Phytoplankton blooms and fish recruitment rate

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Abstract

The relationships amongst phytoplankton and zooplankton production, and fish larval survival to recruitment is examined through linking two generic models. It is first demonstrated that the phytoplankton-zooplankton models can be appropriately combined with a zooplankton-larvae-recruitment model. The combined model reveals some general principles. Recruitment tends to be a domed-shaped function of initial fish egg production. "Bloom" phytoplankton conditions are important for high recruitments. The timing and duration of fish egg production is important in determining recruitment through their impact on the phytoplankton bloom. It is argued that optimal recruitment would be obtained if the duration of larval feeding was less the duration of the phytoplankton bloom; a hypothesis which is testable.

1 Introduction

A key relationship in a dynamical evolution of fish populations is that between "stock" of adult fish of a particular species and "recruitment" of new adults to that stock at the end of their complex journey from egg to maturity. That this journey is fraught with perils is witnessed by the fact that, for example, a female cod lays about 20 million eggs in her life time. Put crudely, if two survive to maturity, we might expect (ignoring fishing) a fairly stable population; if only one survives we should soon see extinction. The majority of egg-production is lost during the planktonic egg stage. However, the duration of the larval stage is typically much longer than that of the eggs, and the larval daily mortality rates are comparable to those of the eggs (see *e.g.* (Harding, Nichols & Talbot 1978)). Larval life is also the period when density dependent regulation of fish populations occurs (Horwood, Cushing & Wyatt 2000).

During the major growth period, a substantial part of the food of the larvae takes the form of zooplankton; in the North Sea, for example, a large part of the food of cod larvae is made up of copepods, especially the calanoids. The character and effectiveness of the feeding strategies of the larvae, and their dependence on the physical environment, especially turbulence intensity, is the subject of much current research. An excellent overview is given in the papers contained in (Marassé, Saiz & Redondo 1997). More generally, the whole relatively poorly understood question of zooplankton population dynamics and its place in the marine ecosystem is the subject of major international research programmes under the overall aegis of GLOBEC. Whilst the lower echelons of the oceanic foodweb, linking herbivorous and omnivorous zooplankton species with photosynthesising phytoplanktonic species and their own nutrient have been extensively studied and modelled (see, *e.g.* (Edwards & Brindley 1999) and references therein), the link through predation of zooplankton by higher trophic levels has been relatively neglected, partly because of lack of observational data. A central objective of GLOBEC is to extend our understanding of this level of interaction through extensive (and expensive!) observational programmes supported and informed by mathematical and numerical modelling and simulation.

The fish-egg-larvae-recruitment cycle has also received wide attention because of its obvious importance to world food supplies. As remarked above, the hazardous progress from egg to mature fish is completed only by a tiny minority, and even at the larval state the survival rate after hatching is typically only c1% (Chambers & A.Trippel 1997). Nevertheless, though always a tiny minority of the hatching larvae, the number of those surviving to maturity and joining the adult fish stock is subject to huge relative fluctuations year by year, a matter of real concern for the fishing industry

Against this background, our main concern here is with the interaction of fish larvae, especially the gadoids, cod and haddock, with their principal planktonic food supply, exemplified in local UK waters and the NE

Atlantic by copepod species. Rather than the detailed form of the interaction, we concentrate on the life history and survival to recruitment of the larvae. Thus we assume simple functional forms and parameterisations at a population level of the interaction, exploring the sensitivity and robustness of recruitment predictions to these assumptions. In this spirit we adopt a mathematical formulation which links a simple model for stock recruitment (Cushing & Horwood 1994), afterwards abbreviated by [CH] with an equally simple model for plankton population dynamics ((Truscott & Brindley 1994), afterwards [TB]).

Briefly, the stock-recruitment relationship as modelled in [CH] depends on the amount of food available for larvae. This relationship has been found to be typically bell-shaped. For small numbers of hatched larvae, increase of their number leads to an increase of recruitment, as at metamorphosis. However, after a certain critical value depending on the availability of food, further increase of initial number of larvae leads to a decrease of recruits. The reason for that is that the large number of larvae consumes most of the available food while young, and then have less to eat while they grow; hence metamorphosis happens later and fewer larvae live long enough to reach it. The experimental evidence of the importance of plankton availability on the larval density dependent mortality has been reviewed *e.g.* in (Horwood et al. 2000).

In model [CH], the dynamics of the larvae food, the zooplankton, is very simple; an initial number of zooplankton is assumed to have a constant growth rate, and to be subject only to loss by grazing larvae. However, the dynamics of zooplankton itself depends on the amount of its food, and should change significantly, say, during the spring phytoplankton bloom. Phytoplankton-zooplankton (PZ) systems have been modelled by many authors; we choose the model [TB] as a simple model describing a phytoplankton bloom by a "prey-escape" mechanism; essentially an "excitable" phenomenon. In [TB], zooplankton mortality has been assumed constant, with no account taken of variations of populations or habits of predators.

In this paper, we take the very obvious step of coupling the models [CH] and [TB]. Thus the food source for fish larvae depends on the zooplankton dynamics, which in turn is coupled to larval populations through the zooplankton mortality term. Though the model is simple and abstract, it contains enough of the key influences and dynamics to throw light on the qualitative relationships between larval fish development and phytoplankton blooms, via the zooplanktonic intermediary. In particular it demonstrates the crucial importance of timing and temporal pattern of spawning relative to the plankton bloom dynamics. This sensitivity, coupled with similar sensitivity to initial populations, may go some way to explaining the observed large variations from year to year in recruitment. Section 2 contains a description of the mathematical model; in Section 3 we present a representative set of numerical results, spanning a range of parameter values used by other authors (see (Edwards & Brindley 1996)), and finally Section 4 discusses their character and significance. Notations are summarised in the Appendix.

2 The Mathematical Model

The model is constructed by coupling the [CH] model for fish recruitment with the plankton populations model [TB] through the zooplankton herbivore in [TB] which constitutes the food source for fish larvae in [CH].

2.1 A model for plankton dynamics

Turning first of all to the plankton population model, we have an equation for the phytoplankton, P, in the form

$$\mathrm{d}P/\mathrm{d}t = k_{\mathrm{TB}}\left(Pr_P(1 - P/P_{\max}) - GZ\right), \tag{1}$$

where $P_{\max}$ is the saturation limit for P and $G(P)$ is the functional form representing the grazing "strategy" of the zooplankton, Z. Following [TB], we assume a Holling type III form

$$G = r_Z P^2/(P_*^2 + P^2) \tag{2}$$

representing a grazing saturating at r_Z for large P, and varying like P^2 for small P. Some justification for such a form may be claimed where food supplies are patchy and zooplankton display some adaptability in their raptorial behaviour. But our main reason for selecting it is the indirect evidence that it yields results which bear a striking resemblance tot he behaviour of observed plankton populations, in which low equilibrium levels of P and Z can be triggered into bloom conditions in which P increases by an order of magnitude or more before falling back again as Z responds to the increased food supply.

