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An evaluation of the utility of spatially-explicit biophysical models in recruitment studies: the
FOCI example.

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Abstract

We have developed a suite of coupled, spatially-explicit biophysical models of the recruitment process for walleye pollock in Alaskan waters, as part of the Fisheries Oceanography Coordinated Investigation (FOCI) program. These models include a three-dimensional circulation model, a bioenergetically-based individual-based model which tracks early **life stages** of pollock through space and time, and a **nutrient-phytoplankton-zooplankton** model which provides a spatially and temporally varying food source for young pollock. In this paper, we **review the** models briefly and discuss what they can tell us about spatial and temporal patterns in the environment of young pollock, and what the implications of these may be for recruitment. We **discuss various** ways of using these models, ie. model experiments, sensitivity analyses and hindcasts and where methods are appropriate, add some cautions derived **from our experience**, and **discuss** developments which are on the horizon in this type of biophysical modelling. We conclude that biophysical modelling provides an excellent framework to examine complex biophysical relationships affecting recruitment, and can significantly aid in our understanding of the recruitment **pro-**

Introduction

We have developed a set of coupled, spatially explicit biological and physical models designed to examine the recruitment process for walleye pollock in the western Gulf of Alaska. Numerical biophysical modelling can help us to explore mechanisms affecting recruitment and the interactions of these mechanisms. Due to the complexity of the involved processes, “progress in understanding how selective forces shape recruitment will depend increasingly on modeling, such as the individual-based approaches now being applied to examine **how** habitat, environment and predation affect recruitment variability” (Pope et al. 1994).

The primary biological model we have developed is an individual-based model of the early stages of pollock life history. Studies of the recruitment process have **often** focused on population-level phenomena, such as correlations among environmental factors, stock factors and recruitment levels, or alternatively, on single processes occurring at the **level** of individual organisms or single life stages, for example predation or starvation. However, the idea is becoming more generally accepted that mechanisms operating on different time, space, or organizational scales may all be important, and that overall recruitment levels are unlikely to be controlled by any one factor, process, or life stage. A complex suite of factors are involved which may act sequentially or simultaneously through compounded nonlinear interactions to affect year-class strength.

Ecologists have increasingly used models which deal explicitly with individuals in order to generate system dynamics (**DeAngelis** and Gross 1992, Judson 1994). These models keep track of a number of distinct individuals within a population, each of which may interact with other individuals or with the physical environment, based on its present state and possibly its past **history**

There were several reasons for our decision to use an individual-based model of the early life stages of pollock in our recruitment studies. First, these models are appropriate to situations where all individuals at the same point in state-space are not assumed to encounter the same environment. Differences in the survival and growth of individuals due to differential histories of exposure to environmental conditions underlie many of our theories about recruitment processes for pollock. Secondly, these models allow us to keep track of individual characteristics over time, and thereby permit examination of the histories of individual fish to attempt to understand why they survived or why they died. Thirdly, these models allow incorporation of complex individual behaviors, such as vertical migrations or learning, which may be important.

We have included a detailed model of the circulation in the western Gulf of Alaska as a critical element of our coupled biophysical models. The inclusion of spatial factors is crucial for understanding the growth and survival of many marine species. Spatial variability in circulation and environmental conditions which causes differential growth and mortality among individual young fish may be important to overall levels of recruitment. For many marine fish species with planktonic early life stages, mesoscale and larger circulation features may influence **the** success of a year class (Incze et al. 1990, Kendall and **Nakatani** 1992, Schumacher et al. 1993, Bograd et al. **1994**), especially in regions with strong and variable currents. Circulation factors may act directly, through transport of early life stages to appropriate nursery areas, or indirectly by mediating encounters of young fish with prey and predators. In regions with complex horizontal current patterns, the trajectories of individual fish may vary widely, causing unique individual histories of exposure to environmental variables, such as temperature, salinity, and predators and prey fields, This may lead to variability in growth or the probability of survival among individuals.

Walleye pollock forms the basis for one of the world's largest single-species fisheries (Kinoshita et al. 1995). Recruitment in this species is highly variable (Megrey et al. 1995). For these reasons, and due to the relative tractability of field studies in the western Gulf of Alaska, this species was chosen for study in the Fisheries Oceanography Coordinated Investigations (FOCI) program. The conceptual life history of pollock is shown in Figure 1. Pollock spawn in late March and early April in Shelikof Strait between Kodiak Island and mainland Alaska, and the eggs and larvae drift downstream (to the southwest) in the prevailing Alaska Coastal Current to the juvenile nursery areas around the Shumagin Islands. Although the transport of early life stages is dominated by advection, there exists a high degree of horizontal and vertical variability of the currents in time and space, and the occurrence of mesoscale eddies, convergence zones, plumes and a deep counterflow are thought to affect the growth and survival of young pollock. Year class strength in this species is thought to be set within the first few months of life (Bailey and Spring 1992), however the particular life stage at which recruitment appears to be determined varies among years.

In this paper we review our progress in modelling the recruitment processes of walleye pollock in the western Gulf of Alaska using this set of coupled biophysical models, in order to assess their utility and to point out some areas in which further work needs to be done. First, we briefly review the set of coupled biophysical models used in this research. Then we discuss several methods of using this suite of models which are appropriate for different purposes. Then, some of the factors indicated by the modelling work as important for good recruitment for pollock in this region are discussed. We review some necessary cautions for users of this class of models, and what we see as the future of this type of modelling in recruitment studies. We finish

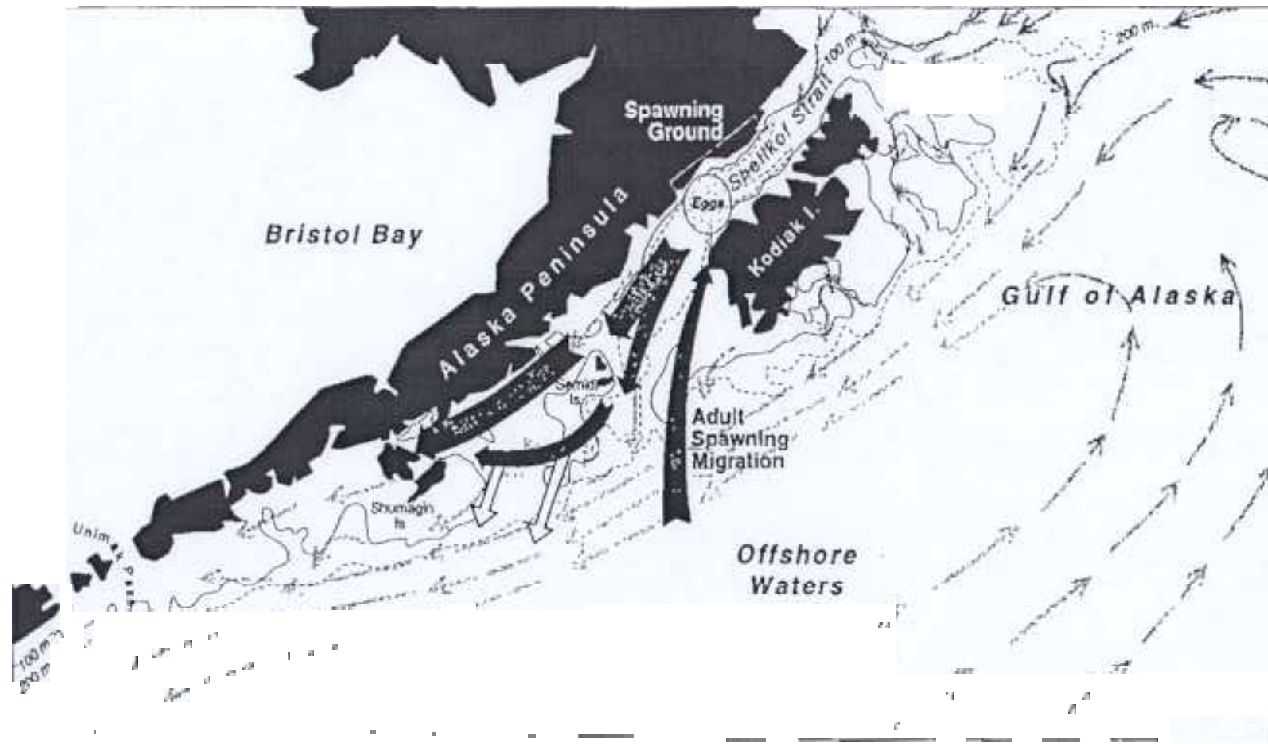


Figure 1. Conceptual life history of Gulf of Alaska walleye pollock showing the spawning area in Shelikof Strait, the downstream movement of eggs, larvae and juveniles, and the return migration of spawning adults.

with some conclusions about how these models have contributed to our understanding of recruitment processes.

Description of FOCI models

The hydrodynamic model (**SPEM**) used in this biophysical modelling effort (described fully in **Hermann** and Stabeno, 1996) is a three-dimensional, prognostic, rigid-lid, eddy-resolving model of velocity and salinity fields in the northern Gulf of Alaska. The model domain (Fig. 2) encompasses the northern Gulf of Alaska, from east of Shelikof Strait to west of the Shumagin Islands. The model, forced by twice-daily winds and monthly fresh-water runoff, solves the hydrostatic, primitive hydrodynamic equations, with wind forcing distributed over the top 20 m of the water column, and buoyancy forcing (due to **runoff**) along the coastline of Alaska. The model employs a curvilinear-orthogonal horizontal coordinate system which follows the irregular coastline. Mean grid spacing in the area between Kodiak and the Shumagin Islands is 4 km. Beyond this region, the grid is expanded to allow for a large recirculation region (essentially this is a way of allowing open boundary conditions for the finely resolved area). The vertical dimension is treated using a variable depth-following (“sigma”) coordinate system, with nine vertical levels.

