinkwater 2005).

Stock-recruitment models with explicit consideration of environmental effects have been widely applied to Atlantic cod populations, indicating environmental variability in the pre-recruit phase. Recruitment models including the effects of temperature (e.g., Planque and Fredou 1999, Solow 2001, Clark et al. 2003, Ottersen et al. 2006, Fogarty and O'Brien In press) and the North Atlantic Oscillation (NAO) as environmental covariates (Solow 2002, Brander and Mohn 2004, Solow and Beet 2007) have been developed. Recruitment conditioned on spawning stock biomass (SSB) increased with increasing water temperature for Arcto-Norwegian cod (Solow 2001) but decreased with increasing temperature in the Irish Sea (Planque and Fredou 1999), the North Sea (Clark et al. 2003) and the Gulf of Maine (Fogarty and O'Brien In press). O’Brien et al. (2000) reported differential temperature effects on North Sea cod recruitment at three levels of spawning biomass; recruitment is lower when SSB is low and temperature exerts a less pronounced effect than when SSB is high. Stige et al. (2006) note that the NAO affects cod recruitment through local hydrographic (temperature and salinity) and oceanographic (turbulence and advection) conditions. Solow (2001) reported a significant relationship between recruitment to the Northeast Arctic cod stock and the NAO winter index during 1973-95 but not for an earlier period (1946-72), implying a change in system characteristics between these two time periods. Relatively weak NAO effects on cod recruitment on Georges Bank and in the Gulf of Maine were found by Brodziak and O'Brien (2005). Brander (2005) suggested that the NAO effect was significant only when spawning stock size was low in an analysis using categorical recruitment and spawning stock size estimates (three levels of each) and aggregated over thirteen North Atlantic cod stocks. Northeast Arctic cod recruitment was more found to be more sensitive to climate influences under changing demographic structures (mean size, mean age and age diversity of spawners (Ottersen et al. 2006). Solow and Beet (2007) developed a recruitment model with interactive climate-population effects for Northeast Arctic cod to test whether the earlier finding of Solow (2002) of differential NAO effects for two time periods was attributable to an enhanced climate response when SSB was low. The dynamics of age specific abundance levels were shown to be significantly related to density dependent and environmental (temperature NAO) factors for North Sea and Kattegat-Skagerrak cod (Chen et al. 2005) employing a generalized additive model structure allowing for non-linear density and environmental factors.

Results from U.S. GLOBEC Georges Bank suggest that climate impacts on zooplankton assemblage structure, and oceanographic conditions affecting turbulence and other factors will potentially strongly influence larval growth with important implications for survival and recruitment. These results were achieved in part through the development of mechanistic individual-based models for cod under the U.S. GLOBEC Georges Bank (Werner et al. 1996, Werner et al. 2001, Lough et al. 2005). Our proposed research will describe the population level consequences of such recruitment variability under different assumed population structures.

The critical importance of potential synergistic interactions between harvesting and climate change in these analyses is clear (see also Kell et al. 2005 for North Sea cod). Clark et al. (2003) and Fogarty et al. (In press) developed age-structured production models for cod in the North Sea and the Gulf of Maine respectively, incorporating temperature effects on recruitment and individual growth. Projections under IPCC high and low emission scenarios were then used to examine the implications of potential climate change on yield and resilience to exploitation. In both systems, a decline in yield and increased vulnerability to exploitation under climate change is predicted.

Pacific Cod

The varying physical environments experienced by different Pacific cod stocks affect both their reproductive and growth rates. Pacific cod stocks in warmer regions tend to have earlier ages of maturity and faster growth rates when food is non-limiting. In the Northeast Pacific, female Pacific cod in the Eastern Bering Sea and Gulf of Alaska have median ages of maturity at approximately 4-5 years (Stark 2007) but decrease to 2-3 years in British Columbia waters (Thomson 1962, Welch and Foucher 1988). A similar pattern is apparent in the Northwest Pacific - female cod from west Kamchatka have a median age of maturity of 6-7 years (Thomson 1962) in contrast to approximately 4 years in waters off Hokkaido, Japan (Hattori et al. 1992).

Warmer winter water temperatures also appear to decrease the fecundity of Pacific cod stocks (Tyler 1995). Similar to Atlantic cod, Pacific cod stocks in warmer waters have substantially faster growth rates than stocks in cooler waters (Ketchen 1964).

Over multi-decadal timescales, ‘regime shifts’ in the Pacific Decadal Oscillation (PDO) are thought to have large effects on population sizes of Pacific cod stocks. Over the past three decades, the Pacific cod stocks in the Gulf of Alaska and East Bering Sea have exhibited multiple-fold increases in population size and catches (Anderson and Piatt 1999, Hunt et al. 2002, Litzow and Ciannelli 2007). Near the southern end of the Pacific cod’s range in the Northeast Pacific, there appears to be little evidence of an increase in population size of the Hecate Strait stock (off British Columbia) after the regime shift around 1976-77. Sinclair and Crawford (2005), tested several recruitment hypotheses, including herring biomass, and found that the variability in recruitment was best explained by changes in ocean transport (proxied by sea level height changes) and spawning biomass.

Approach

Overarching Question

How do environmental variability and differences in population structure (life history parameters and point of action, i.e., changes in growth rate or survival rate at specific ages) interact to produce observed differences in population dynamic responses to a variable environment?

