THE ROLE OF INVERTEBRATE PREDATORS

John H. Steele

Woods Hole Oceanographic Institution

Introduction

The context of this discussion is ecosystem structure and dynamics in temperate shelf regions such as Georges Bank and the North Sea. There are two complementary aspects:

(1)   The partition of energy flow at annually averaged time scales

(2)   The dynamics of ecosystems in response to shorter-term perturbations such as the spring outburst.

It will be argued that invertebrate predators, especially "jellies", are critical to both aspects, and we are limited by the lack of data on abundance, behavior. and metabolism of this component of the marine food web.

Energy Flow

Most diagrams for energy flow in temperate shelf environments introduce invertebrate (or "other") carnivores as a significant component of the pelagic system. Steele (1965) allowed them to eat 75% of herbivore production in the North Sea with only 25% going directly to fish. Jones (1984) compared two periods in the North Sea with Georges Bank. In all these cases, less than 25% went to pelagic fish. However, Jones divided other carnivores into two groups: (1) those that were food for the pelagic fish and (2) "invertebrate carnivores", which were an end point in the web. The species in this latter group were not defined but presumably would be gelatinous.

These long-term flow charts emphasize the importance of this last component and the general lack of quantitative information. Nearly all the other nodes have much better data, so that this other-carnivore box provides a free choice of a value to balance the budget.

For the North Sea, Fraser (1970) calculated an average seasonal cycle for *Pleurobrachia pileus* and illustrated the marked interannual variability (Fig. 3). Due to the methods of collection, the absolute values are in doubt.

For Georges Bank, Davis (1984) demonstrated that "even at conservative estimates of consumption, predators are able to control the copepod populations" (Fig. 1). Davis quotes feeding rates (as percent body carbon) of 20% for the jellies. But Reeve (1980) gives a value of 1500% for *Mnemiopsis*. This number (x15) has been used by Ross-et al. (in press) as a growth rate for predators in a Scottish sea loch and is surely too high (Kremer 1979).
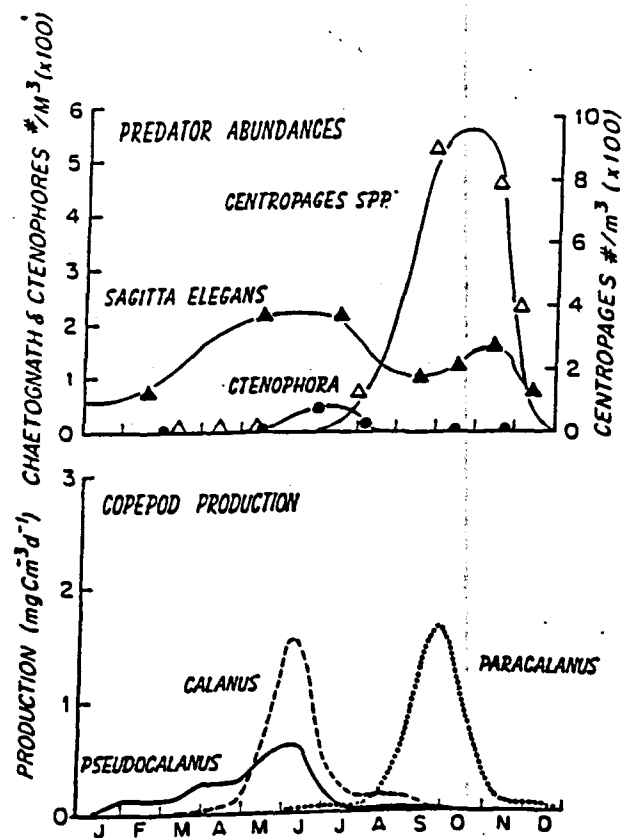
Fig. 1. (Top) Predator abundances on Georges Bank approximated from field data. (Bottom) Seasonal production curves for herbivores generated by model simulations. (Davis 1984)

As a last example, the invertebrate predators in Dabob Bay (Bollens et al. 1992) show marked seasonal patterns which match well with the herbivores (Fig. 2).

The general conclusion from the energy flow budgets is that invertebrates are the dominant source of herbivore mortality. Fish are significant but not the controlling component.

