4.0 Overview of modeling efforts - Cisco Werner and Dennis McGillicuddy

A variety of modeling approaches are being used in the Globec program to study how interactions between zooplankton population dynamics and physical circulation create space/time variability in abundance of the target species. Information on vital rates is essential to these efforts, although the means by which the vital rates data are used differs amongst the various applications. In the so-called "forward problem," a mathematical representation of the organism's population dynamics is incorporated into a circulation model. The coupled model is initialized with a set of observations, integrate forward in time and then compared with the next set of observations. A successful outcome results in minor discrepancies between observations and predictions, and the model solutions thus can be used as a basis for diagnosis of the processes controlling the observed behavior. Unfortunately, satisfactory completion of the forward problem is not always achievable due to limitations in the models, the observations, or both. Adjoint data assimilation methods provide an alternative approach which is particularly useful in such cases. These techniques can be used to determine the model inputs (*e.g.* parameters, forcing functions, *etc.*) that minimize the misfit between observations and predictions, thereby producing an optimal solution from which the underlying dynamics can be gleaned. Examples of both forward (Lynch *et al.*, 1998; deals with *Calanus finmarchicus*) and inverse (McGillicuddy *et al.*, 1998; deals with *Pseudocalanus, spp.*) approaches are described below.

Individual based models (IBMs) represent yet another approach to coupled physical–biological problems of this sort. In this technique, the equations representing the organism's population dynamics are integrated on ensembles of lagrangian particles which are moved about by the prescribed circulation. A major advantage of this approach is that diagnosis of the simulated physical–biological interactions along lagrangian trajectories is relatively straightforward. However, it is often impractical to compute enough ensembles to generate eulerian field estimates with robust statistics. Miller *et al.* (1998) used an IBM for *Calanus finmarchicus* in the Gulf of Maine / Georges Bank region, and results from that effort are described briefly below.

Linking zooplanktonic trophodynamic models to larval fish models is in its initial stages. The full coupling will require 3-D and time-dependent representation of physical and biological variables, some of which are still uncertain, such as behavior, prey preference, etc. However, a simple conceptual model has been developed for larval fish feeding on stage-structured prey populations, in an Eulerian framework (Lynch *et al.* 2000; see description below). The model combines simplified contemporary models of larval fish trophodynamics, zooplankton population dynamics, and hydrodynamic turbulence. The Eulerian view allows instructive maps of larval feeding and (potential) growth rates for individual prey species, alone or in combination.

4.1 An example of the forward problem: Biological/physical simulations of *Calanus finmarchicus* population dynamics in the Gulf of Maine (Lynch *et al.*, 1998).

A site-specific, coupled biological/physical model is described for the dominant winter-spring copepod in the Gulf of Maine (Figure 1). The biological portion describes temperature- and food-dependent progression through 13 life stages in an Eulerian (concentration-based) framework. The population is transported in a flow field depicting the climatological mean conditions in 2-month "seasons". Behavioural assumptions account for depth selection and two limiting cases are contrasted: dispersal throughout the water column, and aggregation in the surface layer. Simulations are inspired by MARMAP observations, with an emphasis on the mid-winter initiation of the annual bloom by diapausing populations, and their role in supplying reproducing populations to Georges Bank during spring.

Mathematically, the population dynamics expressed on the right hand side of the advection-diffusion-reaction equation in Figure 1 represents a conveyor belt among 13 successive life history stages:

$$R_i = \frac{C_{i-1}}{D_{i-1}} - \frac{C_i}{D_i} - \mu_i C_i$$

with D_i the stage duration and μ_i the mortality rate for stage i. Appropriate adjustments at the end points and adult branch points are implied. Stages with duration exceeding 1 day (at $5°C$) are subdivided to control developmental diffusion which is inherent in the Eulerian approach.

Average developent times D_i are sensitive to both temperature and food availability. Generally, increasing temperature T decreases the stage durations, D_i. These are traditionally related through Belehradek equations of the form $D_i(T) = a_i(T - \beta)^\alpha$, where β and α are constants and a_i is a stage varying parameter. Parameters used in this model for Egg through C5 are based on a recent rearing experiment by Campbell *et al.* and appear in Table 1. The estimate for immature females is based on Plourde and Runge (1993). Stage durations of males and mature females are treated as infinite.

Food effects are less precisely known. The stage duration equation above holds for maximal development rate assuming non-limiting food concentrations ($\geq 400\mu gC/l$). We assume that Eggs, N1 and N2 do not feed (Marshall and Orr, 1955; Carlotti and Radach, 1996). For the other stages, we expect that stage durations will increase as food concentrations are reduced. Campbell *et al.* (1998) indicate an increase by almost a factor of 1.5 for food levels of 50 $\mu gC/l$ and a factor of 2 for food levels at $25\mu gC/l$. Durbin et al (1995) observed stage durations of 24.8 days for C4's at 11° in the field, under food limited conditions.

