Chapter 14

IMPORTANCE OF VARIATION IN ALGAL IMMIGRATION AND GROWTH RATES ESTIMATED BY MODELLING BENTHIC ALGAL COLONIZATION

R. JAN STEVENSON
Dept. Biology, Univ. Louisville, Louisville, Kentucky 40292 (USA)

ABSTRACT

A simple mathematical model of immigration and growth was used to study diatom accumulation, species composition, and diversity patterns during colonization on clay tiles. Accumulation patterns of dominant species and the entire assemblage were accurately predicted by the model when immigration parameters were iteratively varied to the best fit. The species that were fast immigrators during early stages of colonization were different than those species with high growth rates. However, modelled estimates of maximum immigration rates during colonization indicated that the fastest reproducers also had the fastest immigration rates during later stages of colonization. Field procedures for estimating immigration rates were probably not as accurate as estimates made with the model. Patterns of species composition and diversity were shown to be strongly influenced by the balance created when different species were fast immigrators and fast reproducers.

14.1 INTRODUCTION

Interest in the modelling approach to studying benthic algal colonization has been stimulated by a need to quantitatively estimate algal immigration and reproduction rates from short-term, temporal accumulation patterns. Since Ivlev's (1933) study of periphyton accumulation patterns on slides in different current velocities, the interpretation of accumulation patterns has recently been used to investigate algal colonization in reservoirs (Hoagland, 1983), in an estuary (Hudon and Bourget, 1981), in temperate-climate streams (eg. Korte and Blinn, 1983; Stevenson, 1984), and in boreal streams (Hamilton and Duthie, 1984). In many of these studies, the interpretation of how algal immigration and reproduction rates varied in different environments and controlled accumulation patterns was important for explaining interactions between the environment and algal assemblages.

Interpretation of algal assemblage dynamics has often been derived from estimates of algal standing crops on substrates from only one date. Differences in accumulation among habitats are often assumed to be the result of differences in growth rates (reproduction - death). However, growth of algae on substrates is not the only important mechanism controlling accumulation. Variation in immigration rates with current velocity has been shown to be a probable cause of differences in algal accumulation around substrates in streams (Stevenson, 1984). Grazing can also affect algal accumulation (eg. Sumner and McIntire, 1982). Thus, a variety of mechanisms determining algal accumulation may vary among habitats and interact to affect accumulation.

In addition to variations among habitats, evidence also suggests that algal immigration and reproduction rates are somewhat density-dependent and vary during colonization. Field estimates of algal immigration rates indicate that organics being adsorbed, secreted, and excreted onto substrates increases immigration rates. Algae, invertebrates, and aggregates of fungi, bacteria, and detritus on substrates also enhance immigration by interrupting currents and reducing shear stress (Stevenson, 1983). Decreases in algal productivity with standing crop (Lamberti and Resh, 1983) and growth habits of algae that maintain them at the surface of developing periphyton mats have suggested that algae compete for light and nutrients (Hoagland et al., 1982; Hudon and Bourget, 1983).

A complete model of algal accumulation should include these complex competitive and predator-prey interactions as well as resource limitation within the environment. However, important insights into the dynamics of benthic algal assemblages can be gained by using simple models while recognizing the limitations and assumptions inherent in the model. Such a model was developed for two reasons: first, to study the sensitivity of algal accumulation patterns to variations in immigration and growth rates and second, to provide a quantitative basis to compare alternative hypotheses for explaining different accumulation patterns in different stream currents (Stevenson, 1984; Stevenson, in press). In the model equation

$$N_{t+1} = I_o + I_m \left(\frac{N_t}{K+N_t} \right) + N_t(e^r), \tag{1}$$

N_t and N_{t+1} were algal abundances on substrates on consecutive days of colonization, I_o was the initial immigration rate onto newly exposed substrates, I_m was the maximum enhancement of immigration as substrates became colonized, K was a constant that related enhancement of immigration to algal abundance on substrates, and r was the algal growth rate. The maximum enhancement of immigration refers to the difference in minimum immigration rates on newly exposed substrates and maximum immigration rates on substrates which have been conditioned by colonizing organisms. Density-dependent competition among algae, algal emigration (detachment from the substrate), and herbivory were assumed to be negligible for purposes of modelling.

