Abstract

A mathematical model based on assumptions of proportionality of filter-feeding insect larvae and their food supply and of the ability of the larvae to substantially reduce the sestonic food supply was developed. The predictions of the model were tested by censusing simuliid blackfly larvae in the outlet stream of a mesotrophic lake. Observed trends in simuliid density agree closely with the predictions. Two seston components (diatoms, detritus) increase downstream contrary to prediction. Potential predators of simuliids were censumed. *Isoperla* spp. decreased with increasing distance below the lake while the perlid stoneflies *Cалиneuria* and *Hesperoperla* seemed to be excluded from the outfall region.

Introduction

Streams which drain lakes are noted for the dense populations of invertebrates which may develop in them (Cushing, 1963; Hynes, 1970; Illies, 1956; Muller, 1955; Ulfstrand, 1968). Lake outlet communities are dominated by filter-feeding insects (Diptera: Simuliidae; Trichoptera: Hydropsychidae, Philopotamidae, Polycentropidae, Psychomyiidae) and other invertebrates such as sponges and *Hydra*. It is usually assumed that this community is maintained by organic material exported from the lake and that the restriction of dense populations to the outfall region implies rapid reduction of the sestonic food supply by physical processes and the animals themselves. Several authors (Chandler, 1937; Maciolek & Tunzi, 1968; Reif, 1939) have documented the decline of seston concentrations downstream from lakes.

In this paper we develop and test a mathematical model for prediction of the abundance pattern of filter-feeders in lake outlet ecosystems and, less rigorously, examine the possible determinants (food supply, predation) of abundance of such animals. Our test populations are simuliid blackfly larvae in the outlet stream of a mesotrophic lake in western Montana, U.S.A. Blackflies are characteristic members of outlet communities and such situations may contribute substantially to populations of the biting adults of some species.

Models and predictions

We considered the availability of food to be the most probable determinant of larval abundance and our formal model concerns interactions of larvae and their sestonic food supply. We also constructed a verbal model of predator-simuliid interactions. Both models were developed prior to design and execution of the field sampling. The observed data were then compared with expectations generated by the models. We emphasize the a priori nature of the research since most investigations in stream ecology rely on posterior analysis instead of tests of formal hypotheses.

The model rests on two assumptions. The first is that larval densities at points along the outlet are proportional to the food supply at that point, or

\[ N = cS \]

where \( N \) is the number of larvae per unit area, \( S \) is seston...
concentration, and c a constant. As water moves down-
stream, seston will be removed by sedimentation and by
the filter-feeding larvae. This compound process may be
written as
\[
\frac{dS}{dD} = -kS - fNS
\]
(2)
where D is distance along the outlet stream. The first term
represents physical losses and k is a fallout coefficient. In
the second term, the rate of removal by filter-feeders
depends on f, a filtering coefficient, and the interaction of
larval density (N) and available seston (S). Substituting
(1) in (2) and combining constants allows us to write
equations in S or N alone:
\[
\frac{dS}{dD} = -kS - f'S^2
\]
(3)
and
\[
\frac{dN}{dD} = -k'N - f''N^2
\]
(4)
Eqn (4) should describe longitudinal changes in black-
fly abundance. However, the integral form of (4) is com-
plex and contains more constants than can reasonably be
estimated from field data. An additional assumption
simplifies the model. If filter-feeders remove the greater
fraction of the seston, the first term of (4) can be deleted
giving
\[
\frac{dN}{dD} = -f''N^2
\]
(5)
The simplified form (5) is much more tractable than (4).
We also believe (5) can be justified on ecological grounds.
Maciolek & Tunzi (1968) found that trophic uptake was
considerably more important than non-biological re-
moval of seston in a California lake outfall. Since (3) and
(4) are quadratic functions of seston concentration, the
second (biological removal) term becomes dispropor-
tionately important as total seston loading increases.
Thus (5) should provide a reasonable approximation in
the outlets of productive lakes while the more complex
model (4) might be required in oligotrophic situations.
The integral form of (5) is
\[
N_D = \frac{a}{D}
\]
(6)
which predicts that larval density \(N_D\) at any point along
the outlet will be proportional to the reciprocal of the
distance \(D\) from the lake. While (6) generates a testable
prediction, it has several drawbacks. The first is statistical.
The model must be tested against sampling data. Since
most insect populations are strongly clumped, a variance-
stabilizing transformation, such as the logarithmic, is
required (Elliott, 1971) before fitted regression lines can
be tested for significance. The second weak point in (6) is
the slope constant \(a\) which includes the effect of initial
seston concentration and the proportionality constant \(c\)
(1). Thus the model predicts that the regression of \(N_D\)
on \(1/D\) should be linear but makes no prior estimate of
the slope of the line. Both problems are easily solved by
taking logarithms of (6) giving
\[
\log N_D = \log a - (b) \log D
\]
(7)
The slope constant \(b\) is inserted to generalize (7) to the
equation of a linear relationship of \(\log N\) and \(\log D\). The
effect of total seston loading appears only in the intercept
term which may be useful for inter-system comparisons
but does not confound the model in the way system rich-
ness does in (6). The arithmetic form of (7) is the power
function
\[
N_D = aD^{-b}
\]
(8)
which, with \(b = 1\), is identical to (6).
In spite of these simplifications and improvements,
the model retains an unrealistic element. Expressions
(6, 7, 8) predict infinite abundance at zero distance. This
impossibility follows from our failure to include space
requirements and other limiting factors in the model. As
a practical matter we did not attempt to test the model at
distances less than 25 m and doubt its validity at distances
less than 10 m. With this limitation in mind we use (7) to
make the following predictions about the abundance
pattern of simulids or other filter-feeders: the relation-
ship of \(\log N\) and \(\log D\) should be linear and, furth-
more, we predict that \(b = 1\).
Although the food limitation hypothesis is reasonable,
we investigated an additional factor in the dynamics of
blackfly larvae. When we began this work we were im-
pressed by the precipitous decline in simulid density over
very short lengths of stream. This decline is so abrupt that