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A model of the predatory impact of larval marine fish on the population dynamics of their zooplankton prey

Stephen M.Bollens

School of Oceanography, WB-10, University of Washington, Seattle, WA 98195, USA

Abstract. A simulation model of the population dynamics of two species of calanoid copepods (*Calanus pacificus* and *Pseudocalanus* sp.) was forced with predation pressure from a generic, hypothetical population of larval marine fish. Results of the model are sensitive to changes in parameters describing the dynamics of both predator and prey populations, including initial numbers, fecundity, growth, mortality, size of prey organisms and feeding selectivity of the predators; the relative importance of these parameters is tested by way of a brute-force sensitivity analysis. Using results from recent ichthyoplankton surveys in Dabob Bay, WA, USA, the model was also forced with predation from populations of larval Pacific herring (*Clupea harengus pallasi*) and Pacific whiting (*Merluccius productus*). Results of the various simulation runs lead to the conclusion that marine fish larvae can significantly impact the population dynamics of their calanoid copepod prey, but that the magnitude of this impact is highly dependent on species-specific values of various population parameters.

Introduction

The role of predation as a structuring force in marine zooplankton communities has been understudied in the ocean, due largely to the difficulties associated with experimental field manipulations in this advective and often inaccessible environment. This has perforce required that community level interactions in marine plankton be investigated through the use of simulation models. However, zooplankton ecologists attempting to model the dynamics of secondary producers have too often had to apply an ill-defined level of mortality due to predation, one based more on convenience and best-fit to observations of zooplankton abundances rather than the life-history patterns and population dynamics of specific predator populations (Steele, 1974; Steele and Frost, 1977; Evans and Parslow, 1985). The feeding dynamics and population growth of predators need to be included to yield more realistic models of plankton dynamics. Given that the sources of predation on zooplankton are many and varied, and that all of them cannot be quantified, priority should be given to those sources that have a dominant effect. An important first step, therefore, is to determine which predators are important and at which stages in their life-histories they are capable of impacting their prey.

While juvenile and adult planktivorous fish are widely acknowledged to be important consumers of zooplankton, the role of the larval stages of marine fish as predators on the plankton is much less clear. Several authors have discussed the metabolic demands and feeding requirements necessary to sustain growth and survival of fish larvae (e.g. Laurence, 1982), but few have considered this predator–prey interaction from the standpoint of the prey. Cushing (1983) made the most elaborate investigation of the problem to date and concluded that the early larval stages of fish are probably too dilute to affect the density of their

zooplankton prey, but that this trend may be reversed as larvae grow. Cushing (1983) did not, however, give full consideration to the dynamics of the prey populations, i.e. the ability of zooplankton to replace themselves through reproduction and growth. In a more general context, Alldredge (1984) has stressed the need to include population growth in any consideration of the predatory impacts of consumers on prey populations.

My intention in this paper is to address the possibility that the earliest life stages of marine fish (i.e. larvae during the first 60 days of life) can significantly impact the dynamics of their zooplankton prey. This work was undertaken not to quantify the impact of larval fish on any one particular population of zooplankton, but rather to place some reasonable bounds on what sort of predatory impacts are possible. That is, I have tried to determine whether this predator–prey interaction is worthy of closer scrutiny and inclusion in future models of plankton dynamics, or alternatively, that this interaction is of little significance to the zooplankton and can thus be safely ignored.

I have considered two species of calanoid copepods (*Calanus pacificus* and *Pseudocalanus* sp.) as prey populations. These two copepods, or closely related species, are frequently abundant in temperate, neritic waters (Marshall and Orr, 1955; Corkett and McLaren, 1978) and are often important prey of larval marine fish (Blaxter, 1965; Hunter, 1980). My approach has been to model the population dynamics of these two copepods under various conditions of reproduction, growth and mortality, including that due to larval fish predation. In order to show general trends and the sensitivity of results to various parameters, the simulation model was initially forced with mortality from a generic, hypothetical population of fish larvae. Subsequently, results from recent ichthyoplankton surveys in a temperate fjord (Dabob Bay, WA, USA) were included in the model.

Methods

Model of prey populations

The dynamics of a population can easily be modeled through the use of Leslie or projection matrices (Leslie, 1945, 1948; Pielou, 1977). Development time, reproductive rate and mortality can be described for each life history stage in the population and changes in the numbers of individuals can be projected over time. Projection matrices have traditionally been constructed such that units of time are equivalent to length of development time between age classes, i.e. at time t there are n_{xt} individuals in class x, all of whom will either die or develop into individuals of class $x + 1$ by time $t + 1$. Thus the probability of development into the next class in each time unit is 1.0; the probability of survival for each age class is then simply a function of stage-specific mortality alone.

I have taken a slightly different approach by allowing units of time (days) to be only a fraction of the total duration of each development stage. This requires that the probability of survival incorporate both the probability of development into the next stage and stage-specific mortality. Figure 1 illustrates a projection matrix (**M**) and column vectors ($\mathbf{n}_x$, $\mathbf{n}_{x+1}$) describing the population dynamics

$$M \times n_x = n_{x+1}$$

$$\begin{bmatrix} 1-P_0 & 0 & 0 & 0 & 0 & 0 & 0 & F_7 \\ P & 1-P_1 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & P_1 & 1-P_2 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & P_2 & 1-P_3 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & P_3 & 1-P_4 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & P_4 & 1-P_5 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & P_5 & 1-P_6 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & P_6 & 1-Z_7 \end{bmatrix} \times \begin{bmatrix} n_{0x} \\ n_{1x} \\ n_{2x} \\ n_{3x} \\ n_{4x} \\ n_{5x} \\ n_{6x} \\ n_{7x} \end{bmatrix} = \begin{bmatrix} n_{0x+1} \\ n_{1x+1} \\ n_{2x+1} \\ n_{3x+1} \\ n_{4x+1} \\ n_{5x+1} \\ n_{6x+1} \\ n_{7x+1} \end{bmatrix}$$

M = projection matrix

n_x = column vector representing population at t=x

n_{0x} = number of female eggs at t=x

n_{1x} = number of female nauplii at t=x

n_{2x} = number of female copepodid stage I at t=x

n_{3x} = number of female copepodid stage II at t=x

n_{4x} = number of female copepodid stage III at t=x

n_{5x} = number of female copepodid stage IV at t=x

n_{6x} = number of female copepodid stage V at t=x

n_{7x} = number of female adults at t=x

P_x = probability of development into class x+1

Z_7 = probability of adults dying of old age = 0.033

F_7 = fecundity of adults (number of female eggs d-1)

Fig. 1. A projection matrix (**M**) and corresponding column vectors ($\mathbf{n}_x$, $\mathbf{n}_{x+1}$) for populations of calanoid copepods under conditions of perfect survival.

of a hypothetical population of calanoid copepods under conditions of perfect survival.