Predictions of algal accumulation patterns by the model provided a significantly good fit to data (Stevenson, in press). I_o was estimated from field collections as 90% of the number of algae colonizing tile substrates during a 24-h period (Stevenson, 1983). I_m was estimated as the difference in 24-h algal accumulations on tile substrates and substrates that had been coated with agar and with surface flows interrupted to simulate colonized substrates. K was estimated to be 2000 cells/cm² (approximate abundance of diatoms after one week). Algal growth rates were estimated during the last 16 days of the 32-day colonization period, when it was assumed that accumulation due to immigration would be negligible compared to accumulation due to reproduction. Algal growth rates were estimated as

$$(\ln(N_{t+1}) - \ln(N_t))/T, \qquad (2)$$

which was the difference in natural log-transformed abundances between day 32 and 16, divided by T, the length of time between dates.

Predictions of this model, particularly for colonization periods greater than 14 days, were affected more by proportionally equal changes in reproduction rates, than immigration rates (Stevenson, in press). An analysis of model sensitivity was done by calculating changes in accumulation patterns when only one factor in the model was changed at a time. Increasing reproduction rates by 50% caused a six-fold increase in accumulation after 32 days. Changing maximum immigration rates was also important because 50% increases caused 55% increases in accumulation after 32 days. The same 50% changes in initial immigration rates and the half-saturation constant (K) caused respective increases and decreases of only 15% in accumulation after 32 days. Changes became more important in maximum immigration than reproduction if colonization periods were short. These results indicate that accurate estimation of immigration and reproduction rates are important for predicting colonization, because variation in both strongly affect algal colonization.

The objective of this modelling study of a benthic algal assemblage was to assess the sensitivity of accumulation rates and community structure to changes in immigration and growth rates of species. Estimates of algal immigration rates obtained by field methods and by fitting model predictions to natural accumulation patterns were compared to study the reliability of estimating immigration. The differences in algal immigration and growth rates among dominant species in a benthic algal assemblage were studied. Then, fast growth rates of late colonists and slow growth rates of rapidly immigrating pioneer species were exchanged to study changes in accumulation rates, species composition, and diversity of assemblages that could result if species were not specialized as fast immigrators or fast reproducers.

Research presented in this paper was based on modelling accumulation patterns of individual diatom species and adding them together to study the entire assemblage, whereas only total assemblage abundances were modelled previously (Stevenson, 1984; in press). Results indicate considerable interspecific variation in algal immigration and reproduction rates, the possibility of algal specialization as immigrators or reproducers, and that emigration and density-dependent competition for nutrients may be important.

14.2 METHODS

Algal abundances on clay tiles were estimated after 1, 2, 4, 8, 16, 24, and 32 days incubation in a stream during the winter when water temperatures were about 2° C (Stevenson, 1983; 1984). Fifteen tiles, in current velocities ranging from 27 to 33 cm/s, were collected on each sampling date. Algae were scraped from tiles and mounted in HYRAX® medium by using vapor-substitution techniques (Stevenson and Stoermer, 1981). At least 500 cells of live diatoms were counted with a Nikon light microscope at 1000X.

Diatoms dominated the assemblage. The ten diatom species with highest relative abundances were chosen for study. Mean abundance on each sampling day was calculated and used to generate a temporal accumulation pattern with which predictions of a model were compared. Field estimates of initial algal immigration rates (I_0) were equal to mean abundances of algae on tiles that had been placed in the stream for 24-h. Field estimates of maximum enhancement of algal immigration rates (I_t) were equal to the sums of both the difference between 24-h abundances on tiles that had been coated with agar and the difference between 24-h algal abundances on tiles with surface flows interrupted and I_0 (see Stevenson, 1983 for details). Growth rates were calculated with natural log-transformed abundances during the last 16 days of colonization (equation 2).

Field and model estimates of algal immigration rates were compared to study the accuracy of estimating immigration rates. Field estimates of I_0 and r were used in a FORTRAN computer program to estimate I_m and K with the model by iteratively varying I_m and K until the best fit with actual accumulation patterns was found. Best fit of model prediction (N_t predicted) with actual accumulation patterns (N_t observed) was calculated with a Chi-squared test (Zar, 1974) using natural log-transformed abundances of algae.

The similarities between field and modelled assemblage abundance, species composition, and diversity (calculated with the Shannon formula; Pielou, 1977) during colonization were studied for accuracy of model predictions of assemblage characteristics. Subsequently, growth rates were exchanged between species that were fast and slow immigrators during early stages of colonization to study sensitivity of assemblage characteristics (abundance, species composition, and diversity) to changes in population characteristics. The two species that were dominant during early stages of colonization and the two species with the highest growth rates were identified. Growth rates of fast reproducers were exchanged with the slower growth rates of the species dominant during early colonization.