The rather scattered evidence on abundance indicates, as one would expect, that the invertebrate predators have marked seasonal cycles. It is difficult to determine the phase difference between the cycles of herbivores and predators, but there is no evidence of marked lags (Figs. 1, 2). This is not surprising, since the available evidence suggests that the growth rates, especially of the jellies (Kremer 1979), are comparable to those of copepods.
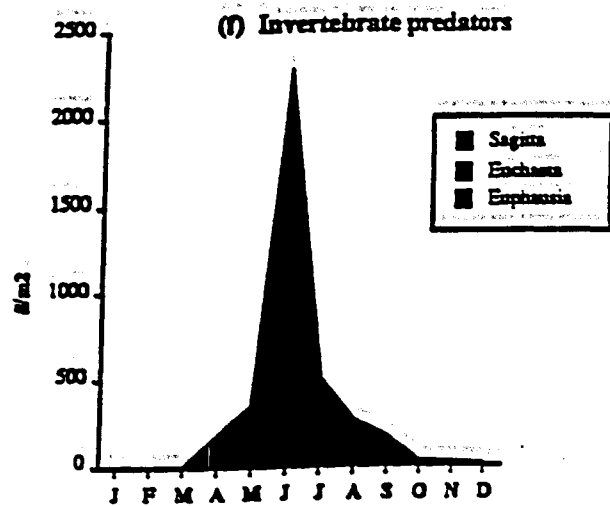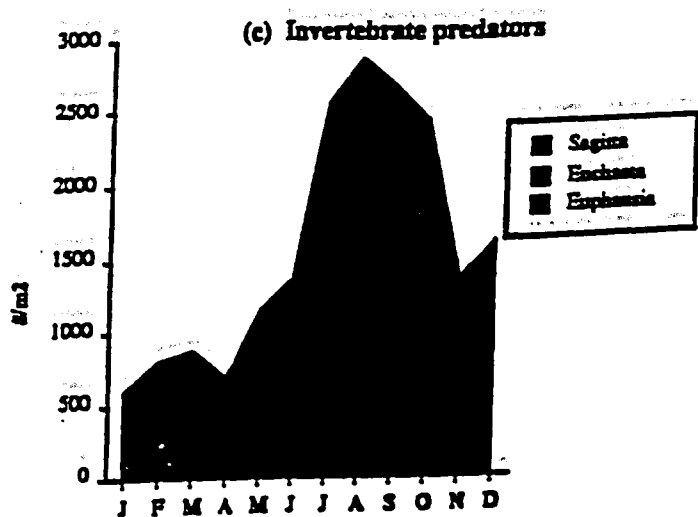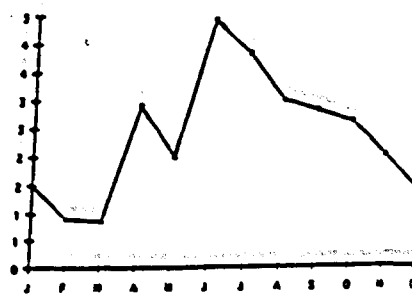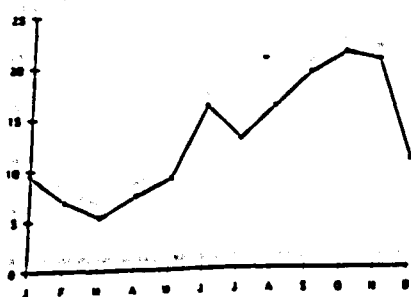
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Fig. 2. Mean annual cycles at two stations in Dabob Bay. (Top) Herbivores. (Bottom) Inverterbrate predators. (from Bollens et al. 1992)

Herbivore-Carnivore Interactions

What is the consequence for the dynamics of having seasonally variable predation on the herbivores? I shall argue that introducing this factor removes two difficulties found in most traditional prey-predator models.

A major problem in plankton models is how to close off the set of equations at the upper end to avoid simulating second- or third-order predators. We need to do this for reasons of simplicity and because there are so few observations on these predators.

Traditionally the herbivorous zooplankton, say Z, are given an equation of the form:

$$dZ/dt = g(Y).Z - d.Z \tag{1}$$

$g(Y)$, the growth rate of Z on its food Y, is usually a non-linear function of Y, e.g., hyperbolic or S-shaped. By contrast, the easiest way to close the model is to assume that the death rate is a constant $\underline{d}$. This implies a predator population that is constant in time and is always able to remove a fixed proportion of Z. If we have no knowledge whatsoever of the predators, then this unrealistic concept is the simplest assumption. But is it appropriate for plankton communities?