Developmental classes progress through successive stages at daily rates that are the inverse of the corresponding development time in days. For example, a class of stage I copepodids at time t with a development time of 4 days will at time $t + 1$ consist of 75% stage I copepodids and 25% stage II copepodids. All naupliar stages are pooled for convenience. Adult females have been given a reproductive life span of 30 days, at which time the remaining survivors die.

Initially, I have taken stage-specific mortality to be a constant proportion of individuals in each stage. While the proportion is fixed for each stage in any one simulation run, the absolute number removed at any time depends on the density of individuals at that time. A proportional rather than a density-

dependent value was assigned to this source of mortality based on the assumption that mortality is due largely to invertebrate predation and recruitment of invertebrate predators would roughly keep pace, with a minimal time lag, with that of prey populations. Figure 2 incorporates a proportional mortality term due to predation into the projection matrix.

In addition to the use of mortality terms in **M** to describe the proportional removal of prey through predation, an absolute, non-proportional amount of mortality can be included by adding a column vector (**X**) whose elements represent the absolute number of individuals removed from each developmental class of the population each day. Figure 3 illustrates how such a vector would be added to the product **M** * $\mathbf{n}_t$ to obtain $\mathbf{n}_{t+1}$. For reasons to be discussed below, this is the manner in which I modeled the effects of larval fish predation on the copepod populations.

$$\mathbf{M} \times n_x - n_{x+1}$$

$$\begin{bmatrix} 1-P_0-M_0 & 0 & 0 & 0 & 0 & 0 & 0 & F_7 \\ P_0-M_0 & 1-P_1-M_1 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & P_1-M_1 & 1-P_2-M_2 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & P_2-M_2 & 1-P_3-M_3 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & P_3-M_3 & 1-P_4-M_4 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & P_4-M_4 & 1-P_5-M_5 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & P_5-M_5 & 1-P_6-M_6 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & P_6-M_6 & 1-Z_7-M_7 \end{bmatrix} \begin{bmatrix} n_{0x} \\ n_{1x} \\ n_{2x} \\ n_{3x} \\ n_{4x} \\ n_{5x} \\ n_{6x} \\ n_{7x} \end{bmatrix} \begin{bmatrix} n_{0x+1} \\ n_{1x+1} \\ n_{2x+1} \\ n_{3x+1} \\ n_{4x+1} \\ n_{5x+1} \\ n_{6x+1} \\ n_{7x+1} \end{bmatrix}$$

Fig. 2. A projection matrix (**M**) and corresponding column vectors ($\mathbf{n}_x$, $\mathbf{n}_{x+1}$) for populations of calanoid copepods experiencing proportional mortality due to predation and old age. All symbols are as in Figure 1, with M_x = proportional rate of mortality of stage x.

$$\mathbf{M} \times n_x + L_x - n_{x+1}$$

$$\begin{bmatrix} 1-P_0-M_0 & 0 & 0 & 0 & 0 & 0 & 0 & F_7 \\ P_0-M_0 & 1-P_1-M_1 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & P_1-M_1 & 1-P_2-M_2 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & P_2-M_2 & 1-P_3-M_3 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & P_3-M_3 & 1-P_4-M_4 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & P_4-M_4 & 1-P_5-M_5 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & P_5-M_5 & 1-P_6-M_6 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & P_6-M_6 & 1-Z_7-M_7 \end{bmatrix} \begin{bmatrix} n_{0x} \\ n_{1x} \\ n_{2x} \\ n_{3x} \\ n_{4x} \\ n_{5x} \\ n_{6x} \\ n_{7x} \end{bmatrix} \begin{bmatrix} L_{0x} \\ L_{1x} \\ L_{2x} \\ L_{3x} \\ L_{4x} \\ L_{5x} \\ L_{6x} \\ L_{7x} \end{bmatrix} \begin{bmatrix} n_{0x+1} \\ n_{1x+1} \\ n_{2x+1} \\ n_{3x+1} \\ n_{4x+1} \\ n_{5x+1} \\ n_{6x+1} \\ n_{7x+1} \end{bmatrix}$$

Fig. 3. A projection matrix (**M**) and corresponding column vectors ($\mathbf{n}_x$, $\mathbf{L}_x$, and $\mathbf{n}_{x+1}$) describing the population dynamics, including absolute mortality due to larval fish predation, of *Pseudocalanus* sp. and *C.pacificus*. **M**, $\mathbf{n}_x$, $\mathbf{n}_{x+1}$ are as described in Figures 1 and 2. L_{yx} is the number of individuals in the y class removed at time x by larval fish predation.

Model of predator dynamics

The hatching of a cohort of fish larvae is assumed to be knife-edged, with the population declining in numbers over time according to the exponential equation:

$$N_t = N_0 \, e^{-Mt} \tag{1}$$

where N_t is the number at time t, N_0 is the initial number and M is the instantaneous mortality rate of the population. Individual larvae within the population will grow in weight according to the exponential equation:

$$W_t = W_0 \, e^{Gt} \tag{2}$$

where W_t is the weight of the larva at time t, W_0 is the initial weight and G is the instantaneous growth rate of the larva.

Furthermore, it is assumed that the total energetic requirement of an individual larva (R), including processes of growth, metabolism and egestion, is related to individual weight according to the allometric equation:

$$R = aW^b \tag{3}$$

Banse (1982) and Vidal and Whiteledge (1982) considered the rates of respiration of several species of small, poikilothermic metazoans and found the value of b to be about 0.8. Citing the similarity of values in b found in weight-dependent rates of respiration and assimilation in zooplankton, Frost (1980) assumed a comparable value of b for the allometric description of weight-dependent individual growth rate.

