

### 3. Growth

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Decisions regarding the representation of feeding and growth in coupled physical-biological models of fish early-life history are intimately linked. The bioenergetics of individual fish represents an energy balance in which any excess energy resulting from the feeding process, once metabolic costs have been paid, can be invested in growth. The specific form of the functional relationship between feeding conditions (or a proxy of those) and growth may vary from a detailed bioenergetic description to a simple empirical, statistical relationship. Modelling the feeding process may not be necessary if the sole objective is to model growth itself, provided that there is no density-dependent impact of cohort abundance on food availability. A number of approaches, of varying degrees of complexity (from high complex mechanistic models to simple phenomenological models), have been successfully implemented in coupled physical-biological models. These include mechanistic bioenergetics models, empirical food-growth models and empirical temperature (age)-growth models. Here we examine each approach, identifying its strengths and weaknesses and providing recommendations for each category of growth model.

There are numerous examples of the application of mechanistic feeding models to forecast growth in coupled physical-biological models (Werner et al., 1994; Werner et al., 1995; Hermann et al., 1996; Hinckley et al., 1996; Werner et al., 1996; Fiksen et al., 1998; Fiksen and Folkvord, 1999; Leising and Franks, 1999; Hinckley et al., 2001; Megrey and Hinckley, 2001; Werner et al., 2001; Fiksen and MacKenzie, 2002; Lough et al., 2005; Maes et al., 2005; Kristiansen et al., in press). Many of these examples have a heritage that can be traced to individual-based models (IBM) in the ecological arena that considered feeding, bioenergetics and growth of larval fish in a simple well-mixed compartment (e.g. Cowan et al., 1993; Rose and Cowan, 1993; Letcher et al., 1996; Rose et al., 1996; Rose et al., 1999). At their heart these models used a simple stochastic scheme for determining encounters with food and whether consumption given encounter occurred. The estimates of consumption were then used in a simple bioenergetic model to forecast surplus energy and hence growth. When applied in a model of a simple well-mixed compartment, the approach assumes random encounters described by a Poisson process. It is conceptually straightforward to include the impacts of environmental factors such as light (Aksnes and Giske, 1993), temperature (Kitchell et al., 1977) and small-scale turbulence (MacKenzie et al., 1994) provided that the distributions of these parameters are known. Parameter estimates used in the models should be specific to the species and ontogenetic stage being modelled and population-specific when evidence suggests it is necessary. Modellers can choose to make parameter values a characteristic of the individual, by drawing parameter estimates from appropriate statistical distributions, or chose to update parameter estimates dynamically to reflect the different histories and trajectories of each individual (Rice et al., 1993). However, the accuracy and precision with which the distribution of these environmental covariates can be defined does introduce uncertainty into predictions of foraging rates (e.g. contrast Sundby, 1997; Visser and MacKenzie, 1998)

There are numerous challenges when applying mechanistic feeding and growth models. The highly detailed nature of these approaches requires a large number of parameter estimates and functional relationships. For example, in their model of the effects of small-scale turbulence on feeding and growth of walleye pollock, Megrey and Hinckley (2001) required estimates for

119 parameters. Thus, application of this approach to any species and ontogenetic stages that have not been very comprehensively studied either requires a substantial amount of prior experimental work (with the associated problems of ensuring realistic conditions applicable to field situations, etc.), or “borrowing” parameter estimates from taxonomically related species, a potentially risky approach given the degree of specialization that is often observed when related species are investigated in depth. Even where this is not a concern, encounter processes between planktonic predators and prey are generally not well quantified. This area is a focus of considerable research (Visser and Kiorboe, 2006) and, while it is beginning to be better understood, empirical work remains a critical need. Inferential approaches can be used to select among alternative parameterizations (Megrey and Hinckley 2001; Fiksen and MacKenzie, 2002; Lough et al., 2005) and sensitivity analysis should be carried out, to inform the modeller about the level of effort worth putting into the detailed parameterization of individual processes. Thus the application of process specific bio-physical models may help inform our understanding of the importance of individual steps in the feeding cycle or growth bioenergetics on recruitment. Within coupled physical-biological models, application of mechanistic growth models presents special challenges. Models require forecasts of the prey community and the physical environment at perhaps two to four orders of magnitude smaller than the minimum horizontal resolution of the hydrographic model. Importantly, many hydrographic properties used in mechanistic feeding models are likely not well conserved. The issue of sub-grid processes in physical parameters has already been discussed in a previous section. The issue of sub-grid processes in biological variables is, if anything, even more challenging. This also includes vertical processes, since vertical environmental gradients are typically strong, and this imposes a particular challenge in modelling the vertical positioning of predators, larval fish and their prey.