14.3 RESULTS

Ten diatoms comprised most of the diatom assemblage on tiles in the stream, ranging from 70% on day 1, to 90% after only 8 days, to 98% by day 32. When

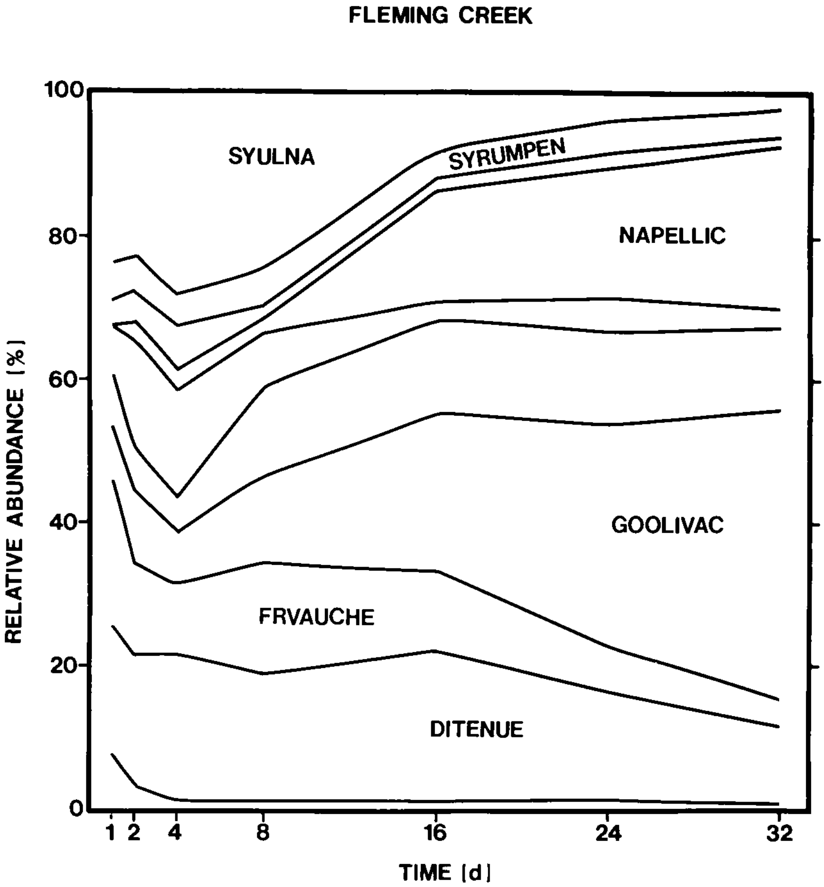

Fig. 14.1. Relative abundances of diatom species found on tiles in the stream during the colonization period. The assemblage has been simplified to the ten most dominant species. DITENUE=*Diatoma tenue*, FRVAUCHE=*Fragilaria vaucheriae*, GOOLIVAC=*Gomphonema olivaceum*, NAPELLIC=*Navicula pelliculosa*, SYRUMPEN=*Synedra rumpens*, SYULNA=*Synedra ulna*.

the assemblage was simplified to include only these taxa (Fig. 14.1), diatoms could be classified in one of three groups: 1) pioneers, with relative abundances decreasing during the colonization period; 2) late colonists, with relative abundances increasing during colonization; and 3) intermediates, with more stable relative abundances than other taxa during colonization. Decreases in relative abundances of *Synedra ulna* and *Fragilaria vaucheriae* from high levels during the first week of colonization (Fig. 14.1) indicated that their immigration rates were faster and their growth rates were slower than other taxa. With growth rates of all taxa ranging between 0.079 and 0.206 (Table 14.1), growth rates of these pioneer taxa, less than 0.1, were the two lowest. The rapidly increasing relative abundances and high growth rates, about 0.2, of *Navicula pelliculosa* and *Gomphonema olivaceum* indicated that they were late colonists and the best reproducers. Relative abundances of *Synedra rumpens* and *Diatoma tenue* were more constant than other taxa. Estimated growth rates of these two intermediate taxa were between those of immigrators and reproducers.

Considerable variation existed among field and modelled estimates of maximum immigration rates and estimates based on classification of the diatoms as either pioneers, intermediates, or late colonists (Table 14.1). Field estimates of maximum immigration rates of late colonists were low, as would be expected from their low relative abundances during the first days of

TABLE 14.1

Estimates of maximum enhancement of immigration rates for six diatom species (I_m·cells·cm^{-2}·d^{-1}) using field and modelling procedures. Chi-squared goodness of fit (X^2, df=4) statistics for model predictions of the accumulation patterns generated by using modelled and field estimated immigration rates are reported with the growth rates (r), initial immigration rates (I_0), and half saturation constants (K) used in the modelling.