In [TB], coupled to the P-equation was an equation for Z of the form

$$\mathrm{d}Z/\mathrm{d}t = Z\left(\gamma G - \mu_Z\right) - k_{\mathrm{CH}} R_{\mathrm{tot}}. \tag{3}$$

where γ is a measure of the efficiency of conversion of P biomass to Z biomass (in our present model, this equation is modified to account for the predation by larvae, see (15) below).

Clearly, $\gamma < 1$, and in [TB] it was assumed that $\gamma \ll 1$. Such an assumption ensures, indeed is necessary for, the occurrence of "excitability". Mathematically this means that some small initial disturbancies from equilibrium undergo a large excursion in phase space before returning to the equilibrium state. Biologically this large (and rapid) excursion represents a bloom, which might arise as one or more physical inputs are changed, for example by seasonal or locally more rapid changes in radiation (spring bloom), by nutrient inputs caused by oceanic upwelling associated with storm systems or by effluence from human activities (sometimes leading to toxic "red tides").

Less obviously, but importantly, the low value chosen for γ represents in a crude way the slower growth to maturity and fecundity of Z individuals. Though, at the *individual* level a conversion rate represented by $\gamma \propto 0.3 - 0.5$ seems reasonable, the [TB] choice of $\gamma = 0.05$ reflects the fact that at *population* level, only a small fraction of the Z population is contributing to the population growth; this is especially true in the circumstances of a bloom, when many of the grazing copepods will be too young to reproduce. A formal extension to age and/or size structured populations, reported in (Clother & Brindley 1999), supports this point and shows that *population* excitability is possible for much higher *individual* conversion rates.

2.2 A model for fish recruitment

The model described in [CH] needs rather more introduction, as follows.

Larva weight [CH] The individual larval weight, $W(a,t)$ is subject to the following constraints:

- Maximum larva weight gain rate per day

$$\Delta W_{\max} = r_L W. \tag{4}$$

- Metabolic costs of a larva per day

$$B_{\rm s} = \sigma W^n. \tag{5}$$

- Maximal amount of food a larva can eat per day:

$$R_{\max} = (\Delta W_{\max} + B_{\rm s})/\beta, \tag{6}$$

  where the conversion coefficient is weight-dependent,

$$\beta = \beta_{\max} - (\beta_{\max} - \beta_{\min})\exp(-jW). \tag{7}$$

- Maximal volume fraction a larva can search per day:

$$p(W) = kW^{\nu}. \tag{8}$$

Moreover, the amount of zooplankton eaten by individual larva per day is calculated according to Holling's type 1 kinetics

$$R(a,t) = \min(R_{\max}, p(W)Z). \tag{9}$$

Note that the argument a shows that this is the ration of the larvae age group a, and $R(a,t)$ will be used to calculate total amount of zooplankton eaten by larvae of all ages a at time t.

Then, assuming that the useful biomass obtained by a larva is a fraction of R,

$$B_{\rm o} = \beta R, \tag{10}$$

we find that the resulting rate of gain (or loss, if negative) in weight is given by

$$\mathcal{D}W/\mathcal{D}t = B_{\rm o} - B_{\rm s}. \tag{11}$$

Here and below, notation $\mathcal{D}/\mathcal{D}t$ stands for

$$\mathcal{D}X/\mathcal{D}t = \partial X/\partial a + \partial X/\partial t$$

in the age-structured case and

$$\mathcal{D}X/\mathcal{D}t = \mathrm{d}X/\mathrm{d}t$$

in the unstructured case, for any quantity X.

Note that, as a consequence of (9), $\mathcal{D}W/\mathcal{D}t \leq \Delta W_{\max}$ (time is measured in units of days).

In case of lack of food, Z, the weight of larvae given by the above equations may decrease or even become negative. This causes formal mathematical problems but in any case is not biologically sensible; if food is so scarce that larvae lose weight, they become extremely weak and quickly die out.

Since this does not happen in the examples used in this paper we ignore the possibility of weight decrease and do not include any terms that would describe corresponding increase in mortality.

Larva number density In the age-structured case, we denote $N(a,t)$ the number of larvae of age a days per unit volume at day t. In the unstructured case, the number density is simply $N(t)$. In either case, after hatching, this evolution means only decrease for every given group of larvae, for several different reasons:

- Non-specific mortality and predation. We assume the relative rate M of this mortality to be age-dependent, as in [CH]:
$$M = \frac{\mu_L}{1+ba}. \tag{12}$$
- Mortality due to starvation. This happens when the weight gain is negative, *i.e.* the metabolic demands are not covered by the amount of food available. In the numerics shown in this paper, this did not happen.
- Metamorphosis. We assume that metamorphosed larvae change their diet and thus withdraw from the considered trophic subsystem. In [CH], metamorphosis was assumed to happen always if a larva reached a certain age or a certain weight. To avoid formal problems related to sudden withdrawal of a whole subpopulation, and to account for intra-subpopulation diversity and for the graduality of the process of metamorphosis, we replaced this sudden transition with a continuous process, with the rate
$$T = C_{T,a} \exp\left(\frac{a-a_T}{\Delta a_T}\right) + C_{T,w} \exp\left(\frac{W-W_T}{\Delta W_T}\right). \tag{13}$$

The resulting decrease in the number of larvae is then described by

$$\mathcal{D}N/\mathcal{D}t = -N\,(M+T.) \tag{14}$$

Larval biomass The total biomass of larvae can now be calculated as

$$L(t) = \int W(a,t)N(a,t)\,\mathrm{d}a$$

for the age-structured model, simplifying to

$$L(t) = W(t)N(t)$$

for the unstructured model, *i.e.* when all larvae are assumed to belong to a single age cohort. This quantity does not enter anywhere else in the system of equations, and was used only for presentation of the results of the calculations.

2.3 The coupled system

Zooplankton biomass increases through consumption of phytoplankton and decreases because of predation by larvae as well as mortality for all other reasons *e.g.* predation by other species; we adopt a form of evolution equations which embodies either the TB or the CH form of biomass increase, viz

$$\mathrm{d}Z/\mathrm{d}t = Z\,(k_{\mathrm{TB}}\gamma G + (1-k_{\mathrm{TB}})r_{Z,0} - k_{\mathrm{TB}}\mu_Z) - k_{\mathrm{CH}}R_{\mathrm{tot}}. \tag{15}$$

Here

$$R_{\mathrm{tot}}(t) = \int R(a,t)N(a,t)\,\mathrm{d}a$$

for the age structured model, or

$$R_{\mathrm{tot}}(t) = R(t)N(t)$$

for the unstructured model, is total larvae predation rate per unit of zooplankton biomass and $r_{Z,0}$ is the constant source of Z biomass assumed in [CH]. Equation (15) reduces to the form of [TB] if $k_{\mathrm{TB}} = 1$, $k_{\mathrm{CH}} = 0$ and to the form of [CH] if $k_{\mathrm{TB}} = 0$ and $k_{\mathrm{CH}} = 1$; in our numerical calculations we take $k_{\mathrm{CH}} = k_{\mathrm{TB}} = 1$.