Currents generated by the model have been compared with those measured by moored current meters and satellite-tracked drifting buoys (**Hermann** and Stabeno 1996). The model reproduces dominant circulation features including the Alaska Coastal Current and the Alaskan Stream, with appropriate cross-shelf structure, vertical shear, and mean transport. Floats tracked at 40 m (the depth of mean larval pollock abundance) using daily filtered model velocity fields compared favorably with observed drifter tracks at that depth (Stabeno and **Hermann** 1996). Discrepancies between the model and data were generally due to the formation of mesoscale eddies

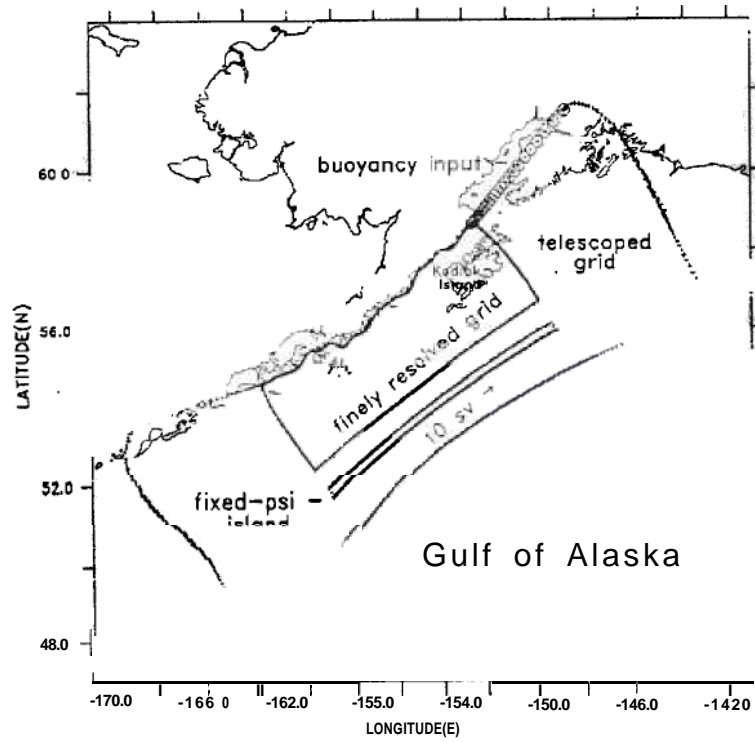


Figure 2. Boundary of the SPEM model grid. Note the telescoping of the grid at the southeastern, northeastern, and southwestern edges of the finely resolved domain. An “island” of fixed barotropic stream function is also shown; barotropic flow is specified at 10 Sv around this island. Circled grid points indicate locations of buoyancy input.

in the model at different times than those observed, although eddy statistics (e.g. **rate** of eddy formation, location) were similar for both. Further details of the model configuration and validation may be found in Stabeno et al (1995), **Hermann** and Stabeno (1996) and Stabeno and **Hermann** (1996).

The individual-based model (IBM) of the early life stages of walleye pollock follows young **fish from** spawning through September of their O-age year (Fig. 3) (Hinckley et al 1996, Megrey and **Hinckley** In Press). It uses a Lagrangian float-tracking scheme to follow fish through space using the daily (time-filtered) velocity fields **from** the SPEM model. The IBM keeps track of many individual characteristics of individual fish. The model is divided into four life stages (egg, yolk-sac larvae, feeding larvae and O-age juvenile) with processes formulated appropriately for each. The processes and parameters associated with them are based, for the most part, on a wide variety of field and laboratory observations on this population.

Mortality is calculated either (1) using a constant rate that differs by life stage, and exponential decline, or (2) using a modified “**superindividual**” method (Scheffer et al. 1995), where an “individual” actually represents a cohort whose numbers decline over time. This method preserves the mesoscale spatial differences between individuals (superindividuals or cohorts) but sacrifices the fine scale differences, as all member of a cohort are assumed to experience the same feeding, metabolism and growth.

Development of eggs is a function of egg age and temperature, and its vertical location in the water column a function of egg size, egg density, and salinity (the latter derived from **the** SPEM model). The size of larvae at hatch is a function of egg size. Degree days are used to determine when the yolk-sac larvae are ready to feed, and when (if they don't feed) they reach the point of no return. Temperatures from the SPEM model are used to calculate degree days. The

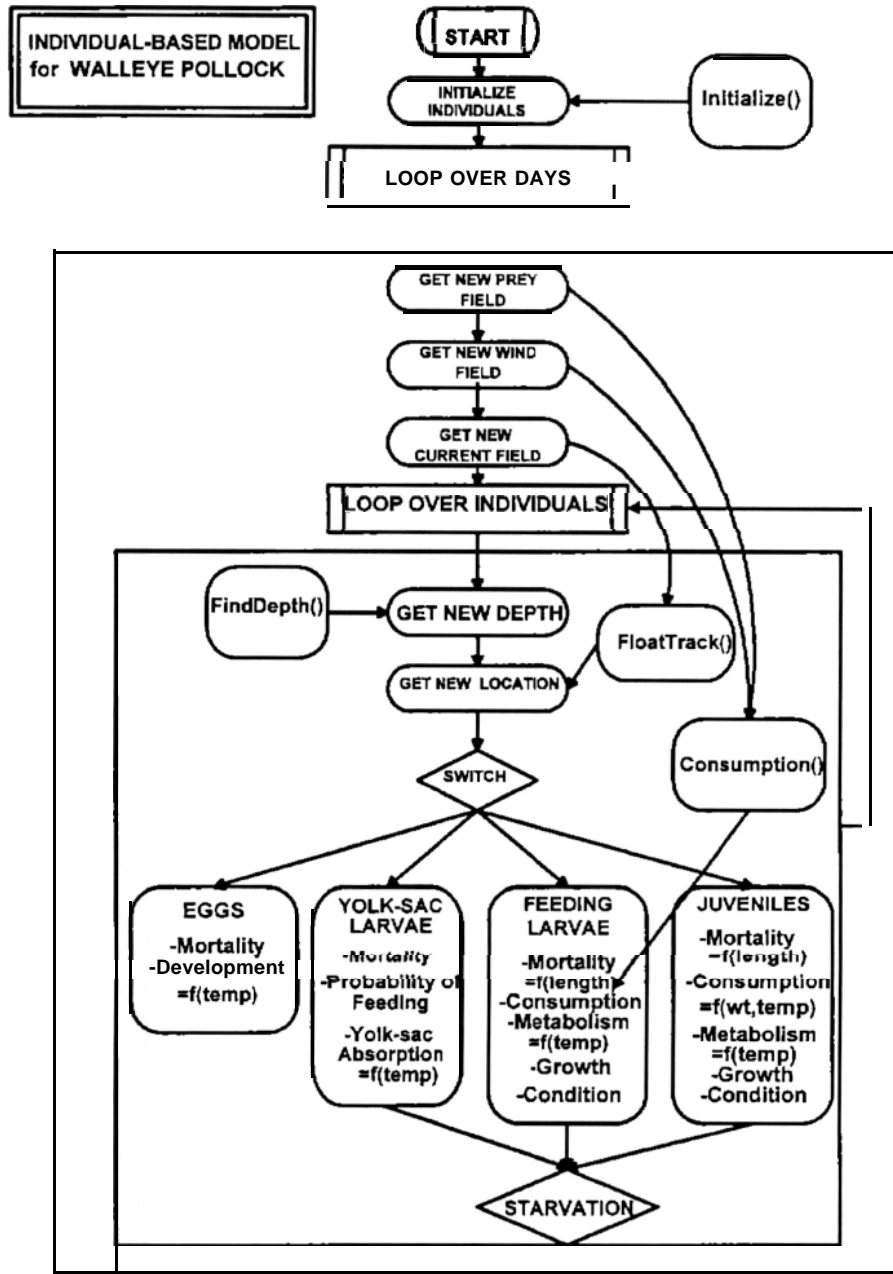


Figure 3. Flow chart of the individual-based model (IBM) of the early life stages of walleye pollock.

probability of feeding is determined by a random number at each time step between **first-feeding** readiness and the point of no return, when the larva dies of starvation. Yolk-sac larvae remain deep in the water **column** until first-feeding readiness, when they move upward in the water **column** to a location in the upper **20-60m**.

Feeding larvae begin **diel** migration when they reach a length of 6 mm. **Diel** migrations are driven by preferred light levels, with a random component of swimming speed derived from **larval length**. Consumption is a function of prey density, wind-generated turbulence and larval body size following the dome-shaped relationship hypothesized by MacKenzie et al. (1994) and MacKenzie and **Kierboe** (1995). This theory proposes that there is an optimum turbulence level (or wind speed) which maximizes consumption by larvae. Both below and above this level, consumption drops off due, respectively, to lowered encounter rates, or decreased catch success. Values of wind speed are input to the model for this process, and use the same data that drives the **SPEM** model. Prey densities used in the model are derived from the **Nutrient-Phytoplankton-Zooplankton (NPZ)** model described next. Prey are divided into life stages, and are consumed by larvae in each larval length classes proportional to the probability of a larva eating each prey category. Feeding larval metabolic rates are derived **from** laboratory studies, which are modified by temperature (derived from **SPEM**).

O-age juvenile depths are derived from random deviates around a mean. There is little information about the consumption of juveniles, so mean daily consumption is a function of **weight and** temperature. Juvenile metabolic rates are derived from laboratory studies.