I have taken the additional step of assuming that the total energetic requirements of a fish larva over time can be described similarly, and that the exponent b has a value of 0.8. This allows equation (3) to be rewritten:

$$R_t = aW_t^{0.8} \tag{4}$$

With the value of b thus determined, the value of a can be found for any single species by knowing the weight and daily ration at any point in time.

Equations (1), (2) and (4) can be combined to yield an expression for the daily energetic demands of the entire cohort of fish larvae, E_t, as a function of time:

$$\begin{aligned} E_t &= N_t * R_t \\ &= N_0 \, e^{-Mt} * a(W_0 \, e^{Gt})^{0.8} \end{aligned} \tag{5}$$

This total daily energetic demand of the cohort of fish larvae was converted from calories per day to number of prey items per day by first applying a caloric-content/dry-wt conversion (Laurence, 1976) and then dividing by the weight of a particular developmental stage of *C.pacificus* or *Pseudocalanus* sp. (Paffen-

hoffer and Harris, 1976; Vidal, 1980; B.W.Frost, unpublished). These numbers were then incorporated into the column vector **X** and applied to the population dynamics of the copepod populations as described above.

Implicit in this approach to modeling the predatory impact of the cohort of larval fish is the simplifying assumption of no functional response in the feeding of the predators, i.e. the number of prey items removed at any point in time is independent of the concentration of prey present and simply a function of the dynamics of the predator populations alone.

Results

Removal rates of larval fish feeding on a static population of prey

To test the hypothesis that larval marine fish can significantly affect the population dynamics of their prey, I first considered the most general case of a generic, hypothetical population of fish larvae feeding on calanoid copepods. This allows me to place some reasonable bounds on the impact marine fish larvae might have on their prey. A hypothetical first-feeding larva weighing 100 μg dry wt was assigned a daily ration of 0.13 cal day^{-1} (Gamble *et al.*, 1981; Bailey, 1983), which projects to 6.69 mg dry wt and 3.74 cal day^{-1} after 60 days of modest growth ($G = 0.07$ day^{-1}). Table I shows the number of prey of a particular development stage needed each day to satisfy the daily energetic demands of a single larva, assuming the larva selects prey of only that stage.

The number of prey items removed each day by a larva can be combined with the densities of predator and prey to calculate a daily removal rate. Assuming 1.0 first-feeding larvae m^{-3} (Cushing, 1983) and a spring-time concentration of *Pseudocalanus*-sized adult copepods of 300 m^{-3} (B.W.Frost, personal communication), the fish larvae would account for a 1.0% daily removal rate if they fed only on adult copepods. Although adult copepods are usually not the preferred food of larval fish, copepods of this size are sometimes taken (Blaxter, 1965; Sumida and Moser, 1980).

In considering the various sources of mortality in *Pseudocalanus* sp. due to

Table I. Number of prey items of a particular developmental class of *C.pacificus* and *Pseudocalanus* sp. necessary to satisfy the daily ration of a hypothetical fish larva at first-feeding ($t = 0$) and after 60 days of growth ($t = 60$)

Dry wt of larva (mg)	Daily ration of larva (cal day^{-1})	Number of prey items needed to satisfy daily ration of larva	
		C.pacificus	*Pseudocalanus* sp.
$W_0 = 0.10$	$R_0 = 0.13$	100 eggs 5.2 NVI nauplii or CI copepodids 0.25 adult females	310 eggs 52 NV nauplii or CI copepodids 3.1 adult females
$W_{60} = 6.7$	$R_{60} = 3.7$	2900 eggs 150 NVI nauplii or CI copepodids 7.2 adult females	9000 eggs 1500 NVI nauplii or CI copepodids 89 adult females

predation, Ohman (1986) found the three dominant predators and their respective daily removal rates in spring to be: the carnivorous copepod *Euchaeta elongata*, 3.5% day^{-1}; the euphausiid *Euphausia pacifica*, 1.0% day^{-1}; and the chaetognath *Sagitta elegans*, 0.5% day^{-1}. These numbers alone suggest that fish larvae might have a significant impact on populations of their copepod prey, perhaps to an extent equal to that of some of the major invertebrate predators. However, these removal rates represent only half of the equation; as stated earlier, any thorough consideration of predatory impacts on prey populations must include rates of reproduction and development of the prey.

Predation from a hypothetical population of larval fish and its effect on prey dynamics

The simulation model of the dynamics of *C.pacificus* and *Pseudocalanus* sp. was first forced with predation from the hypothetical population of fish larvae. Initial values and sources for all parameters used in the description of prey and predator dynamics are given in Tables II and III. These estimates are from the

Table II. Initial values, ranges, and sources of parameters used to describe the population dynamics of *C.pacificus* and *Pseudocalanus* sp.

Parameter	Species	Initial value	Range	Source
N_0 (m^{-3})	*C.pacificus*	203	41–1015	Marshall *et al.* (1934)
	Pseudocalanus sp.	306	61–1530	Marshall (1949)
Development time (egg to adult)	*C.pacificus*	24 days	none	Vidal (1980) Landry (1983)
	Pseudocalanus sp	25 days	none	Landry (1983)
F (female eggs day^{-1})	*C.pacificus*	25	5–25	Frost (1985) B.W.Frost,unpublished
	Pseudocalanus sp.	1.8	none	Frost (1985) B.W.Frost, unpublished
M (day^{-1})	*C.pacificus*	0.06	0.03–0.18	assumed
	Pseudocalanus sp.	0.06	0.03–0.12	Ohman (1986)

N_0 is the initial number of copepods; F is the egg production rate; M is proportional mortality due to sources other than larval fish predation.