			Field Estimated			Model Estimated		
Diatom Species	r	I_0	I_m	K	X^2	I_m	K	X^2
Pioneers								
Synedra ulna	0.079	10.5	262.	2000	0.53	118.	200	0.26
Fragilaria vaucheriae	0.095	9.0	39.	2000	2.80	193.	250	0.23
Intermediates								
Synedra rumpens	0.164	2.2	31.	2000	2.23	176.	950	0.27
Diatoma tenue	0.128	7.9	108.	2000	1.93	656.	1950	0.33
Late Colonists								
Navicula pelliculosa	0.206	0.1	2.	2000	160.	1312.	4300	0.69
Gomphonema olivaceum	0.193	3.3	42.	2000	2.67	1060.	4150	0.18

colonization, however unexpectedly low field estimates were also observed of a pioneer and intermediate species (Table 14.1).

Modelled estimates of maximum immigration rates indicated that pioneers were the fastest immigrators only during early stages of colonization (Fig. 14.2) and that late colonists were actually the fastest immigrators, as well as the fastest reproducers, during later stages of colonization. Although late colonists had higher I_m than pioneers, the estimates of algal abundances (K) needed to increase immigration to maximum rates were also higher for late colonists than pioneers. Thus, immigration of late colonists increased most

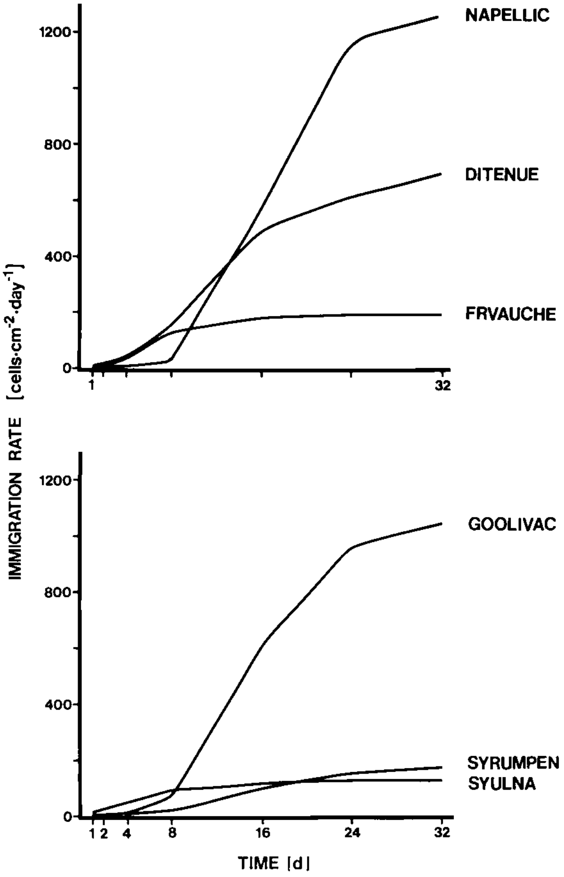

Fig. 14.2. Immigration rates estimated by modelling of six diatom species during the colonization period. See Fig. 14.1 for species abbreviations.

rapidly during later stages of colonization and immigration rates of pioneers were enhanced rapidly during early stages of colonization.

Comparison of observed accumulation patterns and those generated when using field and modelled estimates of maximum immigration rates indicated that field estimates probably underestimated maximum immigration rates (Fig. 14.3). Significantly good fits of observed accumulation patterns were generated by using both field and modelled estimates of immigration (Table 14.1), however