Completion of the final stages of oogenesis is highly dependent upon external food supply (Plourde and Runge 1993; Runge and Plourde 1996; Hirche 1996a; Niehoff and Hirche 1996). Thus the stage duration of the immature female is lengthened as food abundance is reduced. The literature suggests that development in the field can be delayed by as much as 1 month (Hirche 1996a) when food is scarce. This could have a significant effect on the first generation as it would delay its initiation and displace it "downstream" in the advective system.

As a point of departure, food effects on development are modeled by decreasing development rate ($\frac{1}{D_i(T)}$) linearly toward zero when food is below a satiation value. (Equivalently, development time varies inversely with food availability, with the Belehradek function representing the lower limit.) The baseline parameters used are summarized in Table 1.

Spawning is an intermittent process. A mature female releases a clutch of eggs over a short period of time (minutes) with longer time intervals (of order 1 day) between clutches (Hirche, 1996a). Generally the interclutch interval d is considered to be sensitive to variations in the environment, while by comparison the clutch size is relatively insensitive. Averaging over many individuals, we model this as a continuous process with constant clutch size of 50 eggs per female:

$$R_e = \frac{50C_F}{d} - \frac{C_e}{D_e} - \mu_e C_e$$

Both laboratory and field experiments have found temperature and egg production to be positively correlated (Hirche 1990; Plourde and Runge 1993; Hirche and Kwasniewski 1997; Runge and Plourde 1996; Hirche et al. 1997). Miller *et al.* (1997) fit the Hirche *et al.* data for clutch interval variations with temperature using the Belehradek function $d = 218 * (T + 9.11)^{-2.05}$, and we use this relation in table 1. This relation holds for superabundant food levels ($> 400\mu gC/l$ in Hirche, 1990). As food concentration is reduced, egg production decreases with a few days time lag before the effect is seen (Runge and Plourde 1996; Hirche 1990). In laboratory experiments at lower levels ($< 300\mu gC/l$), Hirche and Kwasniewski (1997) observed both a tendency for increased interclutch interval and decreased clutch size. Plourde and Runge (1993) also saw pronounced reduction in egg production in the field for ambient levels $< 1.25\mu gChl/l$. We approximate this effect in the same way as development rate: decreasing the egg production rate linearly to zero when food is below a satiation value ($150\mu gC/l$). Like the food effect on female development, this is a critical parameterization relative to the initiation of Generation 1.

Stage-dependent mortality is represented. Generally, it is assumed highest for earlier life-stages stages (Aksnes and Blindheim 1996). Male mortality is assumed higher than female mortality (a factor of 5 herein), reflecting observations of relative abundance in the field. Predation is likely to be the dominant source of mortality (Davis 1984a,c; Madin et al 1996; Sullivan and Meise 1996) at least over Georges Bank. It is not easily quantified. Predation risk from visual predators would decrease with depth (Aksnes and Blindheim 1996); and diel migration may be triggered by the presence of predators (Durbin et al., 1995). At this time, the details of predator abundance and distribution, and the behavioural response to same, must await a fuller understanding.

Temperature and food effects on mortality are not represented directly. Hirche(1987) found that the animal has a high tolerance to temperature variation. One direct effect of food limitation would be to increase the susceptibility to predation (Kleppel et al. 1996); but we have insufficient empirical support. The effects of temperature and food on stage duration, and therefore on exposure to early stage predation, are captured as indirect effects. Another direct effect would be that of female diet on viability of eggs and early nauplii (Laabir et al., 1995; Uye, 1996). This is not represented; instead it is bundled into the limitation on egg production, avoiding the production of eggs which are not viable through stage N2. We have adopted baseline mortality estimates in Table 1 as lower limits. Additional detail must be inferred at present.

Baseline population dynamics are initiated on January 1 by activating a diapausing population (G_0) based on 10-year mean abundance and distribution from the MARMAP program (Figure 2). The abundance and distribution of G_0 adults is reproduced with a three-layer model, spatially variable mortality, an extended period of activation, no food limitation, and a large, heretofore unobserved source of diapausing C5's near-bottom.

Reproduction modeled in this system shows significant development of generation 1 (G_1) over the Gulf of Maine in February-March, which is not observed (Figure 3). Delay of

Table 1: Vital Rates for *Calanus finmarchicus* (days), at 5°C and 10°C. Development times are given by the Belehradek form $D(T) = a(T - \beta)^{\alpha}$ with $\alpha = -2.05$ and $\beta = -9.11°C$.