Table III. Initial values, ranges, and sources for parameters used to describe the population and feeding dynamics of the hypothetical population of marine fish larvae

Parameter	Initial value	Range	Source
N_0 (m^{-3})	1.0	0.2–5.0	Cushing (1983)
G (day^{-1})	0.07	0.05–0.09	Cushing (1983)
M (day^{-1})	0.05	0.03–0.07	Cushing (1983)
R_0 (cal day^{-1})	0.13	0.065–0.26	Bailey (1983)
	(25 μg C day^{-1})		Gamble *et al.* (1981)
Feeding selectivity	CI copepodids only	eggs–adults only only	Blaxter (1965) Hunter (1980)

N_0 is initial number of larvae; G is instantaneous growth; M is instantaneous mortality; R_0 is daily ration of a first-feeding larva weighing 0.10 mg dry wt.

literature, assuming springtime conditions in temperate, neritic waters. All rate processes were adjusted to 12°C. The model was run for 60 days. The extent to which the results of these simulation runs are dependent on the initial values of the parameters was tested by way of a brute-force sensitivity analysis, i.e. the individual parameters were allowed to vary singly through a rather large, yet reasonable, range of values and the results inter-compared.

Prior to the inclusion of predation from larval fish, the simulation model was run under conditions of perfect survival, resulting in unrealistically large population sizes of both species of copepod after 60 days (3.1×10^5 m^{-3} for *Pseudocalanus* sp.; 1.8×10^8 m^{-3} for *C.pacificus*). Subsequently, a constant, proportional amount of daily mortality (6.0%) was applied to all developmental stages. This value is based on Ohman's (1986) work with invertebrate predators of *Pseudocalanus* sp. adult females. While different stage-specific mortality rates have been observed in calanoid copepods (e.g. Mullin and Brooks, 1970), proportional mortality is assumed, for the time being, to apply equally to all developmental classes of both copepod species. The proportional mortality term can be thought of as including all sources of mortality other than that due to larval fish predation. Even with this mortality factor included, a striking increase in numbers of adults of both species was realized after 60 days (1.1×10^4 m^{-3} for *Pseudocalanus* sp.; 5.5×10^6 m^{-3} for *C.pacificus*). While such high resulting densities are unlikely to ever occur in nature (especially those for *C.pacificus*), this can be considered as ideal bloom conditions for the copepods. (If predatory impacts are capable of significantly reducing prey numbers under such favorable conditions, the impact would be expected to be even greater under conditions of more realistic population growth of the copepods.) Given that this daily mortality rate was the same for both species, the much greater increase in population size of *C.pacificus* is, by definition, due to the greater intrinsic rate of increase (r) of this species.

The addition of an absolute, non-proportional amount of mortality due to the feeding of the hypothetical cohort of fish larvae (as per Table III) was subsequently made to the model. In this and most subsequent runs of the simulation model, results are presented in the form of the percentage reduction of the prey populations due to the inclusion of larval fish predation in the model (Figures 4 and 5). Complete results of each run of the simulation model (initial and resulting population size of both prey species) are available from the author upon request.

Results of the initial inclusion into the model of predation from the cohort of larval fish are shown in Figure 4A (standard run). Both populations were reduced in size, but *Pseudocalanus* sp. to a much greater degree (24.6%) than *C.pacificus* (0.4%). These results represent the combined effects of differential prey size and potential for increase (r) in the two copepod populations. *Calanus pacificus* has both a larger body size (fewer numbers of individuals needed to satisfy the predator population) and greater intrinsic rate of increase (more rapid population growth) than *Pseudocalanus* sp. (Frost, 1980). These two effects result in *Pseudocalanus* sp. being much more heavily impacted by the cohort of larval fish predators. The body size and population growth rate effects were