Metamorphosed larvae We calculate the biomass of metamorphosed fish via the metamorphosis rate and larva weight throughout all the age groups,

$$\mathrm{d}F/\mathrm{d}t = \int T(a,t)W(a,t)\,\mathrm{d}a,$$

for the age structured model, or

$$\mathrm{d}F/\mathrm{d}t = T(t)W(t)$$

for the unstructured model. Again, this quantity does not enter anywhere else in the system of equations, and was used only for presentation of the results of the calculations.

Initial conditions, hatching and aging In the unstructured model, N_0 represents the initial larvae number density as hatched at day t_i,

$$W(t_i) = W_0, \qquad N(t_i) = N_0, \tag{16}$$

assuming $N(t) = 0$ for $t < t_i$. The age argument a in the age-dependent functions M, T was then understood as the time since the hatching day t_i, *i.e.* $a = t - t_i$.

In the age-structured model, hatching dynamics were represented by initial conditions for the $a = 0$ boundary:

$$\begin{aligned} &W(t < t_i, a) = W_0, \qquad N(t < t_i, a) = 0, \\ &W(t \geq t_i, 0) = W_0, \qquad N(t \geq t_i, 0) = \begin{cases} N_0/t_h, & t < t_i + t_h, \\ 0, & t \geq t_i + t_h \end{cases} \end{aligned} \tag{17}$$

i.e. the initial weight W_0 was chosen the same for all hatching days, and the hatching rate was equidistributed in the interval from day t_i to $t_i + t_h$, with N_0 being total number of hatched larvae. As the time and age steps in the calculations were 1 day, the unstructured model was essentially a special case of the age-structured model with $t_h = 1$. This corresponds to an assumption of a conceptually isolated packet of water where only one lot of larvae are hatched.

Finally, the initial value of P and Z were taken as

$$P(0) = P_0, \qquad Z(0) = Z_0. \tag{18}$$

The mathematical model then comprises equations (1), (11), (14), (15), with boundary and initial conditions (16) to (18) as appropriate.

3 Numerical Results

3.1 Qualitative behaviour

Figures 1 and 2 illustrate the behaviour of the model at $k_{\mathrm{CH}} = 0$ and at $k_{\mathrm{TB}} = 0$ respectively, when the model is reduced to its prototypes [TB] and [CH].

The phytoplankton-zooplankton part of the model, corresponding to the [TB] prototype, exhibits excitable, threshold behaviour. This is illustrated on Figure 1, which shows solutions of the model at $k_{\mathrm{CH}} = 0$, *i.e.* with larvae dynamics switched off, and phyto- and zooplankton dynamics, including the parameters values, exactly as in [TB]. Two cases are shown, a subthreshold perturbation of the stable equilibrium, and a superthreshold perturbation which represents a phytoplankton bloom. In the the subthreshold case, the initial concentration of phytoplankton is chosen arbitrarily slightly above the equilibrium value. The resulting increase in phytoplankton biomass is relatively short and weak, and causes no substantial increase in zooplankton. In the superthreshold case, the initial concentration of phytoplankton is 2.5 times higher but its subsequent increase is rather prolonged, for about a month, very significant, by an order of magnitude, and leads to an order-of-magnitude increase in the zooplankton. Note that the post-bloom concentration of phytoplankton is much smaller than the pre-bloom, as it has been almost entirely consumed by the increased zooplankton. The exact value of the post-bloom phytoplankton is rather sensitive to the details of the model; however, within the framework of the model, this has little significance for the zooplankton dynamics, for which there is too little food anyway and where dynamics after the peak is a gradual decay determined by the mortality coefficient.

Figure 2 illustrates the behaviour of the model at $k_{\mathrm{TB}} = 0$, *i.e.* with phytoplankton dynamics switched off, and zooplankton and larvae dynamics, including the parameter values, exactly as in [CH]. The right panel illustrates stock-food-recruitment dependence, *i.e.* number of metamorphosed larvae as a function of initial

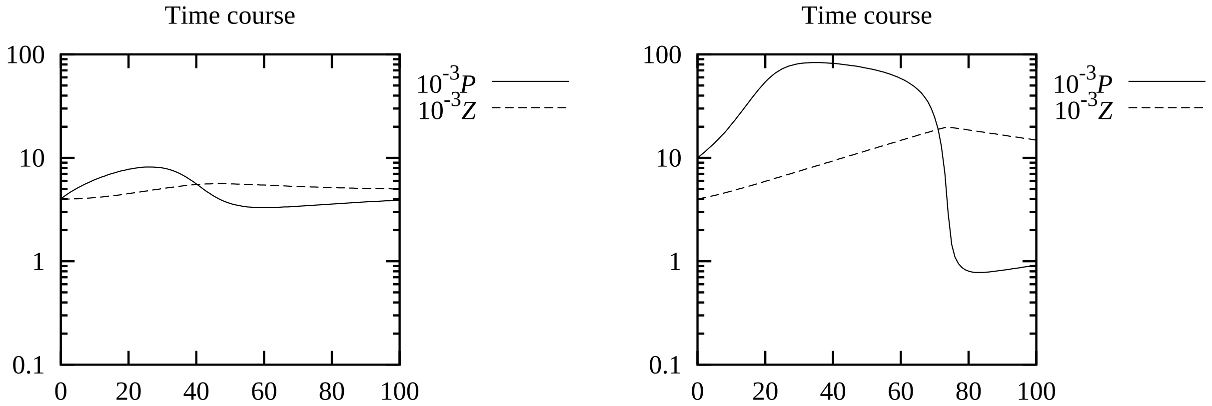

Figure 1: Trajectories for the PZ subsystem [TB] ($k_{\mathrm{CH}} = 0$). Two different initial conditions: subthreshold, $P_0 = 4 \cdot 10^3$ (left panel) and superthreshold, $P_0 = 10 \cdot 10^3$ (right panel).

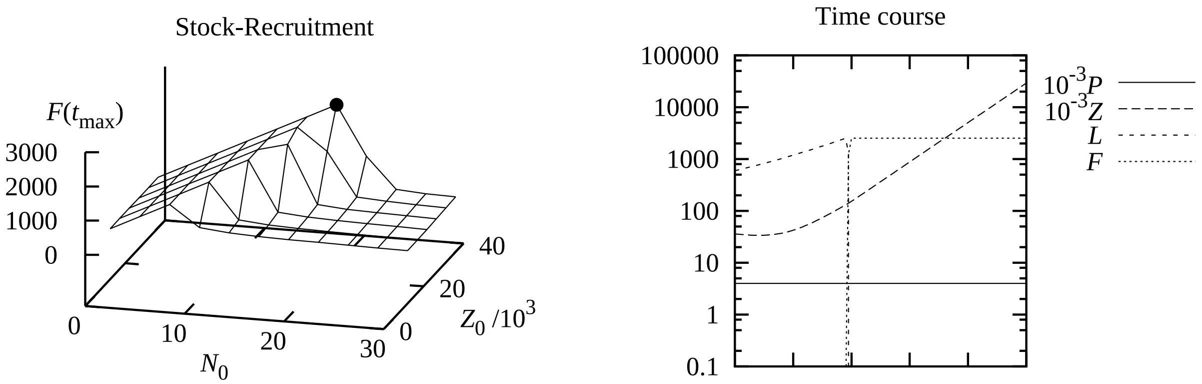

Figure 2: Stock-recruitment relationship (left panel) and time profile (right panel) the zoo-larvae subsystem [CH], $k_{\mathrm{TB}} = 0$. On this and later figures, the black dot on the left panel designates the point for which the time profile of the solution is shown on the right panel. Note that the initial value of Z on the profile here, $Z_0 = 40 \cdot 10^3$ is 10 times higher than $Z_0 = 4 \cdot 10^3$ in the [TB] model profile of Figure 1. The choice of parameters here corresponds to that considered in [CH].

larvae and zooplankton number, for other parameters fixed. The typical feature of this dependence, discussed in detail in [CH], is that for every value of Z_0, there is an optimal value of N_0, given by N_0^*. When $N_0 < N_0^*$, increase of N_0 causes increase of the recruitment, since their food is abundant and they always grow at maximal speed. When N_0 exceeds N_0^*, larvae consume more of the food while they are young; as they grow further the food is limited, and they take longer to reach the metamorphosis weight, leading to increased cumulative mortality and reduced recruitment.

