6 Application 3: recruitment prediction

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6.1 Definition

What do we mean by recruitment prediction? The first thing to consider in defining this term is the time horizon of the prediction. Short-term predictions mean the use of individual-based, coupled physical–biological models (ICPBM) of fish early life history to predict annual recruitment, most usually to aid managers of fish stocks. These predictions may be made via indices or other measures of prerecruitment or recruitment, derived from ICPBM output, that correlate well with other independent, reasonable predictors of recruitment (derived from stock-assessment models, reasonable independent juvenile or prerecruit surveys conducted with acoustic or trawl, or other net-based survey methods). These may be used alone or in conjunction with other predictors, such as spawning-stock biomass. Actual numerical estimates (of the correct magnitude) derived from ICPBM may be possible, but only if certain conditions are met (e.g. the super-individual method, proportionality indices, or other methods of relating model indices to real population numbers are used, and spawning-biomass or egg-production estimates as initial conditions are included). A benefit of these indices is that they could serve as a replacement for expensive juvenile surveys.

Under this definition, the forecast window for recruitment predictions would be limited to the number of years from spawning to recruitment for each species of interest. This is because of the fundamental lack of predictability of regional and small-scale ocean physics. These prediction windows will be different for each species owing to differences in the unique aspects of a species’ life history.

Longer-term recruitment predictions that are likely under different future scenarios (e.g. of climate, fishing, or ocean variability) may also be derived from ICPBM through the use of the models to gain a mechanistic understanding of the important biophysical processes underlying recruitment variability. This knowledge may, for example, help us to understand simple correlations between biophysical factors and recruitment, and when such correlations may or may not hold up.

The development of recruitment predictors from ICPBM requires careful consideration of what we mean by recruitment. There are many ways of defining recruitment. The operational definition depends on the purpose or goal of the prediction. Are we predicting recruitment for management purposes? If so, then recruitment is often defined as the number of fish entering the exploited segment of the population, where the meaning of “exploited segment” depends on the distinctive attributes of each fishery (i.e. gear type, time and space scales). If examining life-history characteristics or gaining ecological understanding is the goal, recruitment could be defined as the number of fish reaching a juvenile nursery area, the number reaching maturity, or the number reaching a particular age, size, or stage.

6.2 Objectives of recruitment prediction

There can be several different objectives for recruitment prediction, and these will affect not only how we select a predictive index from the model, but how the ICPBM itself is constructed and its relevant physical and biological details. Recruitment prediction may be undertaken to test our understanding of the processes that affect recruitment. ICPBM may be developed to clarify mechanistic processes underlying correlations between physical or biological factors and recruitment. Recruitment pre-
6.3 Indices of recruitment from ICPBMs

When using ICPBMs to aid in the prediction of recruitment, an index that appears to correlate well with recruitment can be used. Often, these indices relate to some underlying theory about recruitment success. Some examples of recruitment or prerecruitment indices that have been, or could be, derived from ICPBMs are (i) the number of larvae or juveniles that reach a specified nursery area, weighted by their residence time there (Parada et al., in review); (ii) the number that reach a nursery area by a particular date, size, or age (Bartsch et al., 2004; Baumann et al., 2006); (iii) indices of larval drift or retention, such as the number going in a predefined direction (Wespestad et al., 2000; Wilderbuher et al., 2002; Stockhausen, pers. comm.) that experience different levels of bottom depth anomalies (Baumann et al., 2006), or a survival rate after a certain number of days of drift (Allain et al., 2007); (iv) indices of overlap of larvae with their prey (Hinrichsen et al., 2005); or (v) indices of juvenile particle density at the end of a simulation to look for density-dependent processes related to recruitment (Baumann et al., 2006).

Indices may be compared with data, for example, surveys of prerecruits or recruits. Indices may also be compared with stock-assessment model estimates of recruitment. In this case, caution is needed. The same data may be used in the ICPBM and the stock-assessment model (e.g. spawning-stock biomass); therefore, the indices produced by the two models may not be independent.

The proper choice of recruitment indices will depend on the objectives of the work, the life history of the species, and theories (conceptual models) of what processes are critical to recruitment variability. The development of a conceptual model (see Section 6.4) can aid in the choice of indices.