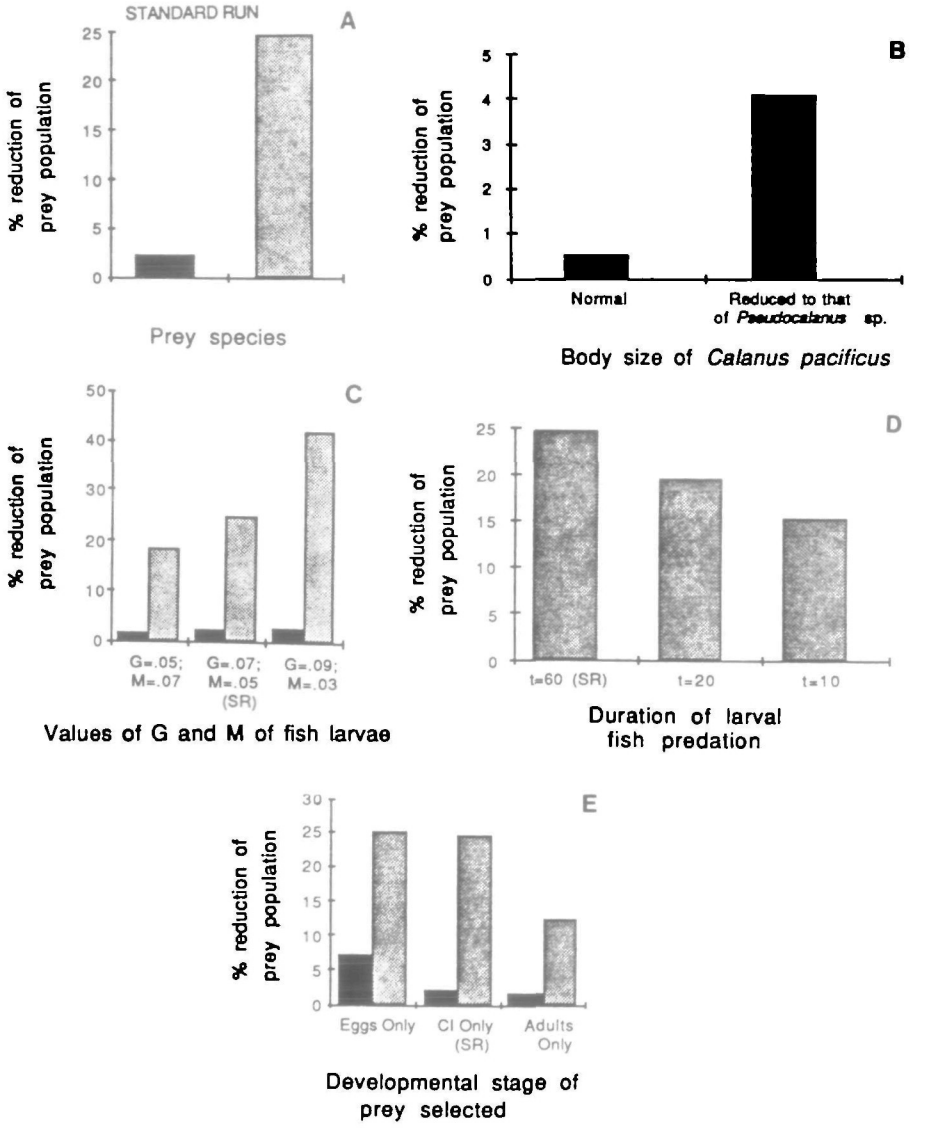

Fig. 4. The effect of varying model parameter values on the per cent reduction of the prey populations (■ = *C.pacificus*; □ = *Pseudocalanus* sp.) due to larval fish predation. (**A**) standard run as per Tables II and III (*C.pacificus* × 5.0); (**B**) effect of reducing the body size of *C.pacificus*; (**C**) effect of varying instantaneous growth (*G*) and natural mortality (*M*) of the larval fish (*C.pacificus* × 5.0); (**D**) effect of varying the duration of larval fish predation on *Pseudocalanus* sp.; (**E**) effect of varying intra-specific selection of prey by larval fish (*C.pacificus* × 5.0). SR = standard run.

separated in a subsequent run of the simulation model, where *C.pacificus* was given the same body size as *Pseudocalanus* sp. (same number of individuals removed by the fish larvae). This resulted in a 4.1% reduction for *C.pacificus* (Figure 4B), compared with a 24.6% reduction for *Pseudocalanus* sp., a

difference in predatory impacts due solely to differential intrinsic rates of increase of the two copepod species. Thus, while both body size and intrinsic rate of increase affect the extent to which predation impacts the prey populations, the intrinsic rate of increase of the prey is the more important factor.

Cushing (1983) has discussed natural mortality (M) and instantaneous growth (G) in larval marine fish and found reasonable ranges of these parameters to be 0.09–0.01 and 0.12–0.04 day^{-1}, respectively, with both parameters usually taking on higher values immediately after hatching and then declining with time. I have made the simplifying assumption of constant rates of mortality and growth over the 60 day larval life span considered, and have thus narrowed my range of reasonable values to 0.07–0.03 day^{-1} for M, and 0.09–0.05 day^{-1} for G. My standard run with the hypothetical cohort of fish larvae (Figure 4A) contains the mid-points of these two ranges ($M = 0.05\ day^{-1}$; $G = 0.07\ day^{-1}$) and thus has the total energy demands of the cohort of fish larvae (equation 5) increasing by a factor of 1.4 over 60 days. Outside limits to the interactive effects of mortality and growth on cohort energy demands can be calculated by using the extreme values of these two parameters in equation 5. Whereas all cases had the same initial conditions (R_0 held constant), using $M = 0.03$ and $G = 0.09$ (low mortality and high growth) resulted in a 12.4-fold *increase* in the cohort energy demands over 60 days, and using $M = 0.07$ and $G = 0.05$ (high mortality and low growth) resulted in a 83.5% *decline* in energy demands over 60 days. Results of the simulation model using these extreme cases of values for G and M are shown in Figure 4C. While the results of these runs show striking differences in the percentage reduction of prey number due to larval fish predation, at least for *Pseudocalanus* sp., the magnitude of these differences in impact is perhaps surprisingly low given the extreme differences in cohort consumption at day 60 under the three different scenarios of growth and mortality. The reason for this goes back to basic life table principles and can be seen in the results from the simulation model presented in Figure 4D.

The effect of larval fish predation was stopped after 10 and 20 days, respectively, and subsequent growth of the prey populations allowed to continue with predation other than that due to larval fish as the sole source of mortality. As shown in Figure 4D, the resulting reduction in population size of *Pseudocalanus* sp. after 10 days of larval fish predation (15.3%) and after 20 days of predation (19.4%) was a large fraction of that realized after 60 days of predation (25.6%), even though consumption of prey by the cohort increased slightly over time. The important inference here is that the dynamics of the predator–prey interaction *early* in time have the greatest impact on the prey. For example, those few adults removed initially cannot reproduce and add individuals to the future population; or conversely, those adults not removed initially will reproduce and result in the production of many times their own number in 60 days.

The feeding selectivity of the fish larvae, as a function of developmental stage of the prey, was also varied in the simulation model. Whereas the standard run (Figure 4A) had the larvae selecting all stage CI copepodids (a rough mid-point

in both size and developmental stage), Figure 4E shows the results of having the larvae meet their daily ration through selection of all eggs, and through selection of all adults. A considerable difference in reduction of prey due to different feeding selectivities was realized in the case of *Pseudocalanus* sp. (25.0–12.3%) but seemed to be less significant in the case of *C.pacificus* (1.4–0.3%). Given that the naupliar and copepodid stages of copepods are the primary food of larval marine fish, the initial assumption of stage CI copepodids being the stage preferentially removed seems to be a reasonable, if also over-simplified, way of representing the *average* feeding selectivity over the 60-day span of larval life.

Altering the initial number of fish larvae present (N_0) by factors of 2 and 5 has the expected results of either increasing or decreasing the percentage reduction of prey due to larval fish predation, as shown in Figure 5A. The same results are shown in Figure 5B for 2-fold and 5-fold changes in the initial number (N_0) of prey organisms. The impact of larval fish under these conditions ranged from 0.5 to 3.6 times that of the standard run (Figure 4A) for *Pseudocalanus* sp. Resulting numbers for *C.pacificus* changed by a corresponding amount, but in all cases resulted in a very small percentage reduction (<2.1%). Identical results were obtained for a two-fold change in the daily ration of the first-feeding larvae (Figure 5C).

Results of varying the value of the proportional mortality term due to other predators by factors of 0.5–3.0 are shown in Figure 5D. For both prey species this has a large impact on the numbers present after 60 days (range of 3.0 m^{-3} to 6.2×10^4 m^{-3} for *Pseudocalanus* sp.; range of 1.5×10^2 m^{-3} to 3.6×10^7 m^{-3} for *C.pacificus*), but only for *Pseudocalanus* sp. does the percentage reduction due to larval fish predation change appreciably, ranging from 19.5 to 100.0%. Even under circumstances of 18% daily mortality for *C.pacificus*, a situation resulting in very modest population growth ($r = 0.033$ day^{-1}), predation from larval fish has only a minor impact on the dynamics of this species (1.5% reduction).