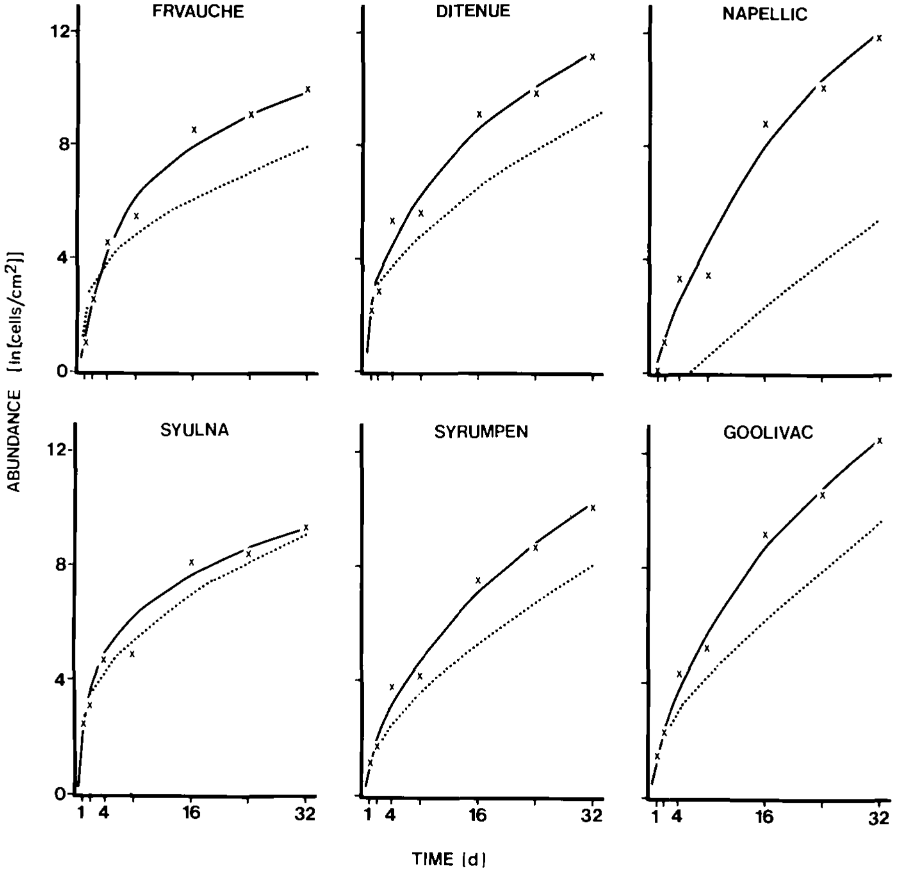

Fig. 14.3. Log-transformed abundances of six diatoms that were predicted by modelling accumulation patterns with estimates of immigration rates obtained with field procedures (dotted line) and with modelling procedures (solid line). Abundances of algae on tiles in the stream are marked with an "X". See Fig. 14.1 for species abbreviations.

lower X^2 values indicated that accumulation patterns were better fit by modelled than field estimates.

Predictions of assemblage accumulation, species composition, and diversity patterns when using modelled estimates of maximum immigration fit actual assemblage accumulation, species composition, and diversity patterns observed in the stream. Small deviations between modelled and observed accumulation patterns were evident among population and assemblage patterns (Figs. 14.3 and 14.4). Modelled accumulation patterns were intermediate between high and low stream abundances on days 4 and 8 respectively. In addition, model predictions for abundances were lower on day 16 than those observed. However, the model was usually quite accurate in predicting diatom abundances on day 32 with a very good fit for total assemblage abundances (X^2 = 0.1856) and population abundances (Table 14.1). Shannon diversity of simplified assemblages (i.e., evenness, because species richness was constantly 10) from the stream was generally lower during the first two weeks of colonization than diversity of the modelled assemblage (Fig. 14.5). A diversity peak in the stream assemblage on day 2 was not observed in the modelled assemblage and diversity was maintained longer in the stream assemblage. In both assemblages

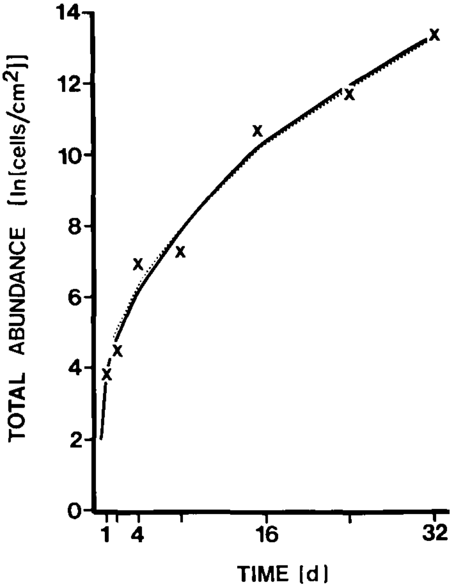

Fig. 14.4. Log-transformed abundances of the ten-species assemblages that were predicted by the model with immigration rates of the species estimated using modelling procedures.

there was a slight increase in diversity between day 8 and 16, which was followed by a decrease.

Results of altering population characteristics to make pioneers into fast reproducers indicated that the high immigration rates of G. olivaceum and N. pelliculosa during later stages of colonization were important. When the fast growth rates of these two taxa were switched with those of the pioneers (S. ulna and F. vaucheriae), final accumulation after 32 days was slightly lower in the altered assemblage (6.61 X 10^5 cells/cm²) than in the unaltered assemblage (6.79 X 10^5 cells/cm²; Fig. 14.6). Abundance of the altered assemblage increased more rapidly than for the unaltered assemblage during the first week of colonization, but more slowly during the second week when late-immigration became more important.