6.4 The need for a conceptual model

Development of a conceptual model of the processes controlling recruitment for each species and area is key to the use of ICPBMs in recruitment prediction, and also to the choice of the proper indices derived from the models. Development of a conceptual
model is a way of organizing what is important, the importance of the roles played by particular processes, and what life stages are affected. If this is neglected, important factors or processes may be missed in the ICBPM.

- Life stages and their duration
- Variation in mortality at each stage
- Biological and physical factors affecting each stage and the “intensity” of the effect
- Processes important within each stage

If different processes at different life stages are thought to be important, it may be necessary to develop different conceptual models for the same species in different areas. For example, the walleye pollock conceptual models for the Gulf of Alaska (http://www.pmel.noaa.gov/foci/forecast/mgt.html; Figure 6.4.1) and Bering Sea (http://www.pmel.noaa.gov/loci/sebscc/results/megrey/bs_concept.html; Figure 6.4.2) contain the same life stages and duration, but they differ with respect to which life stages experience the most variability in mortality and the factors that influence mortality and survival. Therefore, somewhat different ICPBMs have been developed, and different indices may be necessary to predict recruitment.

![Diagram](Image)

Figure 6.4.1. Gulf of Alaska walleye pollock conceptual model (from Megrey and Wespestad, 1997).
Conceptual models are not stagnant. They evolve as new information and understanding become available. For example, the original Gulf of Alaska pollock conceptual model (Figure 6.4.1) has recently been modified to include the effects of regime-scale climate impacts, as well as predation and competition effects (species-to-species interactions) known to be important at the ecosystem level (Bailey, 2000; Bailey et al., 2005; Megrey and Macklin, unpublished report).

6.5 Forecasting accuracy

How accurate do recruitment forecasts have to be before they become useful? This is a difficult yet relevant question that needs immediate research attention. A recent paper by De Oliveira and Butterworth (2005) offers a concrete example of a possible approach. The premise in this paper was that environmental indices that provide short-term predictions of recruitment have the potential to improve the average yield from highly productive resources that sustain recruit fisheries without an associated increase in risk (of resource “collapse”). This paper’s authors asked the question, how accurate does an environment-dependent, spawner–recruit relationship have to be before it affects management decisions? Specifically, what are the benefits of using environmental indices to set appropriate total allowable catches? Through a controlled simulation experiment, they concluded that an environmental index needs to explain roughly 50% or more of the total variation in recruitment ($r^2 \geq 0.5$) before the management procedure starts revealing benefits in terms of the summary performance statistics for risk and average catch. Having similar quantitative information on recruitment forecasts from ICPBM models would help frame the circumstances in which it could prove to be of benefit.

If an index derived from an ICPBM is to be used for recruitment forecasting, it is critical to assess its accuracy and to build trust in its ability to forecast.

6.6 Techniques for forecasting

Forecasts can take many different forms. They can take the form of quantitative annual estimates of absolute abundance (e.g. there will be 5.5 billion recruits next year). We do not believe these are very useful, and they are difficult to produce with any
accuracy and precision. They can also be qualitative. For example, the forecast could be given in terms of recruitment being in a particular state—below average, average, and above average (low, medium, and high)—with appropriate methods used to define, in operational terms, states such as long-term averages or quantiles (33%, 50%, or 66%) based on observed recruitment trends. Rothschild and Mullen (1985) give a good example of how recruitment information (from data or models) can be usefully described by non-parametric classification based on Markov chains. Finally, a recruitment forecast could be the result of an ensemble estimate from numerous stochastic-forecast implementations. The forecast can be delivered as a probability statement; for example, the probability of achieving a given recruitment level or state based on x conditions and y assumptions is 10%. The most appropriate form depends on many factors including many that have been discussed above, such as for whom the forecast is being prepared, how it will be used, the required accuracy, and the required forecast horizon.