All simulation runs to this point assumed maximum egg production rates (excess food) for the two species of copepods, resulting in exceptionally high population growth, especially for *C.pacificus*. Both laboratory (Runge, 1984) and field (Frost, 1985) experiments indicate, however, that the egg production rate of *C.pacificus* varies with phytoplankton abundance. The effects of both mild and moderate food limitation on *C.pacificus* were included in the simulation model by reducing the egg production rates by 40 and 80% respectively (Figure 5E). Natural populations of *Pseudocalanus* sp., on the other hand, have a more constant egg production rate that seems less affected by natural variation in food availability (Frost, 1985), and I have therefore retained the maximal egg production rate for this species. Results of these runs indicate that even under conditions of moderate food limitation and more modest population growth, larval fish predation has a very small impact on the dynamics of *C.pacificus*.

Finally, I attempted to combine some of the effects of various parameter changes to include an extreme yet still reasonable case of high larval fish predation on the two species of copepods. In the case of *Pseudocalanus* sp., I

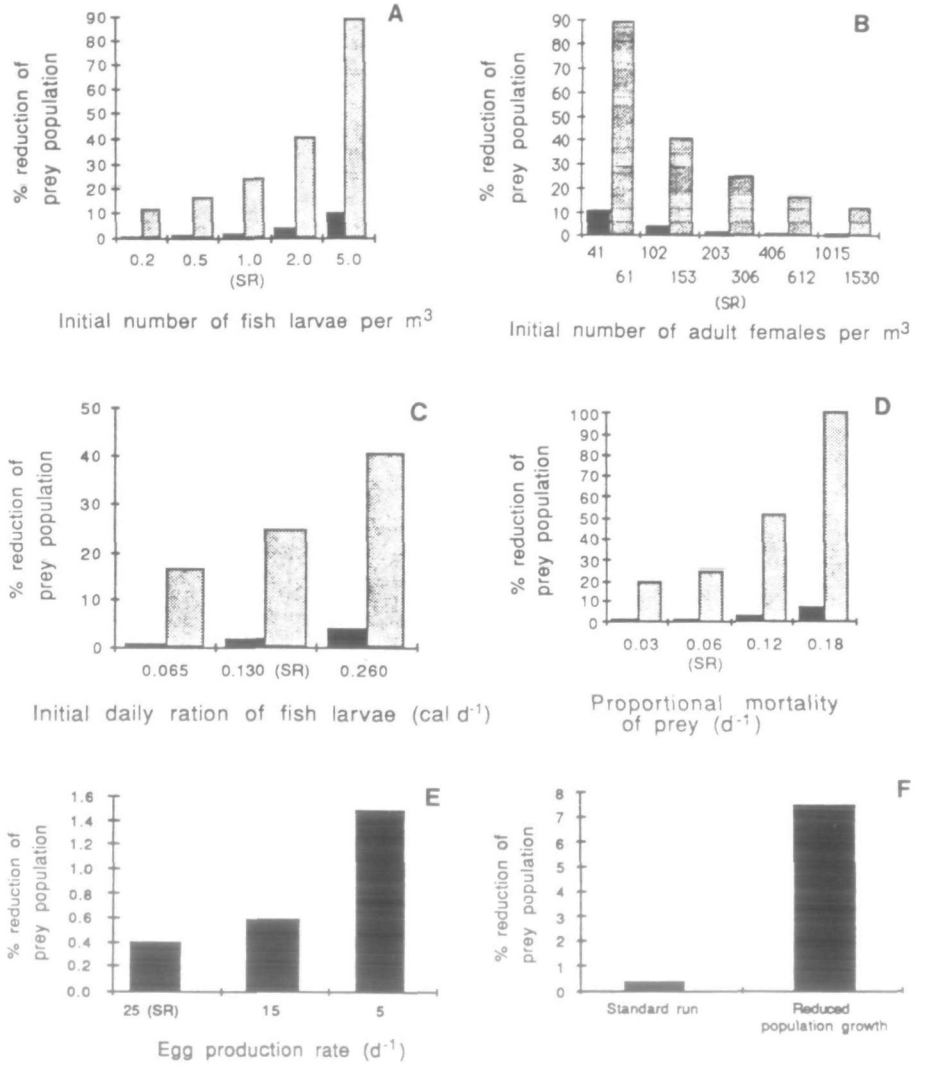

Fig. 5. The effect of varying model parameter values on the per cent reduction of the prey populations (■ = *C.pacificus*; □ = *Pseudocalanus* sp.) due to larval fish predation. (**A**) Effect of varying initial number of fish larvae (*C.pacificus* × 5.0); (**B**) effect of varying initial number of prey (*C.pacificus* × 5.0); (**C**) effect of varying initial daily ration of fish larvae (*C.pacificus* × 5.0), (**D**) effect of varying proportional mortality of prey (*C.pacificus* × 5.0); (**E**) effect of food limitation in *C.pacificus*; (**F**) effect of reduced population growth in *C.pacificus*. SR = standard run.

doubled the initial number of fish larvae and held proportional prey mortality at 12% day^{-1}. In considering these changes prior to the addition of fish larvae, the population of *Pseudocalanus* sp. realized a very small decline in numbers after 60 days (from 306 to 258 m^{-3}). When the mortality due to larval fish predation was added, the population of copepods went extinct at day 51. The same conditions were applied to *C.pacificus*, with the additional inclusion of an 80%

reduction in the daily egg production rate due to food limitation. These changes resulted in very modest population growth over 60 days (r = 0.026 day^{-1}) and a 7.4% reduction in prey numbers due to larval fish predation (Figure 5F).