Figure 3 illustrates the behaviour of the full model for the set of parameters given in the figure caption. This choice of parameters is not the standard choice of [CH], namely, the PZ subsystem is stronger, but is within the observed limits as reported in Edwards & Brindley (1996). Comparison of figures 2 and 3 shows that inclusion of the phytoplankton dynamics in this case does not change the dynamics of larvae qualitatively, and there is reasonable quantitative agreement; the large increase in Z on Figure 2 after day 50 has little effect on recruitment, which is completed by then.

We must however caution that not too much significance should be read into quantitative agreement. Quite modest variations of parameter values can cause large quantitative changes, as exemplified, for example, by Figure 4, calculated for the "standard" parameter values used by [TB] and [CH] respectively. In this case, the carrying capacity of phytoplankton as assumed in [TB] is very much lower than in Figure 3 and is not sufficient to sustain zooplankton concentration sufficient for the larvae development if their number is as large as in Figure 3. Similar qualitative behaviour is observed for correspondingly smaller larvae populations, but note the difference of scale of N_0 on Figures 4 and 3. We return to this point in the later discussion.

The time profile of the right panel of Figure 4 shows that the peak recruitment in this case has been achieved solely at the expense of the plentiful original stock of zooplankton which has been steadily decreasing throughout as the phytoplankton has been heavily suppressed; this is in contrast to the situation shown on Figure 3 where the zooplankton growth has been sustained by a phytoplankton bloom, despite grazing by larvae. This contrast between recruitment in Figures 3 and 4 poses a question, can the effect of a phytoplankton bloom enhance recruitment for *low initial values* of the zooplankton, and if yes, for what conditions? This has motivated the further study described below.

3.2 Exploiting the phytoplankton bloom

Numerical experiments with the model suggest that a rather delicate balance between initial conditions is required for fish larvae to benefit from the phytoplankton bloom. To illustrate this point, we show some representative examples. The left panel of Figure 5 shows that successful recruitment can be achieved either at large initial values of zooplankton Z_0, provided that the hatching larvae number N_0 is within reasonable limits (see the distant part of the graph), or for lower values of Z_0 (labeled by the black dot), provided that N_0 is rather precisely valued. For this case the initial biomass concentrations of phytoplankton was chosen at around the the bloom value. Deviation of Z_0 or N_0 to either side from their optimal values leads to a sharp decrease in the recruitment number.

The reasons for metamorphosis decrease away from this local maximum are illustrated on the next four figures, in which this particular example serves to illustrate several important sensitivites of wider importance. In theneral it is important that high Z lasts long enough for the metamorphosis to complete, which in turn requires that high P also lasts long enough. Thus we see that

- Hatching number N_0 lower than the local maximum point leads to slightly higher values of Z which cause the premature end of the phytoplankton bloom (Figure 6).
- Higher N_0 leads to a lower value of Z and retarded larvae growth, with consequent delayed metamorphosis and increased mortality, *i.e.* by the same mechanism as described in [CH] model (Figure 7).
- Lower Z_0, again, by standard [CH] mechanism, slows down larvae growth, and decreases recruitment via a delay of metamorphosis (Figure 8).
- And, finally, higher Z_0 leads to a premature suppression of the phytoplankton bloom, with subsequent reduction of zooplankton itself which, again, decreases recruitment (Figure 9).

3.3 The role of the hatching time

Success of recruitment depends not only on the parameters of the PZ subsystem, but also on the state in which this subsystem is at the day the hatching starts. The state of the PZ system will itself depend on the time. The next series of figures (10–13) illustrates the effect of different larval hatching times. The PZ system is started

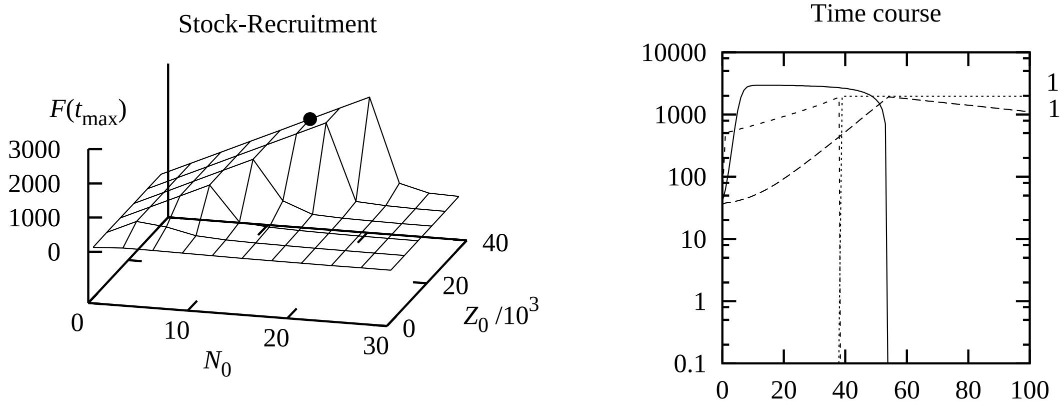

Figure 3: Stock-recruitment relationship and selected time profile and for the full model, *i.e.* $k_{\mathrm{TB}} = k_{\mathrm{CH}} = 1$, where parameters for the PZ subsystem were chosen to match the conditions considered in [CH] ($r_P = 1$, $P_{\max} = 3 \cdot 10^6$, $\gamma = 0.15$).