The problem is that this seemingly innocuous assumption results in two serious paradoxes. If Y_0, Z_0 are the equilibrium solutions, then from (1),

$$g(Y_0) = d$$

This means that the equilibrium value for the prey, Y_0, is independent of the value of Z_0 and of the equation for Y. It depends only on the coefficients in $g(Y)$ and on $\underline{d}$. Thus for different growth rates for Y, the phytoplankton and herbivore values Y_0, Z_0 can vary quite independently. This is at odds with most observations (e.g., McCauley et al. 1988).

The other problem, the paradox of enrichment (Rosenzweig 1971), arises because simple plankton models with this formulation (1) readily go unstable, displaying very large amplitude oscillations that are usually considered unacceptable.

What should we do to escape from these paradoxes? Obviously the idea is to make the equilibrium solution of (1) depend on both Y and Z, and so we need to reconsider the simple form of the closure term. We could propose setting up another equation for carnivores, but this just pushes the closure problem to a higher trophic level and requires the use of unknown or dubious parameters for the carnivore equation (Ross et al., in press).

The rate of predation depends on the number of predators and on their feeding behavior. Both aspects will depend on the density of Z in some complicated manner. To avoid setting up another equation, we can replace d.Z by a non-linear function $d(Z).Z$, where $d(Z)$ represents the co-variation of predation with Z.

There are many possible forms for $d(Z)$ (Steele and Henderson 1992), including hyperbolic functions and time delays. The observations described in the previous section do not permit much elaboration of functional form. However, they are sufficient to indicate that invertebrate predators are usually dominant and that they vary in a manner roughly in proportion to the herbivore density without too great time lag.

For these reasons, the simplest functional form which captures the essence of the observations is to take $d(Z) = f.Z$ so that at equilibrium:

$$g(Y_0) = f.Z_0 \tag{2}$$

This relation provides a link between Y and Z. Further, for most forms of the equation for Y (Steele and Henderson 1992), the equilibrium solutions are stable (Fig. 3).

To summarize: the two formulations, Fig. 3, show the equilibrium relations of Z_0 to Y_0 for

    (a) the original independent solution (1)

    (b) the variable predator function (2).

There are many other formulations, but Fig. 3 shows the essential mathematical difference between (a) and (b). It is this distinction which ensures that the latter does not fall into the paradoxical problems of the "classical" form.

Discussion

(1) The available evidence suggests that invertebrate carnivores, principally gelatinous, are the dominant predators on the pelagic herbivores in temperate shelf regions.

(2) These organisms have marked seasonal variability and, to a first approximation, vary with herbivore abundance.

(3) These factors have a major impact on our theoretical perceptions of plankton dynamics at the general N/P/Z level.

Qualitatively, predation rate increasing with herbivore density acts as a brake on too-large oscillations in the herbivore population and thus contributes to the stability of the system. In more detail, this moderating effect can also prevent the growth rate of individual copepods from varying too widely and so maintain relatively uniform life spans (Steele and Henderson 1992). This relative constancy, at any location and temperature, is in accord with the conclusions of Huntley and Lopez (1992) that copepod growth rates are not greatly affected by food limitation.

More detailed models of the life cycles and strategies of copepods must depend upon better information on their predators—and their behavioral responses to predation pressure. Knowledge of these factors is more important for herbivore dynamics than further data on their own metabolism.