Prey dynamics with predation from larval fish in a temperate fjord included

In an effort to add a greater degree of realism to the model, I used the results from recent (1985–1986) ichthyoplankton surveys in a temperate fjord (Dabob Bay, WA, USA) to describe the populations of larval fish predators. While many species of larval fish occur in Dabob Bay, Pacific herring (*Clupea harengus pallasi*) and Pacific whiting (*Merluccius productus*) are the two dominant species during spring time (S.M.Bollens, unpublished). Furthermore, these species have been the focus of feeding studies concerned with selection (Sumida and Moser, 1980; Checkley, 1982) and daily ration (Bailey, 1983; Gamble *et al.*, 1981) of larvae. This allows for species-specific descriptions of both predator and prey populations in the model.

Table IV gives the values for all parameters used in the description of the two larval fish populations in Dabob Bay. Initial values of parameters used to describe the dynamics of *Pseudocalanus* sp. and *C.pacificus* remained unchanged from those in Table II. In the case of *Pseudocalanus* sp., *M.productus* accounted for a 4.1% reduction in numbers, whereas *C.harengus pallasi* accounted for a much larger, 18.4%, reduction in prey numbers (Figure 6). Neither species of larval fish was able to significantly affect the population of *C.pacificus* under conditions of extremely rapid population growth as provided for by initial parameter values (Figure 6). Even when population growth of *C.pacificus* was slowed through increased mortality (12%) and food limitation (80% reduction of egg production rate), *C.pacificus* numbers were reduced by only 0.9% by *M.productus* and 1.9% by *C.harengus pallasi.*

Discussion

Results of the various runs of the simulation model indicate that predation from a cohort of larval fish can significantly affect the dynamics of calanoid copepod

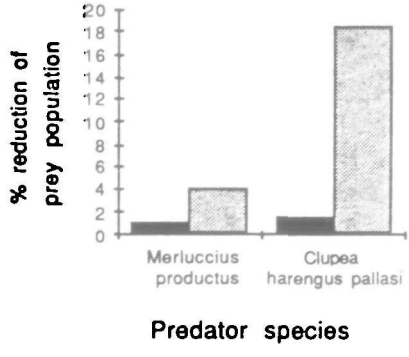

Fig. 6. The percentage reduction of prey populations due to predation from larval fish in Dabob Bay, WA. (■ = *C.pacificus* × 5.0; □ = *Pseudocalanus* sp.)

Table IV. Initial values and sources for parameters used to describe the population and feeding dynamics of larval *M.productus* and *C.harengus pallasi* in Dabob Bay, WA, USA

Parameter	*C.harengus pallasi*			*M.productus*		
	Initial value		Source	Initial value		Source
N_0 (m^{-3})	2.4		S.M.Bollens, unpublished	1.6		S.M.Bollens, unpublished
G (day^{-1})	0.07		Cushing (1983)	0 07		Cushing (1983)
M (day^{-1})	0.05		Cushing (1983)	0 05		Cushing (1983)
R_0 (cal day^{-1})	0.130 (25 μg C day^{-1})		Bailey (1983)	0.14		Gamble *et al.* (1981)
Feeding selectivity	Stage	Frequency	Sumida and Moser (1980)	Stage	Frequency	Checkley (1982)
	egg	0.35		egg	0	
	naupli	0.23		nauplii	0 71	
	copepodids	0.20		copepodids	0.29	
	adults	0.22		adults	0	

N_0 is initial number of larvae; G is instantaneous growth rate; M is instantaneous mortality rate; R_0 is daily ration of first-feeding larvae at $t = 0$ (W_0 = 0.067 mg dry wt for *M productus* and 0.10 mg for *C.harengus pallasi*).

prey populations. The magnitude of this effect is dependent on the values of many parameters used to describe the dynamics of predator and prey populations. I have tried to consider a broad enough range of parameter values to include any situation that might reasonably occur during spring-time conditions in temperate, neritic waters. A comparison of results from the various simulation runs suggest the following hierarchy of importance of parameters, from most critical (greatest sensitivity of model to parameter changes) to least critical (least sensitivity of model to parameter changes).

The maximum intrinsic rate of increase (r_{max}) of the prey population

While not a parameter *per se* in the model, this term incorporates fecundity and development times of the copepods into a measure of potential population growth. *Calanus pacificus* has a considerably higher r_{max} than *Pseudocalanus* sp. due largely to the much greater optimal daily egg production rate of *C.pacificus* (Frost, 1980). Under conditions of excess food and equal mortality, this allows a population of *C.pacificus* to grow much more rapidly, with a concomitant decrease in the impact of predation from larval fish. This is true even if a moderate amount of food limitation is applied to the egg production rate of *C.pacificus*.

If these two species of copepods can be taken as representative examples, seemingly similar prey species (e.g. suspension-feeding calanoid copepods) can exhibit strikingly different population dynamics and thus vastly different susceptibilities, on the population level, to impact from any one predator. This is underscored by the fact that in virtually all cases considered here, larval fish predation has a negligible impact on *C.pacificus*, yet often has a very substantial impact on *Pseudocalanus* sp. This result highlights the danger of over-generalizing in the construction of functional groups, and suggests the need for greater species-specific information.

Size of prey organisms

Size of prey determines the number of prey organisms required to meet the total energetic demands of the cohort of fish larvae. As shown in Table I, this number is much greater for the smaller *Pseudocalanus* sp. Given the construction of this model, the smaller of the two copepods will thus experience greater predation pressure from the cohort of larval fish by virtue of its body-size alone.

Another important aspect in considering the size of prey, and one not incorporated into this model *per se*, is the size-selective feeding of the predators on an inter-specific basis. While I have allowed for selection of prey based on developmental class within a given species, I have forced the predator population to feed on only one population of prey. That is, I have considered *intra*-specific size selection, but not *inter*-specific size selection of predator feeding. Given a spectrum of available food organisms, larval fish (Checkley, 1982) and adult planktivorous fish (Koslow, 1981) select prey items based, in part, on their size. Indeed, the much greater susceptibility of *C.pacificus* individuals to predation by juvenile and adult planktivorous fish may be a major

factor keeping blooms of these rapidly-growing copepods in check. Such interspecific selection is likely to be very important in determining which prey species are ultimately impacted by any one predator population, and should thus be more fully considered in future investigations.