Deviations in diversity patterns between altered and modelled assemblages correlated with the change in population characteristics. Diversity of the altered assemblage decreased more rapidly during the first week of colonization and increased more rapidly during the second and third weeks of colonization than the unaltered assemblage (Fig. 14.5). The more rapid early decrease in diversity of the altered assemblage was due to the enhanced growth

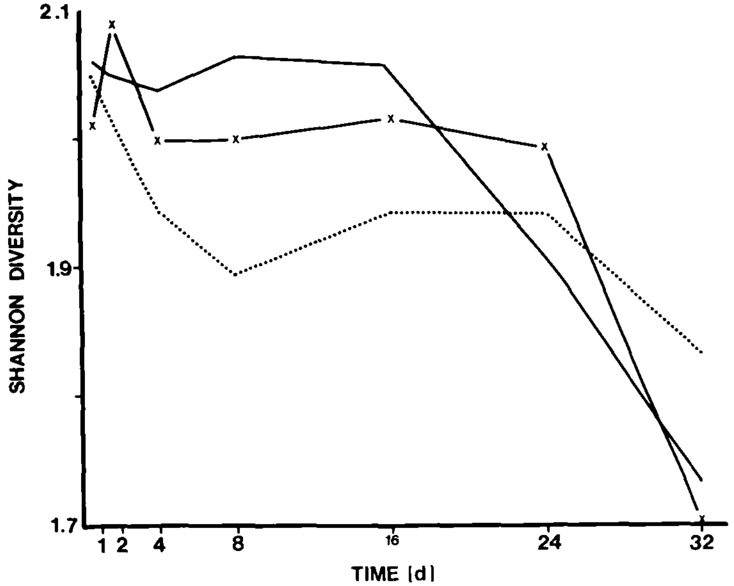

Fig. 14.5. Shannon diversity of ten-species assemblages on tiles in the stream (solid line connecting "X"s), when modelled with unaltered (solid line) and altered (dotted line) population characteristics.

rates of pioneers, which increased the unevenness of population abundances that had been balanced by faster growth of late colonists in the unaltered modelled assemblage. The subsequent mid-term increase in diversity, which was greater in altered than unaltered assemblages, was caused by evenness increasing as fast, late-immigration rates of late colonists started to increase rapidly. Similarly, high diversity was sustained longer in the altered assemblage than in the unaltered and stream assemblages, because the species with the fast, late-immigration rates no longer had fast growth rates.

Unlike species composition patterns in modelled and stream assemblages, relative abundances were relatively constant throughout the colonization period in altered assemblages (Fig. 14.7). Pioneers in the altered assemblage did not comprise substantially smaller proportions of assemblages at the end than at the beginning of the colonization period, because they now had fast

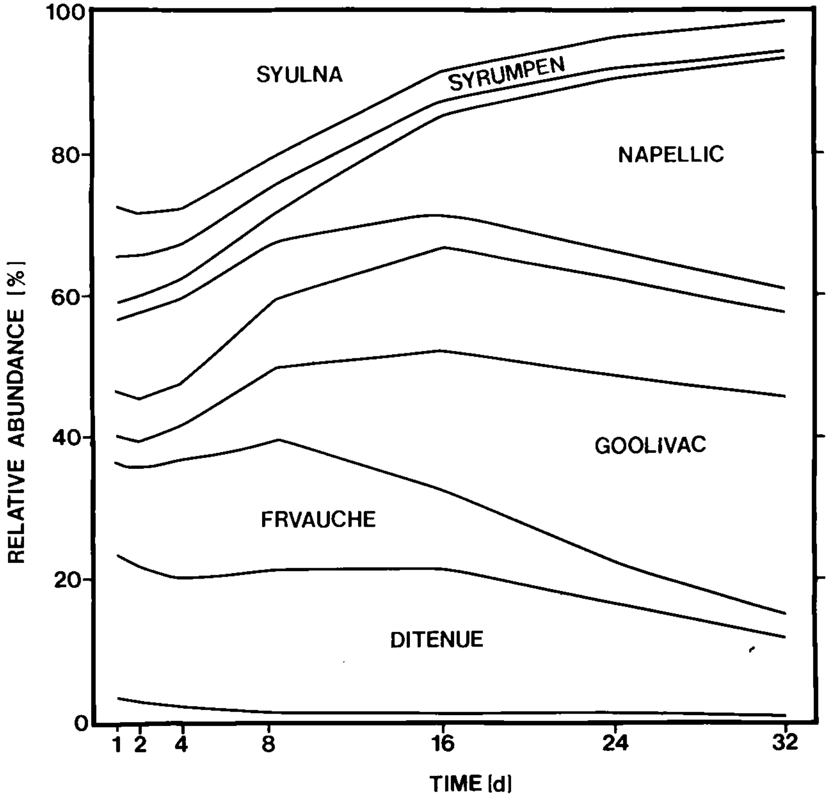

Fig. 14.6. Relative abundances of diatom species during the colonization period when the assemblage was modelled with unaltered estimates of population characteristics. See Fig. 14.1 for species abbreviations. Unlabeled spaces are same species as those in respective locations in Fig. 14.1.

growth rates. Relative abundances of late colonists, now with the slowest growth rates, did not decline during later stages of colonization as relative abundances of other species with slow reproduction rates had in modelled and stream assemblages. The fast late-immigration rates of late colonists were able to sustain their relative abundances, even though pioneers were growing faster.