An **NPZ** model was developed in order to include the effects of a temporally and spatially varying food source on young pollock, mainly the feeding larval stage (Fig. 4) (Hinckley et al. In prep). The NPZ model is similar to the open ocean ecosystems process models of Frost (1987,

**Nutrient-Phytoplankton-Zooplankton
Model**

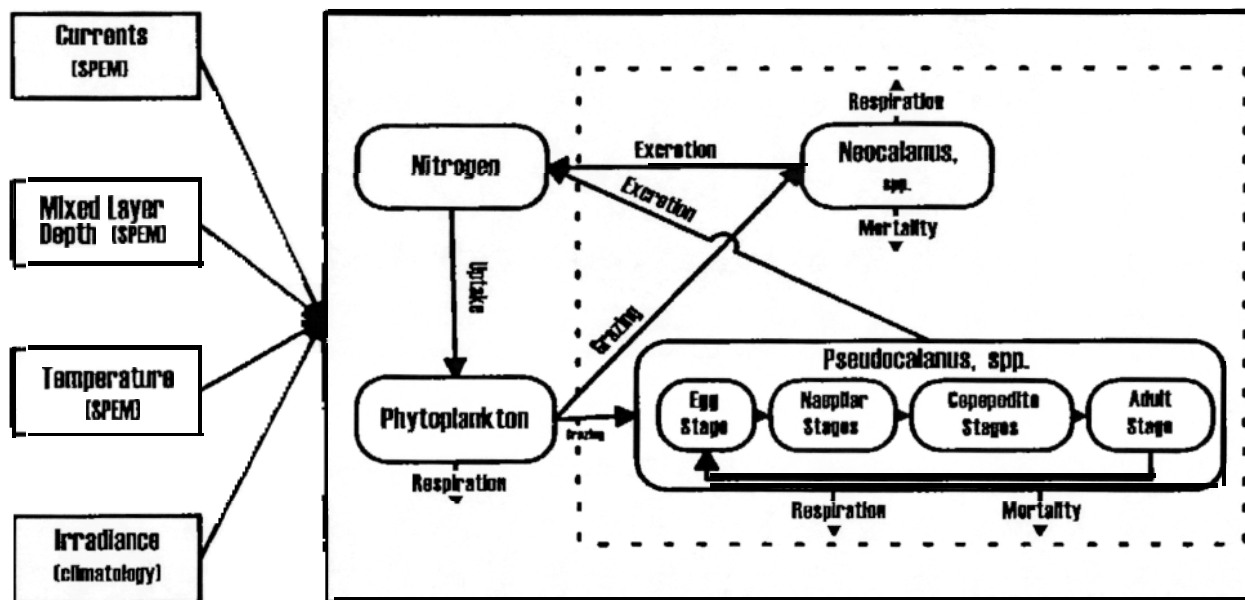


Figure 4. Flow chart of the NPZ model. *Pseudocalanus*, spp. stages modelled are egg stage, five naupliar stages, five copepodite stages and adult stage.

1993) **suitably** modified for our coastal region. *Neocalanus* spp., the biomass-dominant **copepod** in the western coastal Gulf of Alaska and Shelikof Strait, is the primary grazer in the model.

Pseudocalanus, spp. is also included as its egg, naupliar and copepodite stages form a major portion of the diet of larval pollock. Each *Pseudocalanus* stage (13 total) is **modelled** with a separate equation. The NPZ model runs from DOY (Day of Year) 70 to 165, through the spring transition, covering the period when the young pollock are in the larval stage. Vertically, the NPZ model has a **3-layered structure**, similar to Frost (1993), with a homogeneously mixed upper layer of variable depth, a vertically stratified layer extending from the bottom of the mixed layer to 100 m depth, and a “bottom” layer where the values of state variables are assumed to be fixed. Further details of both biological models may be found in **Hinckley** (1999).

Models are not run concurrently, as the SPEM model takes much longer than the **IBM** and NPZ models to run. We therefore run the SPEM model once for each simulated year, storing filtered output of velocities, temperatures and salinity (**Hermann** et al. In Press). Then the **NPZ** model is run using the SPEM velocities, mixed layer depths and temperatures as driving variables, and storing the three-dimensional fields of *Pseudocalanus* stage densities. Lastly, the **IBM** is run using output from the SPEM and NPZ models, and storing output of larval characteristics such as location stage, age, length, weight, etc (Fig. 5). Note that there is no dynamic linkage between the NPZ model and the **IBM** model, ie. larval fish have no impact on the density of their **prey**.

Methods of using models

We ran a series of 6 hydrodynamic model years to provide the forcing functions for a series of biological model runs. We then ran the biological models in three modes. The first was

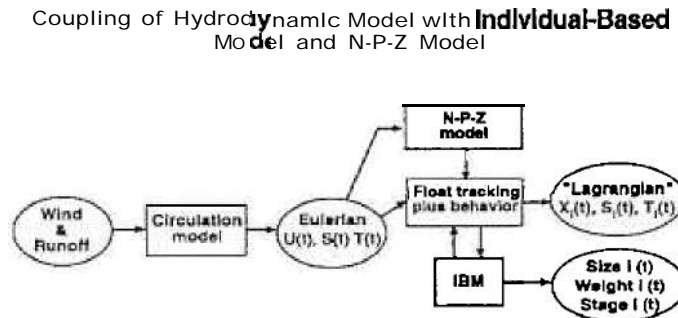


Figure 5. Summary of coupling between SPEM, NPZ and IBM models.

a **hindcast** mode (Hermann et al. 1996), where we tried to duplicate observed initial conditions, such as spawning location, and certain parameters that were specific to the particular year. We then plotted output such as distribution of different life stages or larval characteristics to assess how well the model fit the observations, and to attempt to diagnose the effect of different physical forcing scenarios for each year on the transport and characteristics of young pollock. Figure 6 shows **modelled** distributions of larvae for the years 1987, 1988 and 1989, contrasted with the observed distributions. It can be seen that the model generally does a good job in hindcasting the distributions, with the possible exception of 1988, where a long tail of larvae is seen in the model output to the southwest. It is possible that the region covered by the field survey in this year was not broad enough however, as it did not cover the area to the southwest.

The second mode of running the models was an experimental mode. This mode is designed to examine the viability of specific hypotheses by using the coupled models in a specified experimental design. An example of this was a simulation done to assess the question of why

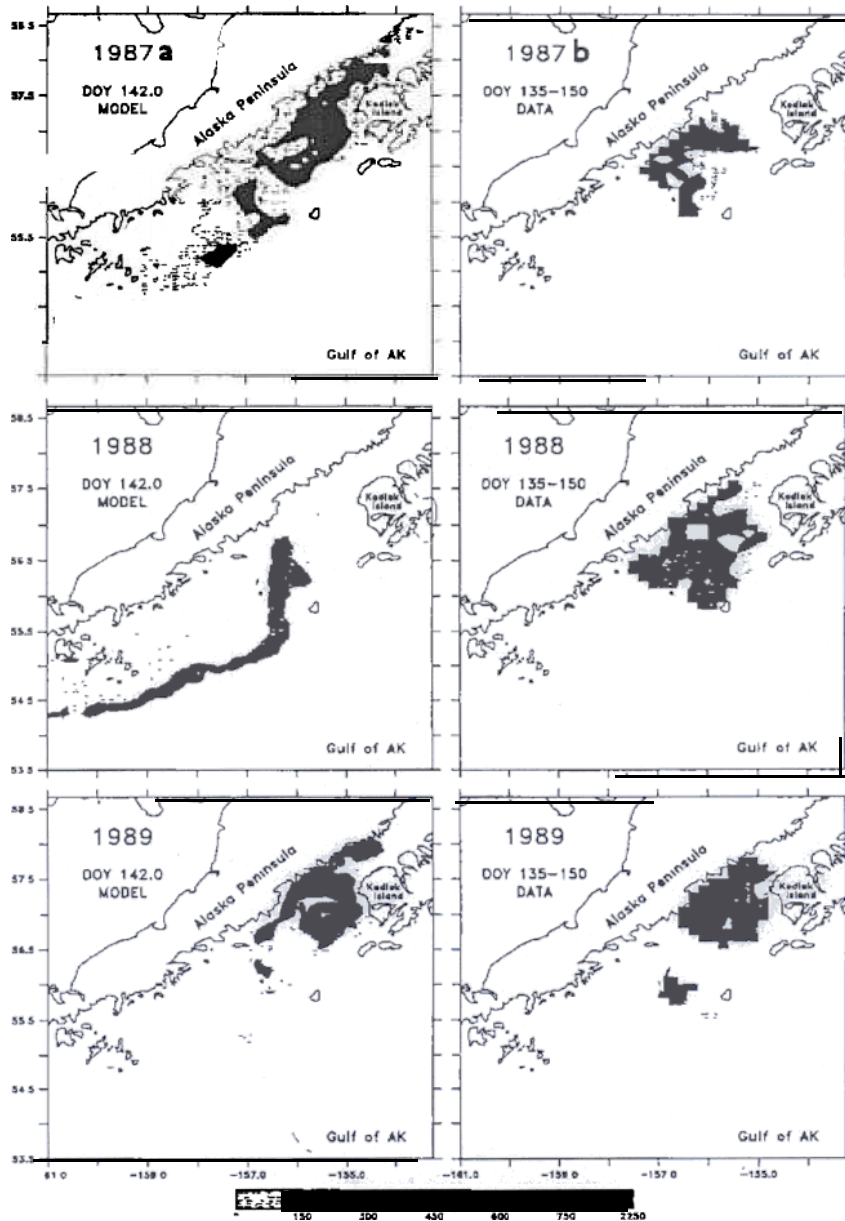


Figure 6. (a) Density of individuals in the IBM model runs on DOY 142 (22 May) for 3 years. Values are numbers of individuals per spatial bin (0.1 degree latitude by 0.2 degrees longitude), converted to larval density (number per 10 m^2). Only non-zero density areas are shaded. (b) Measured larval density for all individuals collected during 15-31 May in each of 3 years. Shaded, contoured areas indicate the spatial extent of the collected data.

the location and timing of pollock spawning in Shelikof Strait is so consistent from year to year (Hinckley et al. In press). The hypothesis addressed was that this consistency was evolved by pollock in this region in order to optimize transport of young stages to the juvenile nursery areas. In this simulation we used a balanced factorial design, where we released eggs from several locations (Fig. 7), times and depths, both inside and outside the observed spawning locations and times.