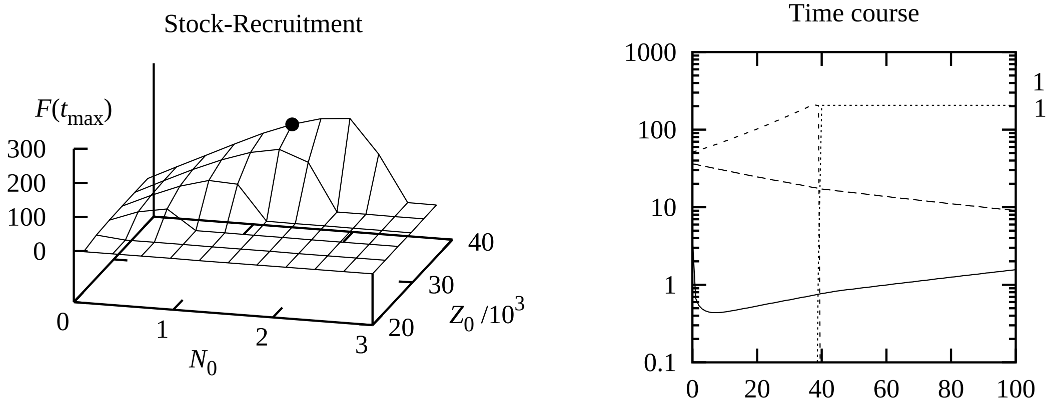

Figure 4: Time profile and stock-recruitment relationship for the full model for the standard set of parameters, in particular, $r_P = 0.3$, $P_{\max} = 1.08 \cdot 10^5$, $\gamma = 0.05$.

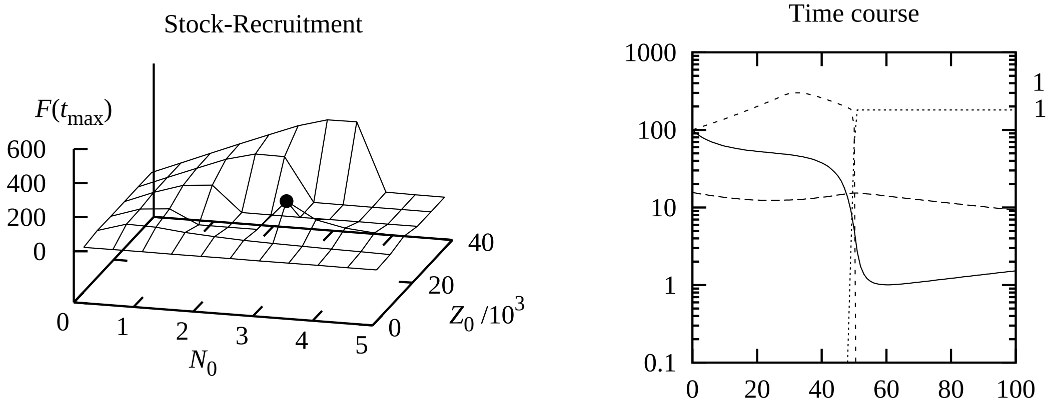

Figure 5: Local maximum of metamorphosis at relatively low initial values of zooplankton. Larvae take advantage of the phytoplankton bloom, ensured by its high initial value, $P_0 = 100 \cdot 10^3$. Other parameters standard.

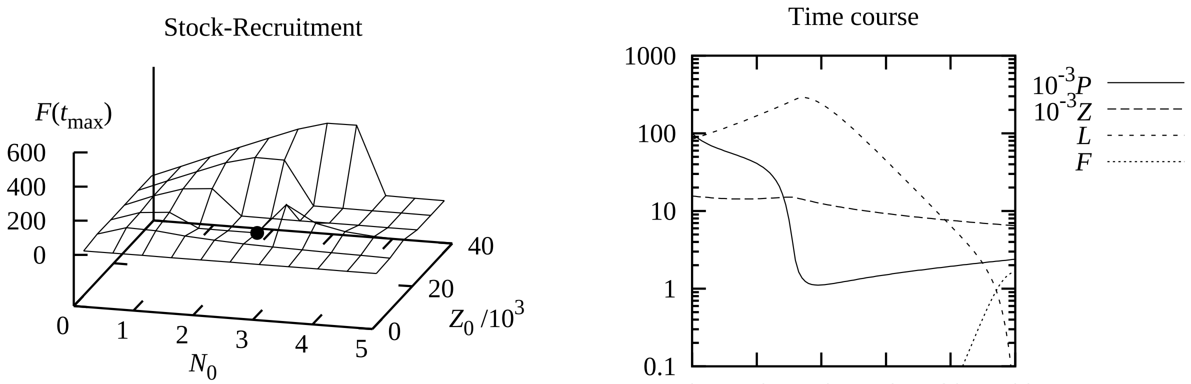

Figure 6: Same as Figure 5, with lower N_0

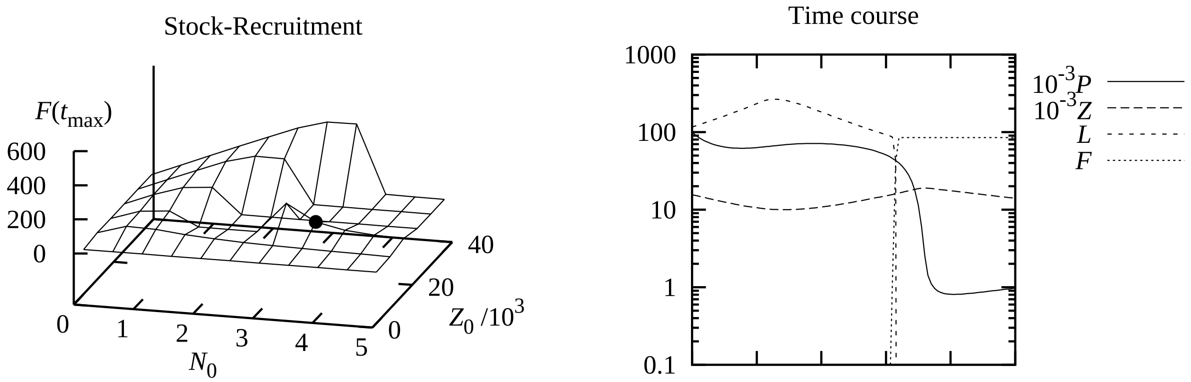

Figure 7: Same as Figure 5, with higher N_0

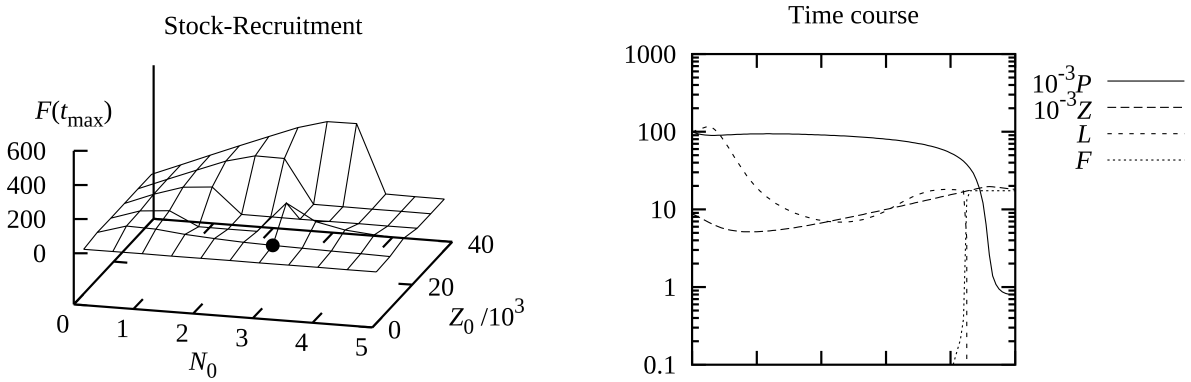

Figure 8: Same as Figure 5, with lower Z_0

at parameter values specified in the legends, and the beginning of hatching (t_i) and number of hatched larvae N_0 varied. The three-dimensional graph for the total biomass of metamorphosed larvae $F(t_{\max})$ as a function of these two varied parameters is shown on the left-hand panels; the right-hand panels, as before, show the time course of the main dynamic variables corresponding to the point represented by the black dot on the left panel.