A caution should be offered regarding the use of recruitment estimates from stock-assessment models to calculate metrics as described above. Changes/updates in annual stock-assessment/cohort-analysis models and resulting recruitment estimates make the most recent estimates of “recruitment” somewhat of a moving target. Stock-assessment models estimate recruitment by summing all fish from a cohort (all individuals with the same birth year) that have died as a result of the fishery (i.e. the catches) and then including the fish that have died from natural causes (also estimated by assuming a particular rate of natural mortality). In other words, the recruitment estimate is the population that would have existed in order to generate the observed catches. The data point of most interest is usually the current year. If a cohort is still contributing to the catch, then in next year’s assessment, an additional year of catches and losses from natural mortality will increase the recruitment estimate relative to the current year. The recruitment estimate will gradually increase over time and finally stabilize once the cohort is completely fished out (i.e. no more individuals of the cohort survive to add to the catches).

6.7 Philosophy of modelling

Approaches to understanding mechanisms that regulate recruitment in fish have increasingly taken an individual-based approach. This approach can be justified on two general grounds. First, field research into recruitment processes in fish has demonstrated that the individuals that survive early life often possess a unique suite of genotypic or phenotype traits that are not simply a random draw from the distribution present at spawning. For example, numerous studies involving otolith microstructure have demonstrated that survivors are selected from a narrow window of the original distribution of birthdates. Other research has revealed selection based on growth rate, size at settlement, spawning location, and maternal influence. Together, these studies have highlighted the fact that we would probably not understand mechanisms regulating recruitment by measuring mean rates; instead, we needed to characterize the sources, patterns, and consequences of variation among individuals in early life traits and understand why the unique subset of traits possessed by recruits conferred a survival advantage.

The second justification for individual-based approaches invokes the importance of spatial processes in regulating recruitment. Sinclair and Iles (1988) proposed a member-vagrant hypothesis in which population persistence relied upon the existence of closed trajectories that allowed surviving larvae to complete their life cycle. Those larvae that “followed” appropriate trajectories became members of the reproductive
population; individuals that “followed” inappropriate trajectories were lost to the reproductive population. This hypothesis, built on the existing understanding of the importance of population structure within a species, emphasizes the importance of the spatial location of larvae at different points in development on their subsequent survival.

Coupled physical–biological models addressing questions involving fish early life histories have typically adopted an individual-based approach. The majority of such models have used a grid-based hydrodynamic model to predict currents at nodes on the grid, which are then used in a Lagrangian particle-tracking algorithm to move particles that represent the early life stages around the model domain. For example, in one of the earliest applications of such models, Bartsch and colleagues (Bartsch, 1988, 1993; Bartsch et al., 1989) considered the trajectories of herring larvae in the North Sea. The model results indicated the importance of a retentive area off the east coast of Scotland. Subsequently, ICPBMs have become more sophisticated in both the representation of the current fields and the biological representation of individual fish. Such models have been used to quantify the contribution of different spawning locations to recruitment, the role of physical processes in regulating feeding, and the influence of mortality on spatial distributions.

However, it is vital to assess and separate the biological motivations for individual-based approaches to the study of fish populations from the computational motivation. Computationally, individual-based approaches are attractive because they elegantly combine the grid-based, spatially specific predictions of hydrodynamic models with biological processes. In so doing, such models portray individuals that differ with respect to their trajectories and thus their exposures to environmental forcing. To ease computational demands, population-level predictions are derived by expanding the predictions for a single particle by a multiplier to represent the contribution to the population. This approach implicitly assumes that all variability in early life history is spatially determined. Simply stated, this approach assumes that all variability is caused by differences among the trajectories followed by individuals, and not by inherent biological interindividual variability. The approach emphasizes the importance of member–vagrant-type ideas at the expense of phenotypic variability among individuals. Not all models make this assumption. A few do include and sample from distributions of traits. For example, in their detailed model of feeding, Fiksen and Mackenzie (2002) sampled from distributions of reactive distances to estimate feeding incidence. However, ICPBMs of the entire early life history that incorporate inherent interindividual variability have yet to be developed. Whether or not the development of such models is important depends entirely on how total phenotypic variability is partitioned between spatially derived sources and inherent interindividual differences. This partitioning is, as yet, unexplored and unquantified.