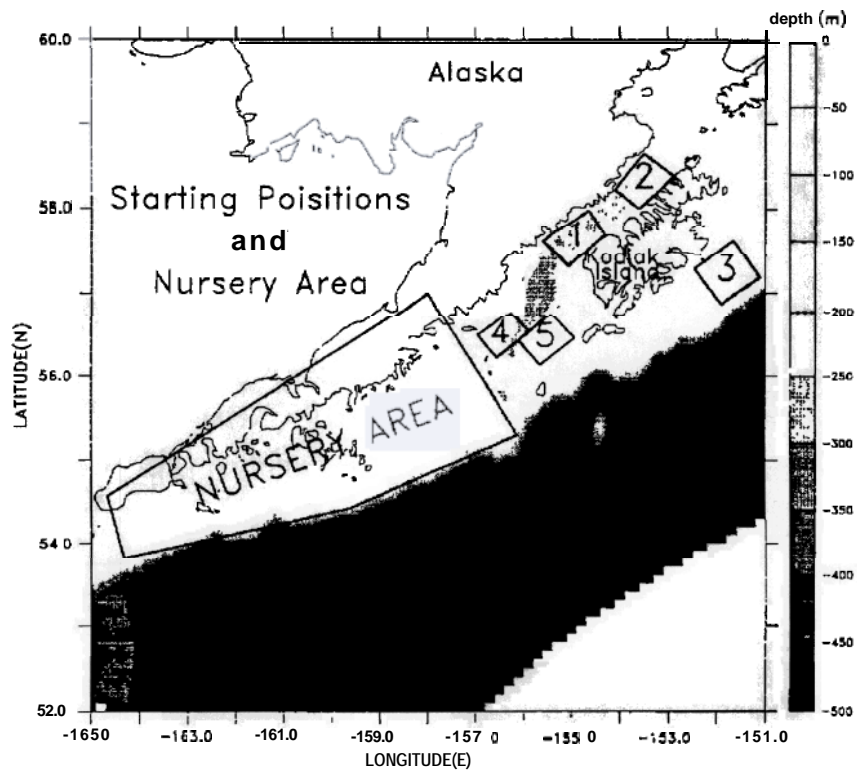


Figure 7. Spawning regions and juvenile nursery area as specified in the model experiment. 1. Central Shelikof Strait, 2. Northern **Shelikof** Strait, 3. Outside Kodiak Island, 4. Northwest **Shelikof** Sea Valley, 5. Southeast Shelikof Sea Valley.

We then **kept** track of how **many** fish **from** each combination of **initial location, time and depth** reached the (observed) juvenile *nursery* area. Figure 8 shows, for example, that eggs spawned outside of Kodiak Island rarely reach the specified juvenile nursery areas. Figure 9 shows **that** many more fish originating **from** the Shelikof **Strait** region reach the nursery area.

The final results of this model experiment were that transport alone could not completely account for the precise spawning location and timing, but transport did narrow the possible window of opportunity. However, when examination was made of the prey fields derived **from** the **NPZ** model for different years as well as transport, it became apparent that a combination of transport and prey spatial and temporal dynamics were **sufficient** to explain the consistency of spawning time and location. This result supports the “match-mismatch hypothesis” of **Cushing** (1972, 1974) which postulates that a match between larval fish production and the production of their prey (both in space and time) is necessary for good recruitment.

The third mode of running the models was in sensitivity analyses. Sensitivity analyses can inform us about not only which parameters are important, but about model formulation, and about mechanisms that are important to recruitment. For example, we did a comparison between two ways of specifying the depth of individuals as it varied with life stage (**Hinckley** et al. 1996). The **first** was **to use an average depth for each life** stage. The second was to use a complex algorithm where depth varied, for example, with salinity in the egg stage, and where **diel** migrations were included in the feeding larval stage. Figure 10 shows tracks of two representative fish, started at the same locations but using the different depth algorithms. It can be seen that the track differs **significantly** between these two ways of formulating depth. Further results of this analysis of sensitivity of the model output to depth were that biological characteristics such as size and weight of larvae between the runs using different depth algorithms (but otherwise exactly the same) differed

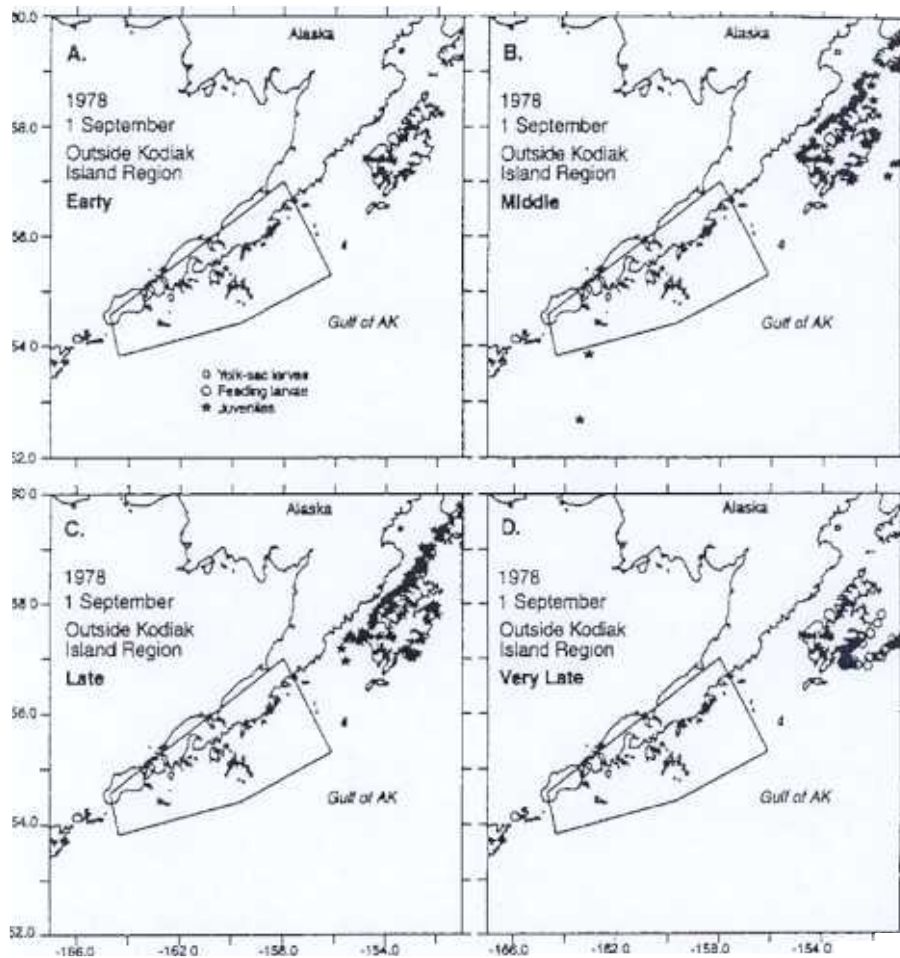


Figure 8. Locations on September 1st of yolk sac and feeding larvae and juveniles from eggs spawned outside Kodiak Island, for 1978. A. Eggs released during the Early spawning time, B. Eggs released during the Middle spawning time, C. Eggs released during the Late spawning time, D. Eggs released during the Very Late spawning time.

