Complex processes in the survival of walleye pollock larvae and forecasting implications

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SUMMARY: The processes that establish the survival of walleye pollock larvae are complex. High frequency events during egg and larval life introduce noise to the dynamics of the population. Forecasts of recruitment must account for this complexity. Initial conditions impacting larval survival do not significantly account for variability in recruitment, but information on abundance near the prediction target are fairly accurate in forecasting year-class strength, following expectations from complexity theory.

KEY WORDS: Walleye pollock, *Theragra chalcogramma*, complexity, complex systems, recruitment, fish larvae

INTRODUCTION

Patterns in recruitment of marine fishes appear to be influenced by complex processes occurring at different scales. High variability, relatively infrequent, and cyclic appearance of strong year classes, as observed for walleye pollock (Fig.1), may be a property of recruitment arising from the
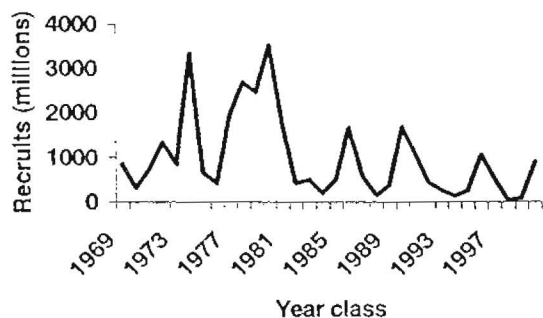

Fig. 1. Dynamics of age-2 recruits in the western Gulf of Alaska population of walleye pollock.

interaction of many different high and low frequency factors that impact survival. For example, the survival of fish larvae is impacted by interactions of biological and physical processes over space scales varying from the perceptual distance of larvae (several millimeters) to climatic events that span ocean basins. Time scales of factors impacting recruitment vary from periods of days to decadal climate regimes and longer.

A complex process is one with a multitude of interacting factors. As a complex process, recruitment is influenced by environmental conditions interacting with biology with nonlinear effects.[1] Fish populations themselves may be part of a larger complex adaptive system, or systems that are to varying degrees self-organizing. Theories of complex adaptive systems suggest that perturbations can push such systems into near chaos and reorganization,[2] similar to what we are currently experiencing in the North Pacific Ocean.[3] Furthermore, slight differences in initial conditions have completely different outcomes on the way a complex system develops, making predictions difficult.

Many factors are associated with larval mortality and survival: predation by invertebrates, cannibalism on eggs, temperature, abundance of prey, prey nutritional condition, storm events, transport into unfavorable nurseries, and growth rates are among the best known. If processes governing the survival of marine fishes are complex, what constraints does this put on our ability to forecast recruitment from initial conditions occurring during the egg and larval stages?

PROCESSES AND SCALES INFLUENCING LARVAL SURVIVAL

Pattern and variability change with the scale of observation both in the physical and biological realms. Turbulence is often described as a chaotic process. At a somewhat higher level of organization, currents in our region of study appear to be complex. While on an even larger-scale, there also appear to be more organized events that are periodic and have consistent effects over large areas, like temperature anomalies related to decadal regime shifts. Likewise, recruitment can be studied on different scales, with

different patterns emerging depending on the scale of study.

The choice of population scale is important to consider as variations in abundance at smaller scales may not be indicative of larger scale patterns. For example, declines in stock abundance may not be reflected on local scales, and vice versa. Spatially restricted studies can be impacted by events on a larger scale, such as migration. On a macro-scale, general patterns may be apparent but they don't demonstrate causes because the mechanisms need finer scale observation.

Larval mortality rates are measured over relatively small space and time scales. For walleye pollock this means over periods of 5 to 20 days and an area of 10 to 30 x 10^3 km^2. Larval mortality, especially in the egg and early larval period, is very high and variable, ranging from about 4% per day to 40% per day.[4] Many factors can impact the survival of larvae and often they are interacting. As an example, larval feeding interactions with the environment will be briefly discussed as a complex process resulting in such high variability in survival.

For walleye pollock larvae, turbulence and mixing are considered important to larval survival. The first-feeding distribution of surviving larvae has been shown to mostly overlap with periods of low wind stress during the first-feeding period, and high winds at that time are associated with low survival[5] (Fig. 2). The implication is that high winds during the
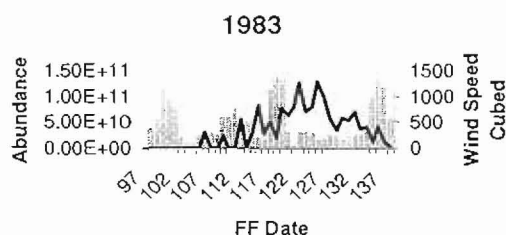

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Fig. 2. Distribution of dates that successfully surviving larvae sampled in late May were at the first-feeding stage (line) compared with an index of wind mixing (wind speed cubed) on that day of year (columns).

first-feeding period disrupt feeding and survival. As further support, larval mortality rates are negatively correlated with wind stress (Fig. 3). Turbulence is thought to impact larval fish contact rates with prey in a nonlinear manner.[6] However, with pollock, not only does turbulence impact prey contact rates, recently it has been shown that pollock larvae will alter their vertical distribution to avoid turbulence.[7] Prey abundance, another factor influencing contact

rates, has been linked with feeding success and mortality rates of pollock larvae[8] and prey levels
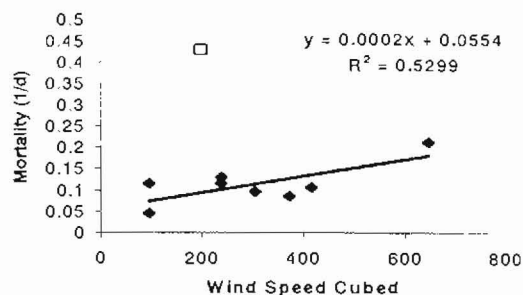