	Belehradek a	D(5°C)	D(10°C)	Satiation, $\mu gC/l$	Mortality, %/day
Eggs	595	2.62	1.41	-	20
N1	387	1.70	0.91	-	15
N2	582	2.56	1.38	-	15
N3	1387	6.10	3.28	100	15
N4	759	3.34	1.79	100	15
N5	716	3.15	1.69	100	15
N6	841	3.70	1.99	100	15
C1	966	4.25	2.28	150	5
C2	1137	5.00	2.69	150	5
C3	1428	6.28	3.37	150	5
C4	2166	9.53	5.12	150	5
C5	4083	17.97	9.65	150	5
Males	-	-	-	-	10
Immature Females	1757	7.73	4.15	150	2
Mature Females	-	-	-	-	2
Interclutch Interval	218	0.96	0.52	150	-
Diapause	-	-	-	-	1

reproduction over the Gulf, and/or severe early-stage mortality, is required to conform with the data. The space-time pattern of this effect is consistent with the observed chlorophyll distribution and timing, and reasonable food-limitation thresholds. Inclusion of this effect initiates the spring *Calanus* bloom in the correct space-time pattern, with significant cohorts of G_0 females and G_1 nauplii over important cod and haddock spawning grounds on Georges Bank. The implication is that G_1 is locally spawned in food-rich waters over Georges Bank by females advected in the food-poor Gulf of Maine surface layer.

4.2 An adjoint data assimilation approach to diagnosis of physical and biological controls on *Pseudocalanus* spp. in the Gulf of Maine - Georges Bank region - McGillicuddy *et al.* (1998).

An adjoint data assimilation approach has been used to study the seasonal variation in climatological abundance of the calanoid copepod *Pseudocalanus* spp. in the Gulf of Maine - Georges Bank region (McGillicuddy *et al.*, 1998). The physical basis of the coupled system is the Dartmouth finite element model, which has been used extensively to simulate the circulation in this region (Lynch *et al.*, 1996). The adjoint method is used to invert for the population dynamics which are consistent with changes in *Pseudocalanus* spp. abundance and the physical transports specified by the hydrodynamic model. An illustrative example of the results from McGillicuddy *et al.* (1998) is shown in Figure 4. From the period January-February to March-April, the inferred biological source term consists of strong growth (red shading) on the crest of the bank and moderate growth (yellow shading) in a coastal strip just offshore of Cape Ann. In the latter location, physical transport has little impact, resulting in a modest accumulation of animals in an area coincident with the patch of local growth. The situation on Georges Bank is quite different, where a balance exists between the advection and source terms. Flow onto the crest across the northern flank of the bank imports low concentrations of animals from the interior of the Gulf of Maine. This results in a strong negative contribution from the divergence of the advective flux. Similar in pattern, of opposite sign, and stronger in magnitude, the source term overshadows advection such that the tendency is for concentration on the bank to increase. Notice that the peak in the source term is slightly "upstream" of the resulting maximum in animal abundance. Diffusion contributes very little to the overall balance of terms in these simulations.

McGillicuddy *et al.* (1998) show that these spatial patterns in net population dynamics vary seasonally according to the animal distributions, the climatological currents, and their orientation with respect to each other. In cases when the flow is either weak or aligned with gradients in organism abundance, changes in concentration over time are dominated by local population dynamics. In situations where the currents are normal to these gradients, complex three-way balances arise between the local tendency, advective transport, and the population dynamics source term. With some notable exceptions, the inferred population dynamics appears generally consistent with what is known about ecological controls such as food limitation and predatory consumption. These inverse calculations do not necessarily produce an incontrovertible representation of reality, but they do provide a mathematical formalism for backing out the ecological variables controlling population distributions. This work is at the very beginning of a scientifically iterative process by which forward and inverse approaches are used in tandem to systematically refine each other.

4.3 Coupling of an Individual-Based Population Dynamic Model of *Calanus finmarchicus* to a Circulation Model for the Georges Bank Region (Miller *et al.*, 1998)

An individual-based life history and population dynamic model for the winter-spring dominant copepod of the subarctic North Atlantic, *Calanus finmarchicus*, is coupled with a regional model of advection for the Gulf of Maine and Georges Bank. The population dynamics model is similar to that used in Lynch *et al.* (1998) described above. Large numbers of vectors, each representing individual copepods with elements for age, stage, ovarian status and other population dynamic variables, are carried in a computation through hourly time steps. Each vector is updated at each time step according to development rate and reproductive functions derived from experimental data. Newly spawned eggs are each assigned new vectors as needed. All vectors are subject to random mortality. Thus, both life history progression and population dynamics of *C. finmarchicus* are represented for the temperatures in the Gulf of Maine-Georges Bank region in the active season. All vectors include elements representing depth, latitude and longitude. This allows coupling of the population dynamics to the tide- and wind-driven Dartmouth model of New England regional circulation. Summary data from the physical model are used to advance vectors from resting stock locations in Gulf of Maine basins through two generations to sites of readiness for return to rest.