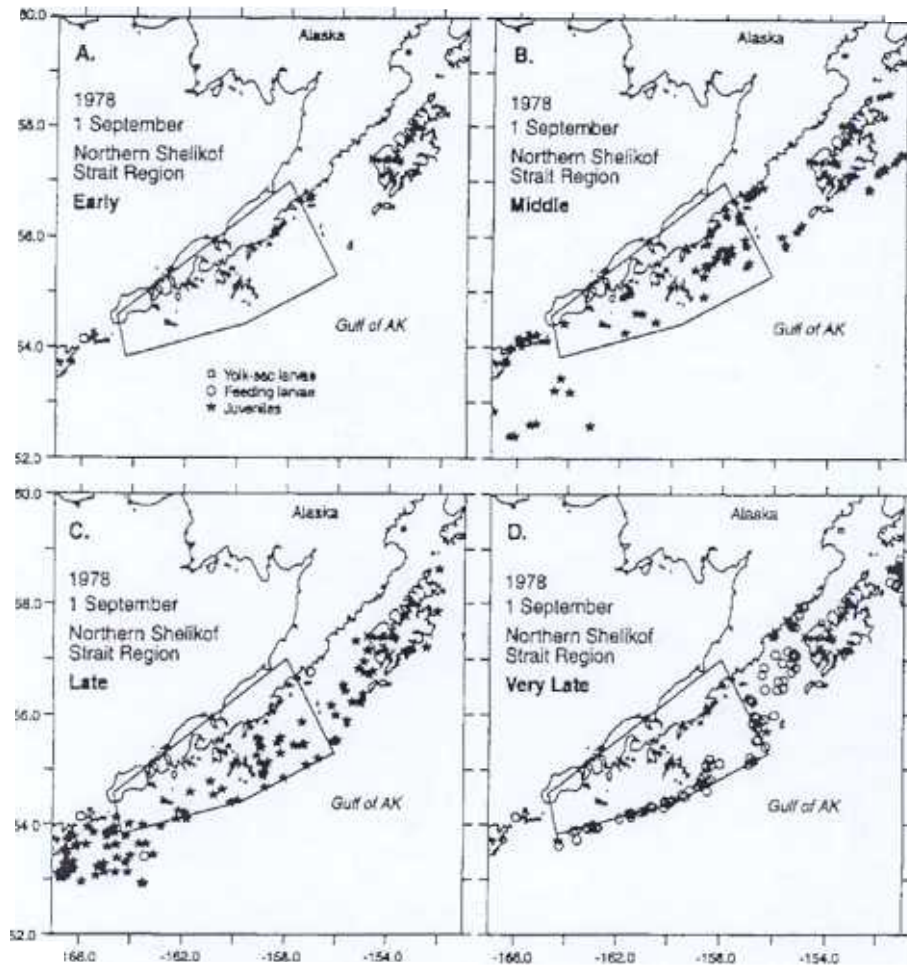


Figure 9. Locations on September 1st of yolk sac and feeding larvae and juveniles from eggs spawned in Northern Shelikof Strait, for 1978. A. Eggs released during the Early spawning time, B. Eggs released during the Middle spawning time, C. Eggs released during the Late spawning time, D. Eggs released during the Very Late spawning time.

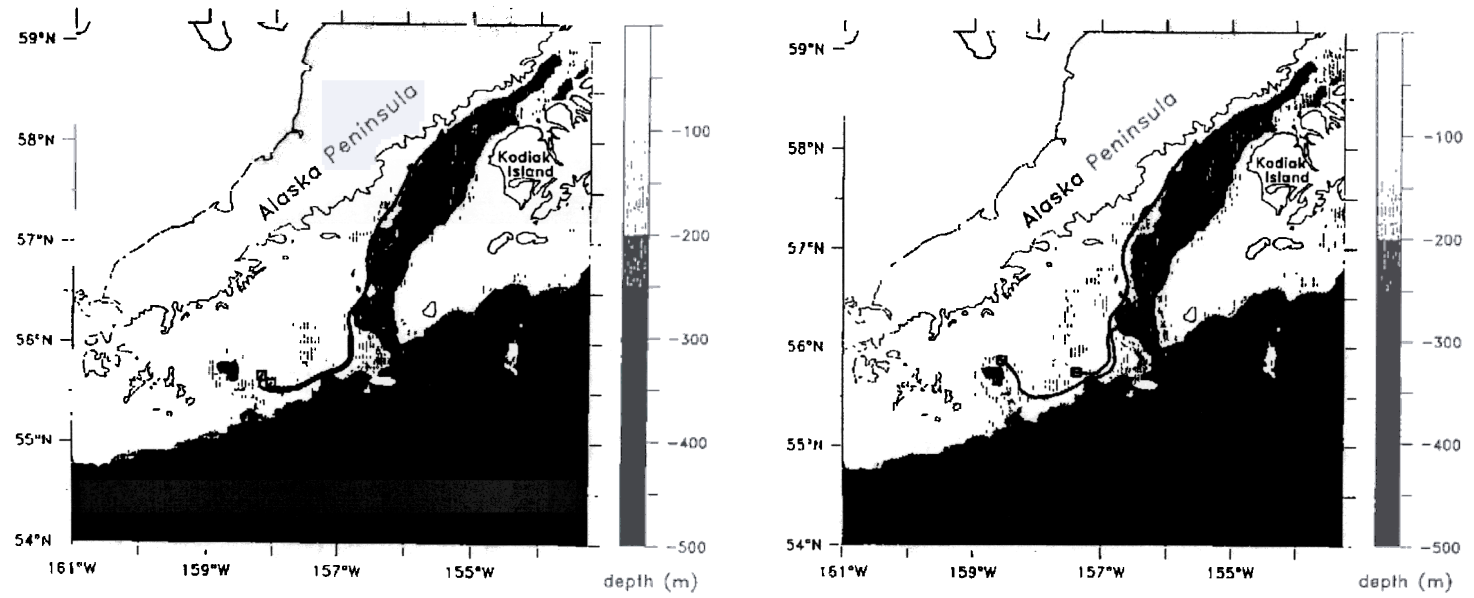


Figure 10. Trajectories of 2 representative floats from the depth algorithm sensitivity analysis. On the left are trajectories which use average depths for each life stage, on the right are those using the complex depth algorithm.

significantly. We also saw, as a result of this simulation, that the depth of individuals was an important factor in whether they successfully made it from the Shelikof sea valley up on to the shelf where the juvenile nursery area was located. These factors have clear implications for recruitment, ie. that factors keeping young fish in the upper waters (prey availability, perhaps less turbulence) aid in transport to the juvenile nursery area from where they recruit back to the Shelikof Strait population of spawners.

A second sensitivity analysis was done of a mechanism by which wind-induced turbulence may cause differences in individual and population characteristics of growth and mortality through an effect on consumption, as hypothesized by MacKenzie et al. (1994) (Megrey and Hinckley In Press). The sensitivity analysis was performed using a Monte Carlo error analysis (Gardner et al. 1983), where model input parameters are drawn from a random distribution in each model run. The Monte Carlo error analysis was implemented using Latin Hypercube Sampling (McKay et al. 1979) in a three-step procedure. The first step involved generating a suite of random input parameter values for the simulation model, the second was running the simulation model to generate a set of output variables, and the third step was a statistical analysis of the model input and output. This sensitivity analysis was done on a one-dimensional version of the IBM, as the three-dimensional version was too computer-intensive to run multiple times.

This sensitivity analysis showed that the optimum wind speed for feeding larval pollock (~7 m/s) was similar to that hypothesized by Sundby and Fossum (1990). This wind speed is not uncommon in the Shelikof Strait region, which indicates that the negative effects on larval feeding of very high winds may indeed occur in this region. The sensitivity analysis showed that feeding and growth processes were very sensitive to reactive distance, and that population characteristics such as mean length, mean metamorphosis date, etc. were very sensitive to parameters

included in this mechanism. The mechanism proved to be a plausible one which might explain the correlation observed between wind speed around the time of first-feeding (Bailey and Macklin 1994) and larval survival. Other possible mechanisms remain to be tested.

Factors supporting good recruitment, as demonstrated by our models

Our biophysical modelling efforts have underlined or revealed several factors which appear to contribute to good recruitment in Shelikof Strait pollock. In some cases, the models have shown us things that were not evident from data and field work. In other cases, the models have underlined and strengthened hypotheses which originally arose solely from data and field studies. These factors include the following:

1. Moderate to strong freshwater runoff, combined with moderate to strong winds (except at first-feeding) appear to contribute to good recruitment, as these contribute to the formation of eddies. 1988 was a year of moderate runoff and strong winds. Figure 11, a contour plot of salinity for 1988, indicates the flow field for DOY 142, in which strong eddy activity can be seen. 1988 was one of the stronger year classes of recent decades.
2. Eddies, especially cyclonic ones, seem to support good recruitment, as these appear to contribute to cross-shelf transport from the spawning area in Shelikof Strait to nursery areas near the Shumagin Islands. Animations of transport of individual fish from spawning to the nursery area (<http://pmel.noaa.gov/~hermann/vrml/lag-multipath-87-bw.wrl>) show that in the presence of many eddies, more larvae are transported from the Shelikof sea valley up onto the shelf area. Larvae which remain in the upper water column in these eddies would be removed from the bottom-following tendency of deep currents which would take them into offshore regions. They would also be more exposed to onshore transport in the upper regions due to the downwelling

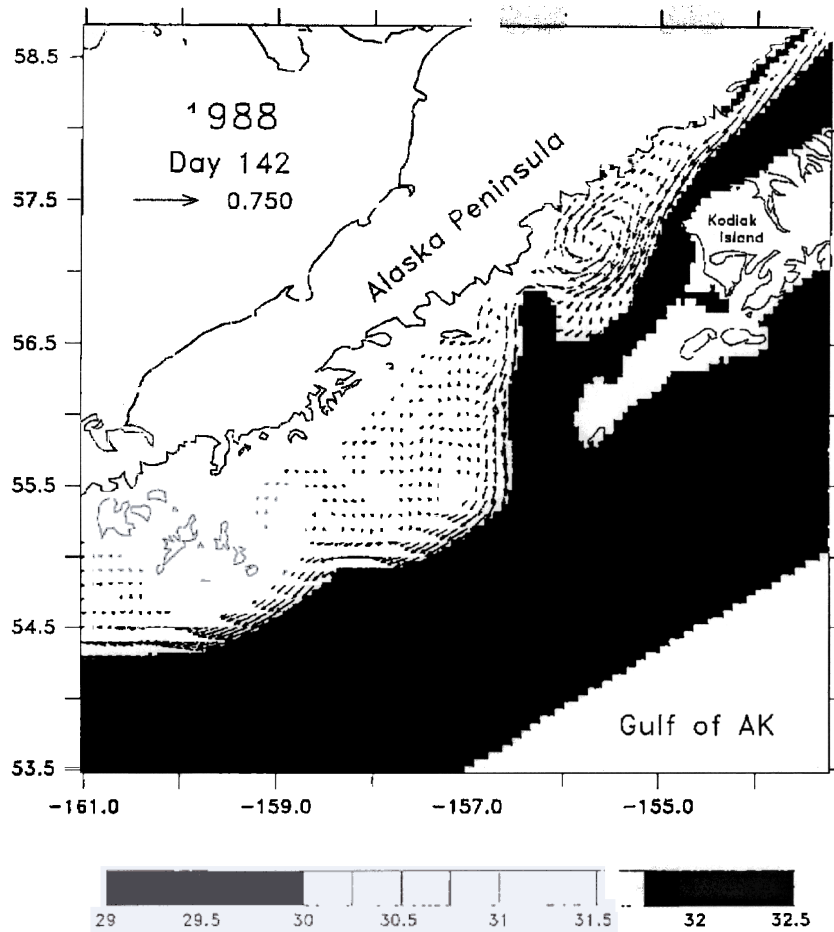


Figure 11. Modelled salinity (in psu) and velocity at 40 m depth on DOY 142 (22 May) for 1988. Key indicates length of 0.75 m s^{-1} velocity vector.

nature of the Gulf of Alaska regime and less exposed to offshore transport in deep regions due to the downwelling.