GLOBEC and other studies have identified a number of examples of relationships between environmental and population change and more often than not those relationships differ over space and even time. Our overarching question is essentially what role has population structure (life history and point of action) played in determining those differences? We have chosen salmon and cod as exemplary taxa because they occur and vary across both the North Pacific and North Atlantic, and together they cover a range of life histories typical of higher trophic level, age-structured populations, from short-lived and semelparous to long-lived and iteroparous. We will catalogue the different population responses of cod and salmon and compare them in the context of current population theory. We realize that this comparative approach is not ideal in the sense that the environment is not identical everywhere, and part of the reason for different population responses is likely differences in the environment. We are therefore asking what part of the differences in population response is due to population dynamics, leaving the part due solely to environmental forcing. Our goal is not just to understand the population responses of salmon and cod, but rather to provide a general increase in understanding of higher trophic level GLOBEC-target species in general. Because of GLOBEC's emphasis on a mechanistic and a population-oriented approach, this seems to us to be a necessary synthesis for GLOBEC to undertake.

This overarching question can also be phrased in terms of an empirical hypothesis-testing program. Given the paucity of examples in which investigators explore the details of population dynamic implications of environmental forcing, a possible null hypothesis would be that: Population dynamics plays no role in determining the differences seen in population responses to a variable environments, that they are due solely to geographic (or temporal) differences in the environmental forcing.

Specific Research Approach

I. Based on population models and theory, how would we expect population structure (both life histories and point of environmental action) to determine the population response to a variable environment, varying over a range of time scales?

Approach to Sub-Question I: The UCD group (Hastings, Botsford and post-doc) will lead the effort to answer this question. They will extend the review and synthesis of population dynamic results included above in the background. They will formulate population models that express the range of population structure and points of environmental action for cod and salmon, with input from Juanes, Fogarty and post-docs. They will first examine changes in equilibrium conditions due to possible spatial differences or slow changes in survival and development rates. They will then formulate linearized models as has been done for coho and Chinook salmon (Worden et al. In prep) and examine the modes of variability in the linear model and the distribution over these modes of forcing at different points of action (Bjornstad et al. 2004, Greenman and Benton 2005). This group will also examine the spectral response of various population structures, and evaluate responses to reddish as well as white environmental variability. Results suggested by linearized models will verified through simulations. The group will then examine persistence using a metric such as the statistics of mean time to quasi-extinction.

We will spend some time on the issue of increasing sensitivity to low frequency variability, identified by Bjornstad, et al. (2004), and its confounding effect on detecting slow climate change. This will involve examination of the low frequency variability through simulation to determine whether it resembles a slowly changing climate signal.

While we have not emphasized spatial interactions in this proposal, we will account for them where appropriate, e.g. where patterns of population covariability over space indicate it.

II. Based on all observations of the responses of **cod** populations to a varying environment across the north Atlantic and north Pacific semi-basins, how consistent are the differences in responses with those expected on the basis of population dynamic theory in sub-question 1?

Approach to Sub-Question II: The UMass group (Fogarty and post-doc) will lead the effort to answer this question. They will review all examples of environmental influences on cod populations more intensively than has been done here, cataloguing the population response in abundance or biomass, the likely points of action and the life history state of the population (e.g., spawning age distribution). The UCD group will contribute information on Pacific cod. They will then use modeling results from the analyses in Sub-Question I to compare the differences in responses by these population to those expected on the basis of population dynamics alone. The resulting publication will synthesize differences on the basis of population dynamics.

III. Based on all observations of the responses of **salmon** populations to a varying environment across the north Atlantic and north Pacific semi-basins, how consistent are the differences in responses with those expected on the basis of population dynamic theory in sub-question 1?

Approach to Sub-Question III: The UMass group (Juanes and post-doc) will lead the effort to answer this question. They will review all examples of environmental influences on salmon populations more intensively than has been done here, cataloguing the population response in abundance or biomass, the likely points of action and the life history state of the population (e.g., spawning age distribution). The UCD group will contribute information on Pacific salmon. They will then use modeling results from the analyses in Sub-Question I to compare the differences in responses by these population to those expected on the basis of population dynamics alone. The resulting publication will synthesize differences on the basis of population dynamics.

IV. Based on the results from sub-questions I-III, what are the general implications for expected results when investigating any higher trophic level species, including cod, salmon and others, in the future?

Approach to Sub-Question IV: Botsford will lead the effort to answer this question with contributions by all others on the project. Because the two focal taxa, salmon and cod cover such a broad range of life histories, the results should be easily translatable to other species. However, some examples of important species may require extension of our existing model runs. A notable example are rockfish on the west coast, which are longer lived than either of our focal taxa.

V. How does the change in adult survival due to fishing influence a population's response to environmental variability?

Approach to Sub-Question V: Botsford and Fogarty will lead the effort to answer this question since they have the most experience with management of marine resources. The basic question to be answered is as adult survival declines due to fisheries removal, how does the response to the environment change? An important aspect will be the effects on the likelihood of population decline to low abundance. This effort will extend the conventional approach to this question based on Spawning Potential Ratio and the "steepness" of the stock-recruitment relationship, which is essentially a static analysis. We will also examine the potential effects of fishery driven selection for run timing.

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