14.4 DISCUSSION

The range of immigration and growth rates among common diatoms was considerable. Differences among immigration rates of species were greater than differences among growth rates. That did not mean that immigration was a more important factor than growth in accumulation. According to extrapolations of a sensitivity analysis, when 50% changes in growth and

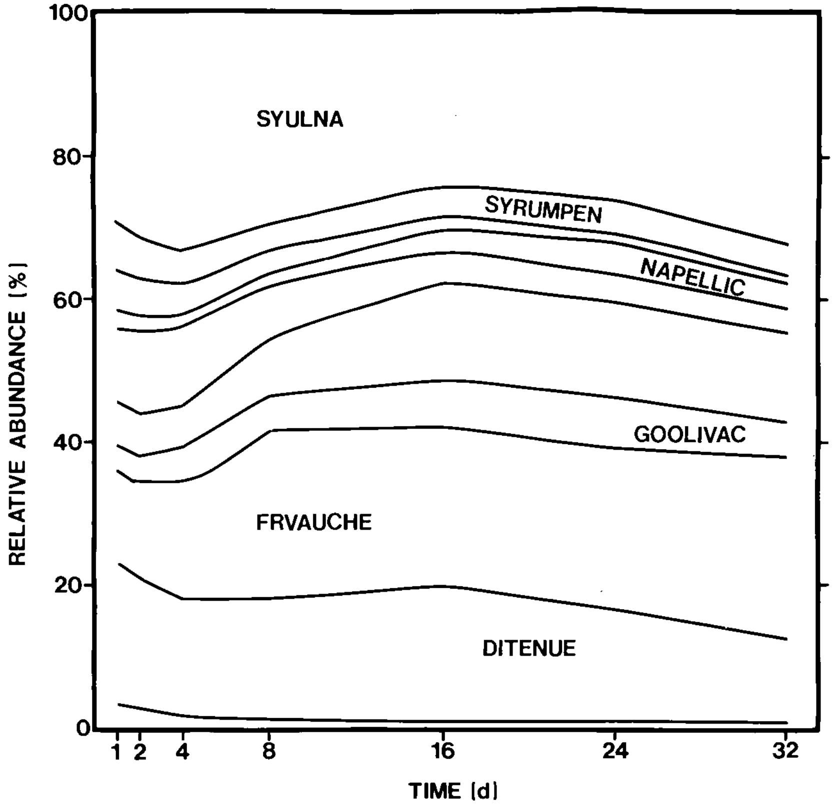

Fig. 14.7. Relative abundances of diatom species during the colonization period when the assemblage was modelled with altered estimates of population characteristics. See Fig. 14.1 for species abbreviations. Unlabeled spaces are same species as those occupying respective locations in Fig. 14.1.

immigration respectively caused six-fold and 50% changes in accumulation (Stevenson, in press), the two-fold differences among growth rates and thirteen-fold differences among immigration rates probably accounted for similar changes in accumulation on substrates after a 32-day colonization. The great differences among diatom immigration rates indicates that immigration, as well as reproduction, can be an important factor in algal colonization and succession on substrates.

Differences in immigration and growth rates among diatom species indicated that some diatoms, in certain habitat conditions, may be specially adapted as pioneer species or late colonists. Pioneer species immigrated most rapidly during early stages of colonization but had the lowest growth rates. If the common suggestion is correct, that nutrient availability to cells decreases with assemblage density, then pioneers may gain a competitive advantage by immigrating rapidly and sequestering nitrogen and phosphorus reserves to sustain low growth rates during later stages of colonization. Late colonists, with fast growth rates and rapid immigration rates during later stages of colonization, may be able to absorb nutrients at lower concentrations (lower K_s) than pioneer species during late colonization when mats and, theoretically, nutrient diffusion gradients develop.