Figure 10 is for parameter values for which in the absence of larvae there is no phytoplankton bloom, so that the PZ subsystem smoothly approaches the stable equilibrium from given initial conditions. This picture demonstrates a nontrivial emergent property of the model: triggering the phytoplankton bloom by hatching of larvae. The left panel shows that, at any value of t_i, the stock-recruitment dependence $F(t_{\max})$ vs N_0 has a characteristic Cushing-Horwoord bell-shape. The optimal point within the considered range of t_i and N_0 is shown by the black dot. The time course of the populations corresponding to this point, is illustrated on the right panel. In the interval of time between $t = 0$ and $t = 25$ the evolution of P and Z is the same as in Figure 1. The event of larvae hatching at day $t = 26$ causes a slight decrease in the zooplankton concentration, which triggers the prey-escape growth of the phytoplankton and subsequent period of bloom between approximately $t = 50$ and $t = 100$. However, by the time the phyto-plankton bloom has effect on the zooplankton population, most of the larvae have already died out so the the recruitment remains very low throughout the considered range of parameters. Thus, in the unstructured model, the effect of a larvae-triggered bloom is unlikely to have significant influence on the rectruitment.

For comparison, Figure 11 shows what happens if in the same plankton system, the same number of larvae hatches over a long period of time. In this case, the phytoplankton bloom caused by early hatched larvae is beneficial for later hatched larvae. The initial period (t between 0 and 50 days) sees development of the phytoplankton, then there is a long period (t between 50 and 100 days) of sustained growth of the zooplankton feeding on the abundant phytoplankton, and the larvae that hatched at the right time to grow up by the end of this bloom period have the best conditions for growth and best chance of survival. Due to the exponential dependence of the larvae survival on the right conditions, this increased chance of survival is more important than the decrease of the hatched larvae number per day because of its spread over a long period. Thus, the overall success in Figure 11, $F(t_{\max}) \approx 100\mu\text{g}/\text{m}^3$, is much higher than $F(t_{\max}) < 10\mu\text{g}/\text{m}^3$ in Figure 10 and is comparable to what is achievable in principle in the plankton system with these parameters, cf $F(t_{\max}) \approx 200\mu\text{g}/\text{m}^3$ on Figures 4 and 5.

As noted in James, Pitchford & Brindley (2001), a phytoplankton bloom initiated exclusively by larvae is unlikely; however, the effect of larvae may enhance the effect of the season and quicken the onset of the phytoplankton bloom. It is therefore interesting to study the success of the larvae in the conditions when the bloom is imminent even in the absence of larvae. This is illustrated on Figures 12 and 13.

Figure 12 shows the unstructured case. The pre-existing phytoplankton bloom has two major effects: (a) the recruitment can reach much larger values, and (b) to do so, hatching should be precisely timed with respect to the bloom. Note that on both figures 12 and 10, optimal recruitment is observed when the recruitment coincides with the end of the phytoplankton bloom.

Next Figure 13 illustrates the effect of spreading of the hatching over a significant period of time. It can be seen that the dependence remains qualitatively the same; the difference is that the dependence is smoother, and the peak recruitment results are slightly lower. The optimal timing in this case is when the *beginning* of the recruitment is at about the end of phytoplankton bloom.

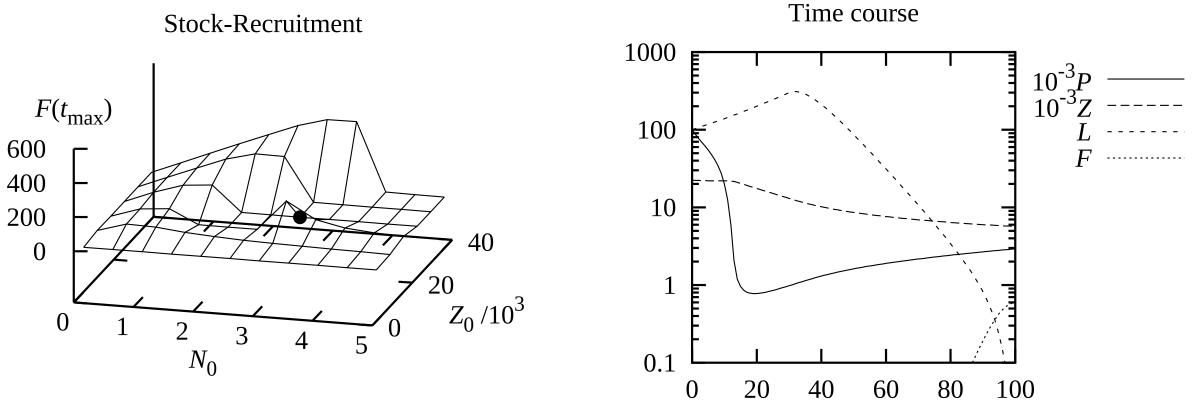

Figure 9: Same as Figure 5, with higher Z_0

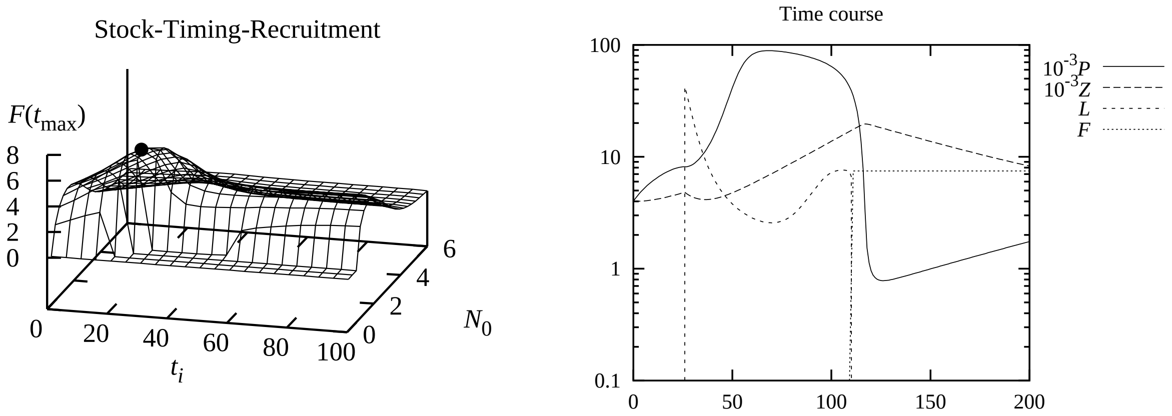

Figure 10: Stock-timing-recruitment relationship, standard set of parameters. Left: stock-timing-recruitment relationship: total biomass of metamorphosed fish, F, as a function of hatching larvae density N_0 and hatching time t_i with respect to the start of the phytoplankton bloom. Right: the time profile of the solution, corresponding to the black dot on the left panel.