An example of model output is shown in Figure 5, in which an ensemble of particles were released from Jordan Basin. In general, supply of *Calanus* stock to Georges Bank comes from all of the Gulf and from the Scotian Shelf. The top of the bank is stocked from western Gulf basins; the Northeast Peak is stocked from Georges Basin and the Scotian shelf. All sources contribute to stock that accumulates in the SCOPEX gyre off the northwest shoulder of Georges Bank, explaining the high abundance recurringly seen in that region. There is some return of resting stock to Wilkinson Basin in the western Gulf, but other basins must mostly be restocked from upstream sources to the northeast. An electronic archive of these results is available in animated form at
`http://www-nml.dartmouth.edu/Publications/internal_reports/NML-98-7/`

4.4 An example of an Eulerian-based/diagnostic approach to linking stage-structured models of zooplanktonic target species and larval fish growth models: Can Georges Bank Larval Cod Survive on a Calanoid Diet? – Lynch *et al.) (2000)*.

A simple conceptual model was developed for larval fish feeding on stage-structured prey populations, in an Eulerian framework. The model combines simplified contemporary models of larval fish trophodynamics, zooplankton population dynamics, and hydrodynamic turbulence. The Eulerian view allows instructive maps of larval feeding and growth rates for individual prey species, alone or in combination.

Decadally-averaged MARMAP surveys of *Calanus finmarchicus* and *Pseudocalanus* spp. were analyzed for the March-April period. Quasi-static population dynamics were used to infer the abundance of the smallest stages from adult female abundance. Computed growth rates show that *Calanus* alone is insufficient

to support the smallest cod larvae (4 and 6 mm), but provides good growth ($\geq$ 10% /day) for large larvae (10, 12 mm); see Figure (6a). *Pseudocalanus* **alone provides generally good growth for all larvae but is mismatched spatially with observed cod spawning and subsequent larval advection; see Figure (6b). Both species together provide good growth, matched spatially with larval cod, for 6 mm and larger larvae; see Figure (6c). A dietary supplement beyond these two species is needed for the smallest (first feeding or yolk-sac) larvae.**

The procedure provides a general method for mapping observations of zooplankton abundance, distribution and reproductive status, and their relevance to larval fish survival. Future work is recommended: continued scrutiny of the turbulent predator/prey interaction is essential; the break point between growing (6 mm and larger) and starving (4 mm) larvae in this study is very sensitive to this parameterization. The role of *Calanus* **eggs in larval fish diet deserves careful evaluation, as they are a major contributor to these modeled rates. Relaxation of the various simplificatons to the population dynamics is an obvious need, and will add considerable complexity to these simple maps. The 2-D analyses used herein need obviously to be generalized to 3-D.**

A postscript version of this paper available at
`http://www-nml.dartmouth.edu/Publications/external_publications/PUB-99-1/`

Figure Captions

Figure 1 (model.ps): The coupled physical/biological model.

Figure 2 (g0.ps): Simulations of generation 0.

Figure 3 (g1.ps): Simulations of generation 1.

Figure 4 (adjoint.eps): Bi-monthly climatological *Pseudocalanus* spp. distributions (adults only) derived from the MARMAP data (number of animals per m^3) for (a) January-February, and (b) March-April. Panel (c) below shows the source term $R(x, y)$ which results from the population dynamics inversion. The remaining panels show the remaining terms in the ADR equation averaged over the period of integration: advective flux divergence (d), diffusive flux divergence (e), and overall tendency (f). Fields in the bottom four rows have been normalized to the bottom depth, so the units are number of animals per m^4 per second. The sign convention is such that the overall tendency equals the sum of advection, diffusion and source terms.

Figure 5 (jord6.ps): An example of IBM output, in which an ensemble of particles were released from Jordan basin.

Figure 6a (CalanusPG.ps): Growth rates (% per day) for larval cod feeding on *Calanus finmarchicus*. Adult concentrations from MARMAP; stage-structure from population dynamics; turbulence from the circulation model. Grey indicates negative growth; regions of 'good growth' (10% /day or greater) are enclosed within the yellow line.

Figure 6b (PCalG.ps): Growth rates (% per day) for larval cod feeding on *Pseudocalanus*. Same detail as Figure 6a.

Figure 6c (CPCalPG.ps): Growth rates (% per day) for larval cod feeding on *Calanus* and *Pseudocalanus combined*. Same detail as Figure 6a.