Fig.3. The relationship between early larval mortality rates and wind speed. The data point marked as an open box was not included in the regression as it was estimated from data collected several weeks earlier than other sampling, and during a cold period.

have been linked with the condition of larvae as well[9]. Larval condition must influence the ability of larvae to locate and capture prey and has a feedback effect on prey. But not only do larvae respond to turbulence, prey also have species-specific reactions to turbulence through avoidance and mixing.[10] High densities of larvae can impact prey number (another feedback condition), and likewise other predators will impact prey numbers. Other interacting factors that are commonly known to be important for larval feeding success include sea surface temperature and light levels. In summary, the impact of many small-scale factors interacting nonlinearly on larval survival can result in many possible outcomes, and is therefore a complex process (Fig. 4).
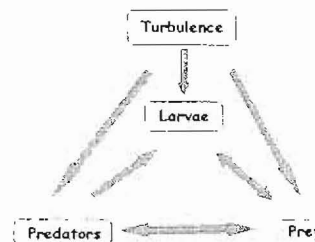

Fig. 4. Schematic picture illustrating the complex interactions between larval feeding, predators, prey and environment.

However, larval feeding is not the only complex process that influences recruitment; predation, advection and disease are complex processes and are important as well. Similar diagrams could be drawn for each of these processes. In particular predation on larvae can be high and is influenced by stage and

condition of larvae, the distribution and abundance of many different predators, their feeding rates, interactions with alternative prey, and environmental conditions.

FORECASTING RECRUITMENT

In the case of walleye pollock, the stage-specific abundances account for a decreasing portion of the variance in recruitment as time from recruitment increases (Figs. 5, 6). Wind mixing and SST are both conditions that influence larval mortality, and these environmental conditions along with egg abundance are the initial conditions in the recruitment process. However, predictions of recruitment from environmental variables and natality are not significant (SST and natality are shown as examples in Fig. 5), as are multiple regression models (for example a regression model with SST, wind mixing and natality as predictors explains little of the variance in recruitment; $R^2=0.0027$, P=0.82).
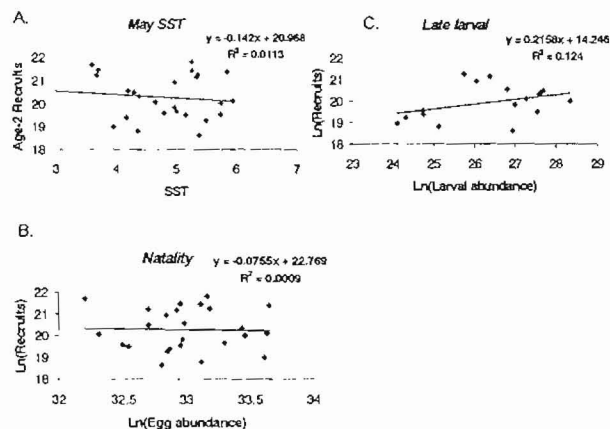

Fig. 5. Regressions between environmental factors (SST) and egg and larval stage abundance and recruitment.

Somewhat closer to recruitment, especially in the sense that the period of high and variable mortality is completed, there is an apparent trend with late-larval abundance, and then a significant trend with age-0 juveniles (Fig. 6). Finally age-1 abundance is a fair predictor of recruitment to the fishery. In conclusion, forecasts from a previous state of the population may be reasonably accurate, but predictions from distant stages, like eggs and larvae, or environmental conditions impacting them, are likely to be inaccurate due to complexity.
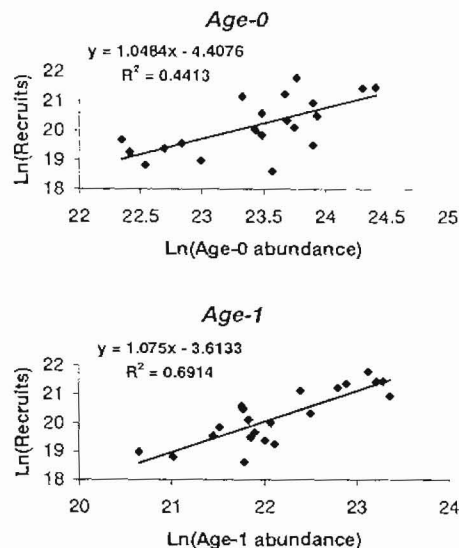

Fig. 6. Regressions between age-0 and age-1 juvenile abundance and recruitment.

CONCLUSION

Survival to recruitment is the cumulative effect of interactions between many high and low frequency events, making it a complex process. Although this study has focussed on early larval survival, constraining or deterministic factors operating at larger scales and occurring later in life may tend to give some order to the recruitment process.

Forecasting recruitment follows what is expected from a complex process, becoming more difficult with increasing time from the event.[11] Accurate forecasts are possible from prior information on the population state, such as abundance at the juvenile stage, but it seems unlikely that accurate predictions will be possible from initial conditions affecting larvae alone. Nonlinear models that incorporate dominant factors influencing survival and accounting for juvenile mortality may hold some promise for the future.[1,12] As well, neural net models currently under development may be useful. The success of such models, and the understanding and predictability of larger-scale processes on recruitment, however, require a better understanding of the mechanisms underlying larger-scale patterns.[13] recruitment.

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