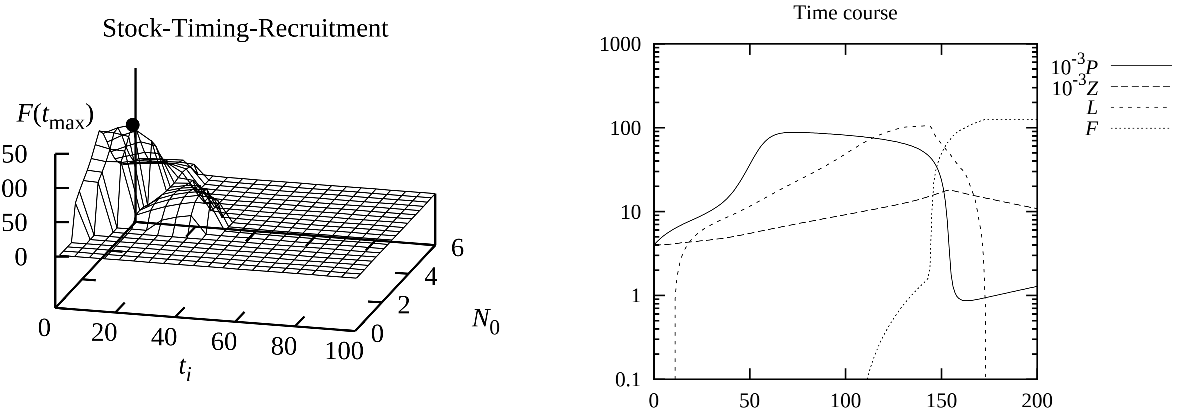

Figure 11: Same as Figure 10, but with hatching spread over 120 days.

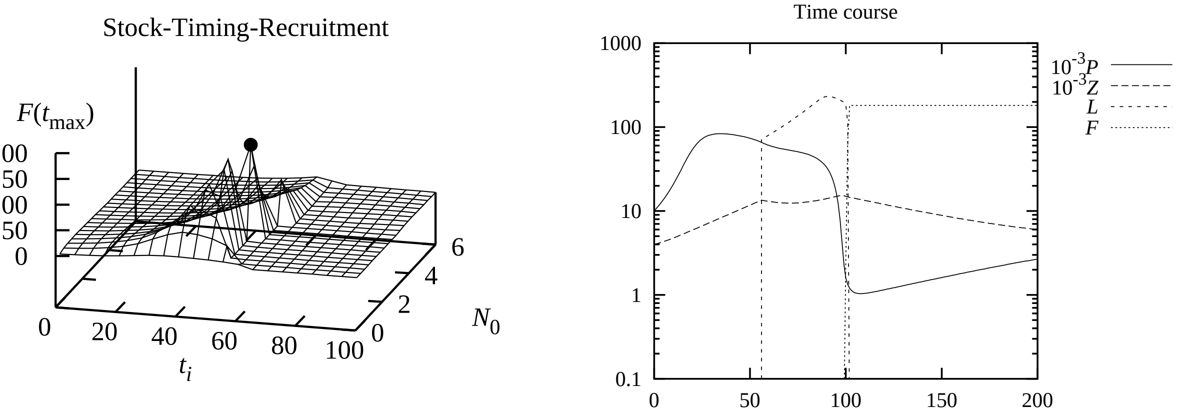

Figure 12: Stock-timing-recruitment relationship. Same as Figure 10, with a higher initial phytoplankton concentration, $P_0 = 10 \cdot 10^3$.

Numerical experiments with further spreading of the hatching period reveal no further advantages, in contrast to the case of the subthreshold pre-hatching state of the PZ subsystem. This is because the phytoplankton bloom in this model, once triggered, is a very robust regime and the small influence of the larvae on the zooplankton does not alter it.

4 Discussion

The numerical results obtained above demonstrate that the *qualitative* features of the results obtained by [CH] persist when the stock-recruitment model is coupled to a dynamic model for plankton populations [TB]. The crucial modification is that the food source (copepods), which in [CH] would grow exponentially in the absence of larvae, is replaced by an evolving copepod population itself dependent on phytoplankton growth through photosynthesis. A striking feature of the results is the sensitivity of the final recruitment total to variations in biological and physical influence. By choosing parameter values and initial conditions well within the ranges used by recent authors (see (Edwards & Brindley 1996)), we can obtain recruitment totals varying by up to three orders of magnitude. Though these variations compare well with observed variability in recruitment (Garrod 1983, Cushing 1996), it implies that accurate quantitative prediction is likely to be difficult. It is possible, nevertheless, to make several general comments.

- In conditions under which strong phytoplankton blooms occur, the accompanying zooplankton population will, in the absence of larvae, vary substantially over time, typically by an order of magnitude.
- This implies that timing of the appearance of larvae is crucial in determining their food supply and eventual metamorphosis — the Cushing Match-Mismatch hypothesis (Cushing 1995).
- In non-bloom conditions, zooplankton populations remain more steady, but typically at levels too low to provide the food supply assumed in [CH]. The qualitative pattern of recruitment resembles [CH], but is much lower (see Figures 3 and 4).
- Hatching of larvae can stimulate the onset of a phytoplankton bloom, by suppressing the concentration of zooplankton and triggering the "prey escape" mechanism for the phytoplankton. This phenomenon is probably typical for trophic chains with more than two species and appropriate time scales.
- Larvae can benefit from the phytoplankton bloom only in a quite narrow range of parameter values, particularly, hatching timing. Any deviation from optimal values leads to fast decrease of recruitment, due to the exponential nature of larvae mortality. This means that single batch hatching (egg laying) is a very high risk strategy; it pays off if the timing is *exactly* right, but on the whole an extended hatching period is advantageous. In this case at least some of the larvae enjoy the most favorable feeding conditions.
- Rough criterion for optimal timing: end of the larval stage (main time of recruitment) should coincide with the end of phytoplankton bloom. In particular, this implies that the duration of larval stage, if possible, should be shorter than the duration of the bloom.

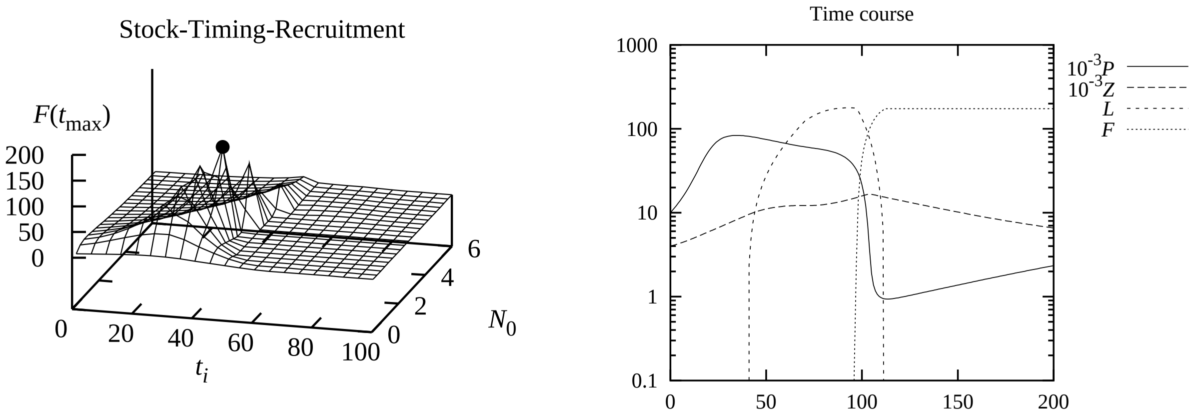

Figure 13: Stock-timing-recruitment relationship. Same as Figure 12, with hatching spread through a month, $P_0 = 10 \cdot 10^3$, $t_h = 30$.