Eddies also appear to contain more food. This has been seen in field work (Canino et al. 1991), and can also be seen in the output of the NPZ model. Figure 12 shows contours of cope-

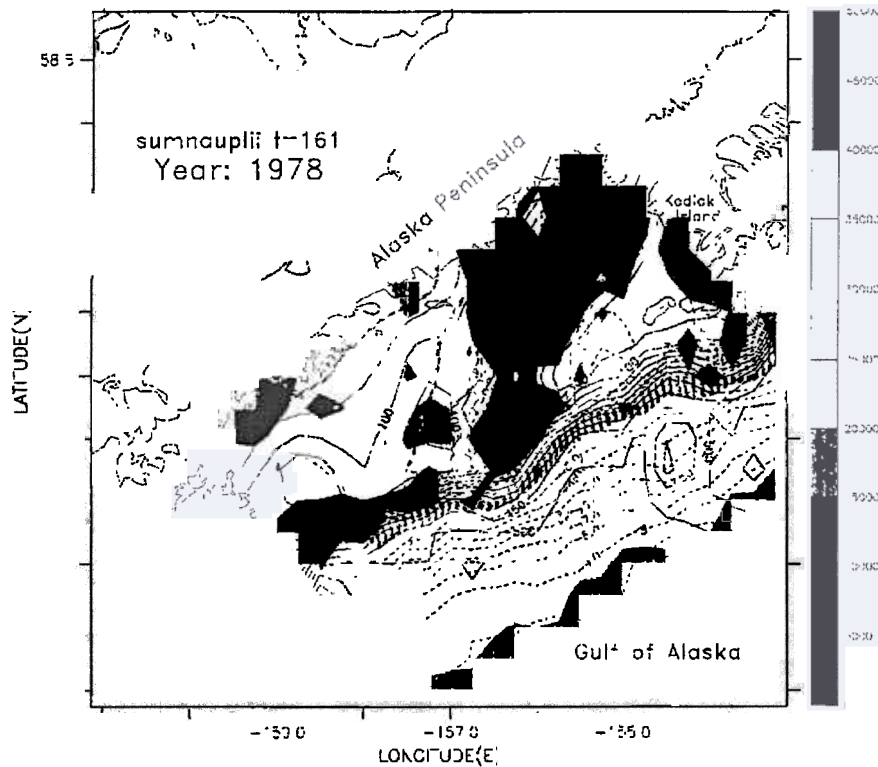


Figure 12. NPZ results for the mixed layer (the sum of the naupliar stages of *Pseudocalanus*, spp. over model domain on DOY 161 for 1978. Color coded by no/m^3 . Red lines represent stream function. Black lines represent bottom contours (m).

pod nauplii, one of the primary food sources for larval pollock, and the stream function derived from the SPEM model, in which eddies can be seen. Higher abundances of food can be found in and around the edges of eddies. This is probably because of the shallower stratification in these eddies and the shallower nutricline. Shelikof Strait is not a nutrient-limited region until after the spring bloom, when nutrient levels in the mixed layer can reach zero. The effect noted, therefore,

would only be significant later in the spring. Conditions within an eddy are likely to be critical to those larvae entrained in them for any length of time.

Bailey and Macklin (1994) and Stabeno et al. (1996) have proposed that retention in eddies may be advantageous to larvae due to an interaction of wind, stratification, and prey conditions. They propose that because cyclonic eddies tend to be stratified higher in the water column, and this shallow stratification retards the penetration of wind-induced turbulence, larvae that would otherwise swim downward to avoid the turbulence can remain in the upper water column where prey are more abundant, facilitating survival. The mechanism of swimming downward to avoid turbulence is not included in our model at this time, however the mechanism which is included, whereby high levels of turbulence interfere with feeding, could equally explain this effect.

3. Retention in the sea valley early in the year (before early May) appears to be beneficial for larvae, as food is low in the regions to the west at this time. Figure 13 shows contours of naupliar abundance on DOY 121, derived from the NPZ model for different years. Areas to the west of the Semidi Islands and to the east of the Shumagin Islands have relatively low abundances of nauplii early on in all years simulated. This is not a region where extensive field work examining food supplies for young pollock has been done early in the year; this modelling work is the first indicator that avoidance of this area may be important to larval success. Field studies in this region early in the year, both to validate the model, and to test this hypothesis, would be useful.

4. It would appear to be beneficial for larvae to remain high in the water column. This helps both by promoting cross-shelf transport, and by keeping larvae in regions of higher prey abundance (see 2, above). One of the results of the sensitivity analysis of the depth algorithms described in the previous section, was that if larvae were placed too deep by the algorithm, there was not

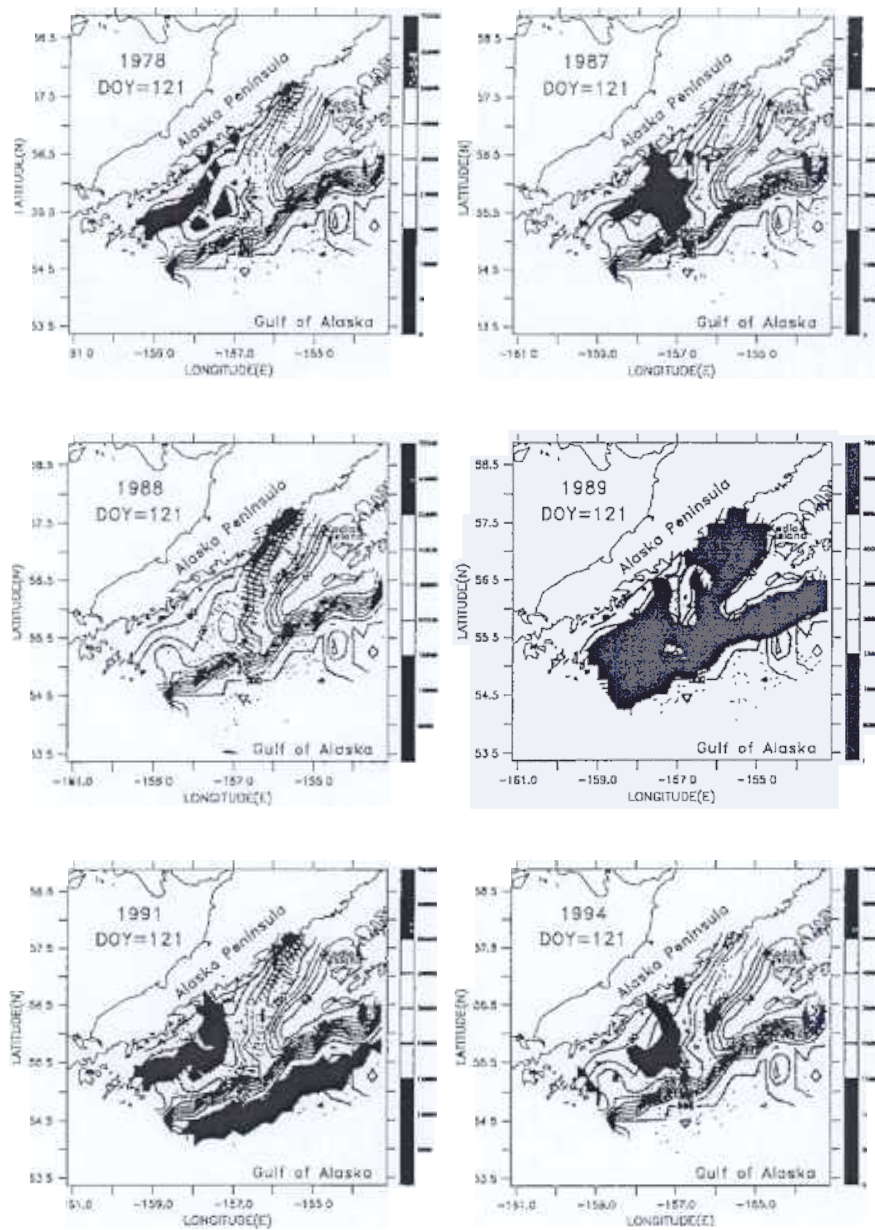


Figure 13. NPZ results for the mixed layer (the sum of naupliar stages of *Pseudocalanus*, spp.) over model domain on DOY 121 for all years. Color coded by no. m^{-3} . Red lines represent stream function. Black lines represent bottom contours (m).

enough food (as predicted by the NPZ model). This sensitivity analysis also showed that larvae and early juveniles which were placed higher in the water column were more likely to be transported nearer to shore (Hinckley 1999).