Other approaches used to model growth rely on empirical relationships. The independent variables in these phenomenological models differ but often include fish age and temperature (Heath and Gallego, 1997; Heath and Gallego, 1998; Brickman and Frank, 2000; Brickman et al., 2001; Mullon et al., 2003; Suda and Kishida, 2003). This approach is motivated by concerns over the accuracy of the representation of sub-grid scale processes in the hydrographic model, as well as other physical and biological variables not necessarily predicted by it, like light, turbidity, and prey fields. The conservative nature of temperature means that it is less sensitive to sub-grid scale concerns, except in the vertical in stratified regions, and therefore likely a reliable foundation for spatially-explicit predictions of growth. Additionally, the approach has the advantage that there is no need to model prey populations, since it is assumed that temperature, in addition to its direct (physiological) effect, acts as a proxy for the environmental changes that tend to correlate with the seasonal temperature cycle (e.g. food availability, daylight length, light intensity, etc.). However, there are also potential pitfalls to this approach if the underlying temperature-dependent growth model is incorrectly parameterized or applied to a population for which it was not developed (Folkvord, 2005). The parameterisation of a temperature-dependent growth model may not be as straightforward as it seems. In particular, matching the spatial scale of the larvae with that of the temperature field can be difficult. For example, earlier approaches (e.g. Campana and Hurley, 1989) used daily temperature estimates for the area of interest (Browns and Georges Banks), common to all larvae in the area, while Gallego et al. (1999) used a particle-tracking model projecting individual larval trajectories over a spatially- and temporally-resolved temperature field to estimate the daily temperature history of individual larvae. Additionally, the phenomenological models are often based on the observed growth of

survivors, which may be different from the average growth observed in the cohort from which they were derived (Meekan and Fortier, 1996). However, Folkvord (2005) has demonstrated that field growth rates are often maximal, although Beaugrand et al. (2003) found that prey abundance influenced recruitment success of North Sea cod. When food is not included in the phenomenological model, the approach also implicitly assumes that there is no food-dependent growth variation, or that such variation is negligible, beyond what may be captured by temperature as a proxy variable. To address this concern, several authors (Leising and Franks, 1999; Bartsch and Coombs, 2004; Bartsch et al., 2004) have included food-dependency in the phenomenological model. This offers the attraction of coupling food to growth, but it reintroduces the difficulties over sub-grid scale predictions of prey distribution already discussed, even if these are generated externally to the model (Bartsch et al. 2004).

Growth and mortality are intimately coupled through a range of mechanisms such as size-dependent predation patterns, starvation and growth-dependent larval stage duration. These mechanisms have received well deserved attention from modellers for quite some time. But growth and mortality are also intimately coupled through larval behaviour, since behaviour promoting growth typically also increases the risk of predation (Lima and Dill, 1990; Walters and Juanes, 1993). Such processes have received less attention in fisheries oceanography, both empirically and in models, although they have been incorporated in ecosystem-based approaches (Pauly et al., 2000). One example is the trade off between being spotted by visually searching predators and the need to find food through visual detection of prey, which is the main forcing of diel vertical migration. Another example is the risk of encountering tactile or ambush predators through increased swimming activity, which also increases the encounter rate with potential prey items. There are also good reasons to argue that such behaviours are state and size-dependent, and that they interact with larval dispersal and drift trajectories. There is a need for approaches adopted from behavioural and evolutionary ecology to improve understanding of these processes.

Another issue is the need to separate between growth and development (ontogeny) in determining sensory and biomechanical abilities of larvae. All models of larval fish early-life history that include larval sensory or other abilities couple such traits to body size, with direct feedback on feeding history. In reality, ontogeny can proceed (for some time) without food supplies, improving larval abilities to find and capture prey, and presently we are ignoring this in our models. However, although some experimental work has already been carried out on the subject (e.g. Skajaa et al., 2004), a greater quantitative understanding of the relative importance of ontogeny vs. growth for predation vulnerability and foraging ability, for example, is still required for most species and ontogenetic stages.

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