Prey mortality, other than that due to larval fish predation

The value of this parameter has a very strong influence on how rapidly the prey populations grow, which in turn largely determines the extent to which larval fish can affect their numbers. Values of this mortality term that result in reduced population growth have the effect of increasing the importance of larval fish predation. Conversely, parameter values that result in increased population growth will have the effect of diluting, or decreasing, the impact larval fish predators have on their prey. In general, model results show fairly high sensitivity to the value of this mortality term. This is all the more important given that mortality is probably highly variable in nature, not only between species, but temporally and spatially as well.

Furthermore, it should be noted that the vast majority of cases considered have resulted in large blooms of copepods. Should the prey populations experience conditions less conducive to growth, such as higher mortality due to other sources of predation, the impact larval fish can have on their prey increases significantly. Indeed, in those few cases considered where the prey population is actually in decline, predation from larval fish severely hastened the crash in prey numbers.

Initial numbers of prey and predators

As expected, the greater the number of predators and the fewer the number of prey initially, the greater is the impact of predation. Results of the simulation model overemphasize this point, however, because of the lack of density-dependent effects on both predator and prey populations. For example, high initial numbers of fish larvae combined with a low density of food organisms might be expected to result in reduced growth, slower development and likely higher mortality of the fish larvae, thus leading to a reduced impact on the prey population. Although such density-dependent regulation mechanisms are not included in this model, the fact that larval fish can significantly reduce the numbers of their prey leaves open the possibility that larvae generate density-dependent larval growth (Cushing, 1983).

Growth and mortality of larval fish

Although the values of these parameters would be expected to vary widely in nature, they have surprisingly little effect on the results of the model. As stated earlier, this result is due to the greater significance to the prey of interactions that occur early in time, a result entirely predictable from basic life table principles. Furthermore, given that the values of larval growth and mortality were chosen to represent the *average* rates experienced by the larvae over 60

days, the two extreme cases where low growth ($G = 0.05$ day^{-1}) was combined with high mortality ($M = 0.07$ day^{-1}), and high growth ($G = 0.09$ day^{-1}) was combined with low mortality ($M = 0.03$ day^{-1}) seem likely to occur only rarely. A reasonable range of values for these two parameters seems, therefore, to generate a fairly narrow range of results.

Daily ration of fish larvae

The daily ration of an individual fish larva at any point in time is almost certainly not a simple function of weight alone, but can be expected to vary due to both instantaneous growth rate and species-specific differences in metabolic rate. Significantly different results are obtained from runs that include a 4-fold difference in the value of this parameter at the onset of feeding, a range that should more than allow for inter-specific differences in this parameter.

Feeding selectivity as a function of developmental class of prey

The results of the model do show some sensitivity to changes in feeding selection, but extreme differences in its value are required to cause significant changes in resulting impacts. Given that the value of this parameter was chosen to describe the *average* selection of larvae over 60 days, reasonable variation in the value of this parameter is unlikely to significantly affect results of the model.

I conclude that marine fish larvae are capable of significantly impacting the population dynamics of their prey. The magnitude of this impact is dependent on many parameters, the values of which are, in many cases, species-specific. In particular, the potential population growth of the prey population seems critical in determining the susceptibility of prey populations to predation impacts. In the two prey species considered here, *Pseudocalanus* sp. is almost always significantly impacted by larval fish predation, whereas the more rapidly growing populations of *C.pacificus* are almost never significantly affected. Although lower and more realistic potential population growth in the case of *C.pacificus* will have the effect of increasing the impact of larval fish predation (e.g. Figure 5F), the relative impact on this species would always be less than in *Pseudocalanus* sp.

Such species-specific values of the parameters used in describing the predator dynamics may be equally critical. In the case of Dabob Bay, *C.harengus pallasi* had a greater impact on the prey populations than did *M.productus*, although this difference was less striking than differences due to the dynamics of the prey populations themselves. The results presented here all point to the need for species-specific information on rate processes of both predator and prey populations.

My conclusions about the potential for larval fish to impact their copepod prey are in general agreement with those of Cushing (1983). However, I have found the period during which the cohort of larvae has the greatest impact on the population dynamics of their prey to be the earliest rather than the latest stages

of larval life. This is true despite the fact that prey items are likely to be more numerous initially (naupliar versus copepodid stages of copepods) and that the energetic demands of the cohort of larvae will likely increase over time. The critical point for the prey, and one stemming directly from basic life table principles, is the dynamics of the predator–prey interaction *early* in time.

My conclusions suggest that zooplankton ecologists seeking to understand the dynamics of copepod populations cannot ignore predation from larval fish as a potentially significant source of mortality. This leads naturally to the question of how best to quantify this impact for any one plankton assemblage in time and space. Two approaches are possible: the use of simulation models, such as were presented here, or large-scale experimental manipulations, such as enclosures. In the case of simulation models, the need is for detailed information on species-specific rate processes, the collection of which is both time-consuming and expensive. Applying the simulation model presented here to the case of Dabob Bay was only possible given that the dominant springtime fish larvae (*C.harengus pallasi* and *M.productus*) and copepods (*C.pacificus* and *Pseudocalanus* sp.) are all fairly well studied in terms of their life-histories and physioecologies. Even so, the model suffers from ambiguities over some parameter values. Other locations and their respective plankton assemblages might be far less amenable to simulated modeling, requiring first that detailed physiological studies of the dominant species be undertaken.

Large-scale experimental manipulations (i.e. enclosures) have been fruitfully applied to predation studies in freshwater plankton systems (e.g. Hall *et al.*, 1970; Lynch, 1979), but have had more limited success in marine environments (e.g. Grice *et al.*, 1980; Houde and Berkeley, 1982). The difficulty in applying this method to an advective, inaccessible environment such as the ocean was stated earlier; so-called 'edge effects' and the need for adequate experimental control and replication exacerbate this problem. Enclosures have the advantage, however, of allowing one to consider more directly effects on the plankton rather than specific mechanisms of predation. Which of these two approaches should be employed would, of course, depend on the particular system being studied. In general, though, simulation modeling would seem preferable where detailed, species-specific information on rate processes is available, and large-scale experimental manipulations the method of choice where such information is lacking and environmental constraints are tractable.

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