5. A broad distribution of high abundances of (modelled) copepod nauplii and copepodite stages, and a naupliar peak in abundance between DOY 140 and 160 are both associated with good recruitment years (Figure 14, 1978, 1988 and 1994). A late bloom (1989) or a narrow distribution of high abundances of food (1987, 1989) may contribute to poor recruitment. This condition may be necessary but not sufficient, as 1991 (Fig. 14) showed a broad distribution of food, yet was a poor year class.

6. Wind speeds near the optimum level for consumption (~ 7 m/s), especially around the time of first-feeding may contribute to good recruitment. Our model includes a mechanistic explanation (the dome-shaped relationship between wind-induced turbulence and consumption) which may underlie the observed correlation between low wind speeds at the time of larval first-feeding and survival. It would be interesting to see how this prediction, especially with regard to the optimal wind speed as predicted by this model and the strength of recruitment, is borne out in the future.

Cautions

During the course of our modelling work in the FOCI program, we have learned much which might be useful for others attempting biophysical recruitment modelling studies. First and foremost, these models are large and complex and computing power has been a limiting factor in our work, especially with regards to the oceanographic models. This should become less of a problem as computers continue to increase in power and decrease in cost. However, "people-power" has been even more limiting, and will probably remain so. Each of the models described

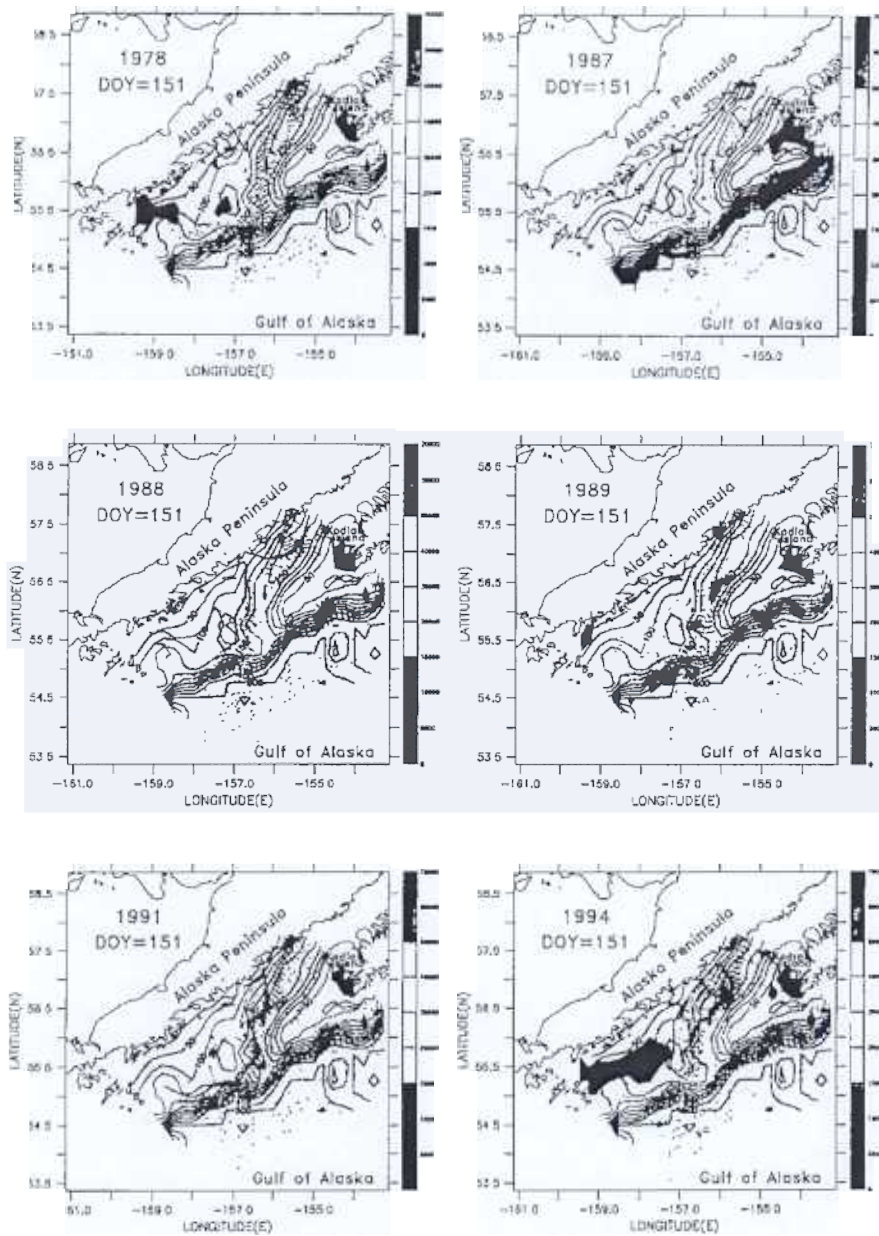


Figure 14. NPZ results for the mixed layer (the sum of naupliar stages of *Pseudocalanus*, spp.) over model domain on DOY 151 for all years. Color coded by no. m⁻³. Red lines represent stream function. Black lines represent bottom contours (m).

has taken many months and years to develop and test. Much validation work remains to be done, and many more simulations with these models are desirable. The availability of standardized and validated code (like the SPEM model) through easily accessible channels (like the world-wide-web) could perhaps accelerate the process.

A large amount of effort must be devoted to understanding how the models are working. Again, they are large and complex, and it is not easy to get a clear picture of what the models are actually doing. The outputs are immense and confusing, and the types of analyses done on these outputs needs to be carefully chosen. Unnecessary complications should be avoided, ie. only those processes thought to be important should be included, and new mechanisms and algorithms should be tested against the simpler versions before inclusion. Calibration and sensitivity analyses are necessary in order to gain insight. We have heard of cases where these types of models replicate some data well, yet with further analysis they are found to contain mechanisms which, by themselves, don't produce sensible results (Dr. J. Anderson, Univ. Wash., Seattle, pers. commun.).

These models, as with all models, are not capable of replicating the data exactly. For example, the circulation model (without data assimilation, which our models do not yet have) can only get currents and mesoscale features right in a statistical sense. This therefore limits the precision with which we can replicate distributions, at a particular spatial scale, of different life stages for any one year, or other biological characteristics. However, "statistically correct" results may be sufficient to develop reasonable hypotheses about sensitivities and mechanisms. Detailed spatial models may be used to address the very issue of predictability itself. By analogy with weather prediction, we may use these models to suggest how far into the future one could reasonably hope to predict recruitment, given a fixed amount of past and present data.

These models are very data intensive. Concurrent and prior field and laboratory studies are irreplaceable as a source of parameters, initial and boundary values, and for model calibration. Effective and frequent communications with those who collect the data and conduct the process studies is essential. We have been lucky in that FOCI is a well-integrated, long-term and ongoing recruitment processes program, which has much data and has had many studies done under its auspices. Despite this, some of our parameterizations and processes must still be drawn from other, closely-related species.

Our modelling work has made it clear that inclusion of more than a single trophic level (ie. that of young fish) is necessary for advances in understanding through the use of these types of models, for example the match-mismatch hypothesis, which needs spatially explicit NPZ and fish IBMs to explore. Our work has given us insight into the important role that the spatial and temporal dynamics of prey play in affecting young fish and the recruitment process. One of the largest gaps in our models, for example, is the lack of data and understanding of spatially- and temporally-explicit mortality processes and predator fields. An improved ability to model the distribution and abundances of predators would undoubtedly advance our knowledge of recruitment further.

A further point is that while our “decoupled” method of saving low-pass filtered velocities appears generally successful, it may exclude some cross-shelf transport pathways, e.g. those due to interaction of vertical migration with tides. Further work to mitigate or avoid this potential problem would be useful.

The future of biophysical models in recruitment studies

Increases in computing power, and decreases in computing costs will make biophysical modelling easier and more accessible to recruitment studies programs. Memory, processing speed and output storage capacity are all critical. We have used a vector-processing supercomputer (Cray YMP) for much of our work. The SPEM model takes about 125-150 CPU hours to run one year simulation on that computing platform, and the NPZ and IBM models about 6-7 hours each to run per model year. We are now starting to run our models "in-house" as faster and cheaper workstations become available. Indeed, a new breed of affordable workstations easily matches the power of older supercomputers. Promising technologies for the future include massively parallel architectures; many oceanographers have already begun to avail themselves of these new resources. Programming for these new architectures is not trivial, however, and a steep learning curve has slowed their adoption by the wider community.

There are several factors which should be addressed to make biophysical recruitment models more useful. One is the need to find methods of sorting through and analyzing complex and voluminous multidimensional model output. Three-dimensional visualization methods (Moore et al. In revision) and graphical user interfaces (Megrey et al. In review) can be very useful in this respect. Work needs to be done to assess the effects of using standard statistical methods on model output where many of the underlying assumptions (such as independence of observations) are not met. Methods of statistically comparing spatially-explicit model output (e.g. the spatial distribution of different life stages) with data are needed, given the consideration outlined above, that the model can never replicate the data exactly. Lastly, methods of assessing model performance need to be developed that take into account the size and complexity of these models (Reynolds and Ford 1999).

Conclusions

Spatially-explicit coupled circulation and biological models can provide an excellent framework for the examination of complex biophysical hypotheses regarding recruitment processes in marine fish. Mechanisms thought to underlie correlations between physical factors and recruitment can be examined and contrasted. Hindcasts of specific years and suites of years can be examined in a holistic manner, very different from the snapshots which are all we can obtain from field surveys and experiments. Individual-based models allow us to track the histories of those fish that survive and those that die, and to diagnose the reasons for the difference. Our modelling effort certainly confirms the notion that small-scale variations in the exposure of individual fish to environmental conditions of transport, temperature, salinity and other environmental scalars, may make an important difference in survival to recruitment. Inclusion of even rudimentary spatial information in the models can radically alter the outcomes (Hinckley 1999).