But how long should we consider a "bloom" to be. One tends to think of exceptional cases of very high algal concentrations, such as red tides. These are however exceptional, driven by a change in the environment or a sudden release from predation. More generally the spring bloom is of an extended character. Off the north-east coast of England in 1976, in a region of fish larval development, the spring bloom of chlorophyll $a > 10^3 \mu\mathrm{g\,m}^{-3}$, persists for over six weeks (Horwood 1982, figs. 5 & 8). On the central station of the Fladen Ground, in the same year, such concentrations lasted for 3-4 weeks (Radach 1983). Similar and longer durations of the spring bloom can be seen in reviews by *inter alia* Cushing (1995) and Mann & Lazier (1996). Consequently it may be reasonable to propose that larval development takes the order of the duration of the spring bloom. However, not only does the spring bloom have different characteristics between and within oceans, but larval development is very sensitive to local temperatures. This gives scope for discrimination and testing of such an hypothesis.

Finally, a major assumption in the [TB] model is that the populations called P and Z are homogeneous. This is clearly not true in practice. The rapid growth rate and short lifespan of individual phytoplankton means that some formal averaging process over a larval lifespan is likely to be adequate in that case. However, the fact that copepod growth rates and lifespans are comparable to that of the predator larvae suggest that age-dependence or, more importantly, size variation in zooplankton is likely to be important. A valuable exercise for the future is then a coupling of a stock-recruitment model to an age-dependent or otherwise variable P-Z model. *e.g.* (Clother & Brindley 1999).

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Appendix: table of notations[1]

Notation	Std (init) val	Units	Meaning
Units			
d			day
m			meter
μg			micrograms
Independent variables			
t		d	time
a		d	age
Dynamic variables			
$P(t)$	$4 \cdot 10^3$	$\mu\mathrm{g\,m}^{-3}$	phytoplankton biomass concentration
$Z(t)$	$4 \cdot 10^3$	$\mu\mathrm{g\,m}^{-3}$	zooplankton biomass concentration
$W(t,a)$	33	μg	weight of one larva
$N(t,a)$	1	m^{-3}	larva number per volume (per day of age)
$F(t)$	0	$\mu\mathrm{g\,m}^{-3}$	metamorphosed fish biomass per volume
Model parameters			
k_{TB}	1		contribution of TB model
k_{CH}	1		contribution of CH model
$P_{\max}$	$1.08 \cdot 10^5$	$\mu\mathrm{g\,m}^{-3}$	TB phytoplankton saturation constant
r_P	0.3	d^{-1}	TB phytoplankton maximal growth rate
r_Z	0.7	d^{-1}	TB zooplankton maximal grazing rate
P_*	$5.7 \cdot 10^3$	$\mu\mathrm{g\,m}^{-3}$	TB zooplankton grazing satiation constant
γ	0.05		TB zooplankton grazing efficiency
μ_Z	0.012	d^{-1}	TB zooplankton non-specific mortality rate
ν	0.2234		CH larvae weight-search volume exponent
k	0.0154	$\mathrm{m}^3\,\mathrm{d}^{-1}\,\mu\mathrm{g}^{-\nu}$	CH larvae weight-search volume coefficient
μ_L	0.089	d^{-1}	CH larvae initial mortality to predation rate
b	0.005	d^{-1}	CH larvae mortality to predation decrease rate
$r_{Z,0}$	0.0875	d^{-1}	CH zooplankton growth rate, regardless of food
n	0.67		CH larvae weight-metabolic cost exponent
σ	2.6	$\mu\mathrm{g}^{1-n}\,\mathrm{d}^{-1}$	CH larvae weight-metabolic cost coefficient
j	0.002	$\mu\mathrm{g}^{-1}$	CH larvae maximal digestive coefficient exponent
$\beta_{\max}$	0.48		CH larvae max digestive coefficient
$\beta_{\min}$	0.135		CH larvae minimal (initial) digestive coefficient
r_L	0.12	d^{-1}	CH maximal larva growth rate
a_T	100	d	CH larvae metamorphosis age
W_T	3165	μg	CH larvae metamorphosis weight
$C_{T,a}$	1	d^{-1}	CH larvae metamph-age rate coefficient
$C_{T,w}$	1	d^{-1}	CH larvae metamph-wgt rate coefficient
Δa_T	3	d	CH larvae metamorphosis age spread
ΔW_T	31	μg	CH larvae metamorphosis weight spread

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[1] The units are for the unstructured model. For the age-structured model, extensive quantities describing larvae age groups are per day of age, *i.e.* have additional dimensional factor of d^{-1}.

Notation	Std (init) val	Units	Meaning
Computation parameters			
P_0	$4 \cdot 10^3$	$\mu\mathrm{g\,m}^{-3}$	initial phytoplankton biomass concentration
Z_0	$4 \cdot 10^3$	$\mu\mathrm{g\,m}^{-3}$	initial zooplankton biomass concentration
W_0	33	$\mu\mathrm{g}$	initial larva weight
N_0	1	m^{-3}	total hatched larva number per volume
t_i	0	d	hatching begin
t_h	1	d	hatching duration
$t_{\max}$	256	d	total calculation time
Δt	1	d	calculation time/age step
Auxiliary functions			
G		d^{-1}	TB amount phyto eaten by zoo per zoo μg per day
$R_{\max}$		$\mu\mathrm{g\,d}^{-1}$	CH maximal daily ration of one larva
R		$\mu\mathrm{g\,d}^{-1}$	CH actual zooplankton biomass eaten by one larva
R_{tot}		$\mu\mathrm{g\,m}^{-3}\,\mathrm{d}^{-1}$	CH amount of zoo eaten by larvae of all ages
p		d^{-1}	CH fraction of volume searched by larvae
β			CH larva food conversion efficiency
B_{o}		$\mu\mathrm{g\,d}^{-1}$	CH biomass obtained by larva from food
B_{s}		$\mu\mathrm{g\,d}^{-1}$	CH biomass spent by larva for energetic needs
ΔW		$\mu\mathrm{g\,d}^{-1}$	CH larva theoretical weight gain rate
$\Delta W_{\max}$		$\mu\mathrm{g\,d}^{-1}$	CH maximal larva weight gain rate
M		d^{-1}	CH larvae mortality to predation rate
T		d^{-1}	CH larvae metamorphosis rate
L		$\mu\mathrm{g\,m}^{-3}$	larvae biomass