Lastly, these notes relate only to temperate shelfs and assume that copepods are the dominant herbivores. This "classical" assumption may not even be true for these environments, but it certainly does not hold for open ocean oligotrophic regions. Yet in these areas, "jellies" are still a dominant component. Thus elucidation of their dynamics is surely a global problem.
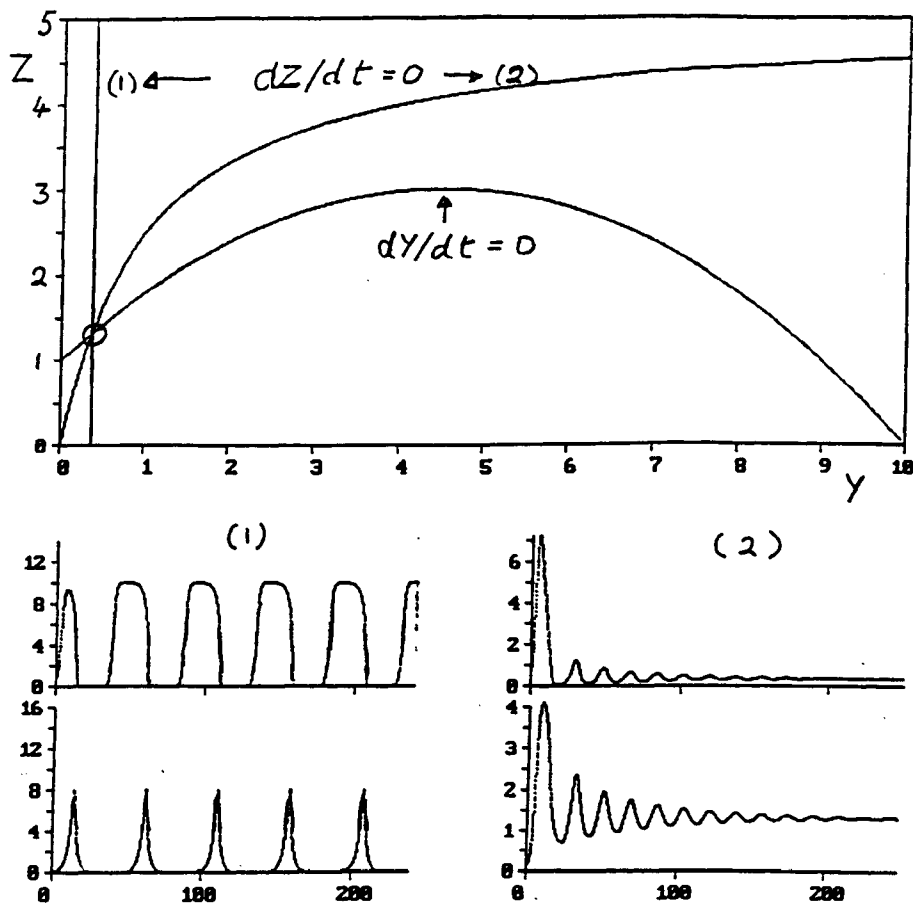
Fig. 3. Upper: Isocline diagram showing equilibrium conditions, where
dY/dt = f(Y) - g(Y).Z
f(Y) = a.Y/(1 - Y/b), g(Y) = Y/(1 + Y)
dZ/dt is from equations (1), (2) in text.
Lower: Solutions from (1) and (2), with appropriate parameter values.

References

Bollens, S.M., Frost, B.W., Schwaninger,H.D., Davis, C.S., Way, K.W., and Landsteiner, M.C. 1992 Seasonal plankton cycles in a temperate fjord and comments on the match-mismatch hypothesis. *J. Plankton Res.* 14:1279-1305.

Davis, C.S. 1984 Predatory control of copepod seasonal cycles on Georges Bank. *Mar. Biol.* 82:31-40.

Fraser, J.H. 1970 The ecology of the ctenophore *Pleurobrachia pileus* in Scottish waters. *J. du Cons. int Explor. Mer.* 33:149-168.

Huntley, M.E., and Lopez, M.D.G. 1992 Temperature-depent production of marine copepods: a global synthesis. *Amer. Nat.* 140(2):201-242.

JGOFS U.S. 1990 Equatorial Pacific modelling workshop (unpublished).

Jones, R. 1984 Some observations on energy transfer through the North Sea and Georges Bank food webs. *Rapp. P-v. Reun. Cons. int. Explor. Mer.* 183:204-217.

Kremer, P. 1979 Predation by the ctenophore *Mneniopsis leidyi* in Narragansett Bay, Rhode Island. *Estuaries* 2:97-105.

McCauley, E., Murdoch, W.W., and Watson, S. 1988 Simple models and variation in plankton densities among lakes. *Amer. Nat.* 132:383-403.

Reeve, M.R. 1980 Comparative experimental studies on the feeding of chaetognaths and ctenophores. *J.Plankton Res.* 2:381-393.

Rosenzweig, M.L. 1971 Paradox of enrichment: destabilization of exploitation ecosystems in ecological time. *Science* 171:385-387.

Ross, A.H., Gurney, W.S.C., and Heath, M.R. (in press) A comparative study of the ecosystem dynamics of four Scottish sea lochs. *Limnol. Oceanogr.*

Steele, J.H. 1965 Some problems in the study of marine resources. *Int. Comm. N.W. Atlantic Fish. spec. pub.* 6:463-476.

Steele, J.H., and Henderson, E.W. 1992 The role of predation in plankton models. *J. Plankton Res.* 14:157-172.