In order that it may become a tool useful for the prediction of recruitment, either in the short- or long-term, several factors need to be addressed in these types of models. First, more timely results are needed. The great amount of computer and processing time needed by these models has hindered real-time simulations, or at least fast turnaround times for yearly predictions of recruitment. Improvements in computer speed should help with this problem, however, personnel time is still an issue. Secondly, a better understanding of mortality processes is needed. Ideally, more attention to the effect of predation, and to the life histories and spatial and temporal distributions of predators on young fish should be performed and incorporated into these models. Thirdly, more complete validations are needed to build confidence in these models. This is an area of ongoing work with our models, and needs to be done more generally with other large complex biophysical models. Finally, the coupling of individual-based models of the early life history

with stage- or age-structured models of older fish would enable us to examine the effects of biological and physical factors all the way to the age of recruitment, and also to examine the effects of climate and harvest in multi-year simulations.

In conclusion, we have found that coupled biophysical models have increased our understanding of recruitment processes in walleye pollock, have allowed us a more holistic view into these processes, and have allowed us to examine hypotheses relating to specific mechanisms underlying correlations between physical and biological factors and recruitment. We encourage others to incorporate this type of modelling in their recruitment studies.

Literature Cited

- Bailey, K.M. and A. Macklin. 1994. Analysis of patterns in larval walleye pollock: *Theragra chalcogramma* survival and wind mixing events in Shelikof Strait, Gulf of Alaska. Mar. Ecol. Prog. Ser. 113: 1-12.
- Bailey, K.M. and S.M. Spring. 1992. Comparison of larval, age-0 juvenile and age-2 recruit abundance indices of walleye pollock, *Theragra chalcogramma*, in the western Gulf of Alaska. ICES J. Mar. Sci. 49: 297-304.
- Bograd, S.J., P.J. Stabenon, and J.D. Schumacher. 1994. A census of mesoscale eddies in Shelikof Strait, Alaska, during 1989. J. Geophys. Res. 99: 18243-18254.
- Canino, M.F., K.M. Bailey and L.S. Incze. 1991. Temporal and geographic differences in feeding and nutritional condition of walleye pollock larvae *Theragra chalcogramma* in Shelikof Strait, Gulf of Alaska. Mar. Ecol. Prog. Ser. 79: 27-35.
- Cushing, D.H. 1972. The production cycle and the numbers of marine fish. Symp. Zool. Soc. London 29: 213-232.
- Cushing, D.H. 1974. The natural regulation of fish populations. In: (Harden Jones, F.R. Sea fisheries research, Elek Science, London, pp. 399-412.
- DeAngelis, D.L. and L.J. Gross. 1992. Individual-based models and approaches in ecology: populations, communities and ecosystems. Routledge, Chapman and Hall, Inc. New York.

- Frost, B.W. 1987. Grazing control of phytoplankton stock in the open subarctic Pacific Ocean: a model assessing the role of mesozooplankton, particularly the large calanoid copepods *Neocalanus*, spp. Mar. Ecol. Prog. Ser. 39: 49-68.
- Frost, B.W. 1993. A modeling study of processes regulating plankton standing stock and production in the open subarctic Pacific Ocean. Prog. Oceanogr. 32: 17-56.
- Gardner, R.H., B. Rojder and U. Bergstrom. 1983. PRISM: A systematic method for determining the effect of parameter uncertainties on model predictions. Technical Report, Studsvik Energiteknik AB Report/NW-83/555, Nyköping, Sweden.
- Hermann, A.J. and P.J. Stabeno. 1996. An eddy resolving model of circulation on the western Gulf of Alaska shelf. I. Model development and sensitivity analysis. J. Geophys. Res. 101: 1129-1149.
- Hermann, A.J., S. Hinckley, B.A. Megrey and P.J. Stabeno. 1996b. Interannual variability of the early life history of walleye pollock near Shelikof Strait as inferred from a spatially explicit, individual-based model. Fish. Oceanogr. 5(Suppl. 1): 39-57.
- Hermann, A.J., S. Hinckley, B.A. Megrey and J.M. Napp. In press. Applied and theoretical considerations for constructing spatially explicit individual-based models of marine fish early life history which include multiple trophic levels. ICES J. Mar. Sci.
- Hinckley, S. 1999. Biophysical mechanisms underlying the recruitment process in walleye pollock (*Theragra chalcogramma*). PhD Dissertation, Univ. Washington, Seattle.
- Hinckley, S., A.J. Hermann and B.A. Megrey. 1996b. Development of a spatially explicit, individual-based model of marine fish early life history. Mar. Ecol. Prog. Ser. 139: 47-68.
- Hinckley, S. A.J. Hermann, K.L. Mier and B.A. Megrey. In press. The importance of spawning location and timing to successful transport to nursery areas: a simulation modeling study of Gulf of Alaska walleye pollock. ICES J. Mar. Sci.
- Incze, L.S., P.B. Ortner and J.D. Schumacher. 1990. Microzooplankton, vertical mixing and advection in a larval fish patch. J. Plankton Res. 12: 365-379.
- Judson, O.P. 1994. The rise of the individual-based model in ecology. Trends Ecol. Evol. 9: 9-14.
- Kendall, A.W., Jr. and T. Nakatani. 1992. Comparisons of early life history characteristics of walleye pollock *Theragra chalcogramma* in Shelikof Strait, Gulf of Alaska, and Funka Bay, Hokkaido, Japan. Fish. Bull. U.S. 90: 129-138.
- Kinoshita, R.K., A. Greig, J.D. Hastie and J.M. Terry. 1995 (draft). Economic status of the groundfish fisheries off Alaska (1994). Socioeconomic Task. Alaska Fisheries Science Center, 7600 Sand Point Way, NE, Seattle, WA 98115. 104 p.

MacKenzie, B.R. and T. Kiørboe. 1995. Encounter rates and swimming behavior of pause-travel and cruise larval fish predators in calm and turbulent laboratory environments. *Limnol. Oceanogr.* 40: 1278-1289.

MacKenzie, B.R., T.J. Miller, S. Cyr and W.C. Leggett. 1994. Evidence for a dome-shaped relationship between turbulence and larval fish ingestion rate. *Limnol. Oceanogr.* 39: 1790-1799.

McKay, M.D., R.D. Beckman, and W.J. Conover. 1979. A comparison of three methods for selecting values of input variables in the analysis of output from computer code. *Technometrics* 21: 239-245.

Megrey, B.A., S.J. Bograd, W.C. Rugen, A.B. Hollowed, P.J. Stabeno, S.A. Macklin, J.D. Schumacher and W.J. Ingraham, Jr. 1995. An exploratory analysis of associations between biotic and abiotic factors and year-class strength of Gulf of Alaska walleye pollock (*Theragra chalcogramma*). In: *Climate change and northern fish populations*. Beamish, R.J. (ed). *Can. Spec. Publ. Fish. Aquat. Sci.* 121: 227-243.

Megrey, B.A. and S. Hinckley. In press. The effect of turbulence on feeding of larval fishes: a sensitivity analysis using an individual-based model. *ICES J. Mar. Sci.*

Megrey, B.A., S. Hinckley and E. Dobbins. Using scientific visualization tools to facilitate analysis of multi-dimensional data from a spatially-explicit, biophysical, individual-based model of marine fish early life history. *ICES J. Mar. Sci.* (In review)

Moore, C.W., A.J. Hermann, N.N. Soreide, C.M. Lascara and G.H. Wheless. Desktop scientific visualization for ocean and atmospheric sciences using Virtual Reality Modeling Language (VRML). *Bull. Amer. Met. Soc.* (In revision).

Pope, J.G., J.G. Shepard and J. Webb. 1994. Successful surf-riding on size spectra: the secret of survival in the sea. *Phil. Trans. Royal Soc. London* 343: 41-49.

Reynolds, J.H. and E.D. Ford. 1999. Multi-criteria assessment for ecological process models. *Ecology* 80: 538-553.

Scheffer, M., J.M. Baveco, D.L. DeAngelis and K.A. Rose. 1995. Super-individuals: a simple solution for modeling large populations on an individual basis. *Ecol. Model.* 80: 161-170.

Schumacher, J.D., P.J. Stabeno and S.J. Bograd. 1993. Characteristics of an eddy over a continental shelf: Shelikof Strait, Alaska. *J. Geophys. Res.* 98: 8395-8404.

Stabeno, P.J. and A.J. Hermann. 1996. An eddy resolving model of circulation on the western Gulf of Alaska shelf. II. Comparison of results to oceanographic observations. *J. Geophys. Res.* 101: 1151-1161.

Stabeno, P.J., A.J. Hermann, N.A. Bond and S.J. Bograd. 1995. Modelling the possible impact of climate change on the survival of larval walleye pollock (*Theragra chalcogramma*) in the Gulf of Alaska. In: *Beamish, R.J. (ed) Climate change and northern fish populations*. *Can. Spec. Publ. Fish. Aquat. Sci.* 121: 719-727.

Stabeno, P.J., J.D.Schumacher, K.M. Bailey, R.D. Brodeur and E.D. Cokelet. 1996. Observed patches of walleye pollock eggs and larvae in Shelikof Strait, Alaska: their characteristics, formulation and persistence. *Fish. Oceanogr.* 5(Suppl. 1): 81-91.

Sundby, S. and P. Fossum. 1990. Feeding conditions of Arcto-Norwegian cod larvae compared with the Rothschild-Osborn theory on small-scale turbulence and plankton contact rates. *J. Plankton Res.* 12: 1153-1162.