There are alternative hypotheses for species being either fast early-immigrators or fast reproducers and late-immigrators. Alternative hypotheses state that immigration rates are more closely related to densities of algae in the plankton than to interactions with benthic organisms and their modifications of substrate conditions. One alternative hypothesis states that immigration rates of late colonists increased only during late stages of colonization because of episodic changes in abundances of algae in the water. Slight increases in discharge could cause such sudden changes in algal drift as more loosely attached algae drift from substrates. I have observed that wind disturbance of submerged macrophytes can disturb macrophytic substrates and cause increases in algal drift. However, discharge during colonization decreased in Fleming Creek and macrophytes were not present during the winter.

Another alternative hypothesis is that immigration and plankton abundances changed with seasonal variation in habitat conditions and with a shift in species best adapted for fast reproduction during successive colonization periods. Thus, pioneers with fast early-immigration rates had high densities in the water because of high abundances on substrates and high abundances on substrates because their reproductive rates were fast in the past; densities on substrates and in the water decreased because their reproductive rates declined with recent climatic changes. The species that are fast reproducers are best adapted to the new ambient conditions of the present colonization period. Consequently, their abundances on substrates and in the water increase and cause an increase in their immigration rates.

Explanations for changes in immigration rates that involve changes in plankton or biotic interactions with previous colonizers are not mutually exclusive, but are complementary. Although plankton abundances were not estimated during colonization in this study, they should be considered in future research; then, immigration rates in the model of accumulation could be related to plankton abundances. It is also probable that immigration rates were related to benthic algal abundance. Other immigration studies have shown that there are differences in diatom immigration abilities, that diatom immigration rates increase during the colonization period, and that immigration of some diatoms probably increase more than others during the colonization period (Stevenson, 1983). Bothwell (1983), however, did not observe increases in immigration rates during colonization of algae on open-cell styrofoam. Actually, Bothwell's observation further substantiates previous observations that development of surface irregularities (aggregates of algae, detritus, bacteria, and fungi) on smooth substrates enhances immigration rates more than organic coatings (Stevenson, 1983). The surface irregularities of Bothwell's substrates probably interrupted flow, and consequently, additional surface irregularity and coating of substrates with secreted mucopolysaccharides had little effect on immigration.

Algal accumulation rates and community structure were sensitive to changes in both immigration and growth rates. The importance of high immigration rates by late colonists during later stages of colonization was evident after exchanging growth rates between pioneers and late colonists. First, there was no increase in assemblage accumulation when pioneers grew faster than late colonists. Assemblage accumulation was expected to be greater if pioneers were also fast reproducers because pioneers would have longer to reproduce on substrates than late reproducers. Previous study with the accumulation model (Stevenson, in press) had shown that immigration accounts for most of accumulation during the first week of colonization, and growth is most important thereafter. The late colonists in that study did not have fast late-immigration rates, as were detected in this study. Faster immigration by late colonists than pioneers was great enough to compensate for the time lost during which growth on substrates did not occur. The importance of late immigration was also evident when late colonists were able to maintain constant proportions of the assemblage. Pioneers comprised successively small proportions of the assemblage when they were slow growers. Again, immigration of late colonists being faster than pioneers was important for generation of these results.

The importance of variations in immigration and growth rates in controlling species composition and diversity was evident in differences for modelled and altered assemblages. Evenness of abundances of fast immigrators and fast reproducers sustained high diversity during the colonization period, whereas diversity decreased when the same species were fast immigrators and fast reproducers. Eventually, when abundances are high and reproduction accounts for most of accumulation, uneven reproduction rates among species caused a decrease in evenness and diversity. The importance of fast late-immigration rates was again evident in a higher mid-colonization diversity increase and in diversity being sustained longer during colonization in altered than modelled assemblages.

The accuracy of results of this study is difficult to address directly. Future research is being done to study hypotheses that developed during this modelling work. Accuracy of results can be addressed here by examining results of other studies and by examining model assumptions.

Results of other field studies indicate that estimates of immigration and growth rates are close to those observed in other studies. Colonizations studied by Ivlev (1933) and by Korte and Blinn (1983) are particularly well suited for comparison because they include early (less than 7 d) samples and the lack of sudden decreases in accumulation indicate that sloughing did not occur. Their accumulation patterns were shaped similarly to those in Fleming Creek. Curves of log-transformed abundances tended to be straight during the last two weeks of colonization, which indicated that growth was the predominant accumulation process. Slopes of these curves, estimates of growth rates, ranged between 0.1 and 0.3 (excluding highest and lowest current conditions in Ivlev's study), which are similar to growth rates estimated in this study. Strong effects of immigration are evident in both data sets. Given growth rates above, increases from 150 to 10,000 cells/cm^2 on days 1 and 3 (Ivlev, 1933) and at least 13,000 cells/cm^2 on day 3 (Korte and Blinn, 1983) were probably the result of high immigration rates. Immigration rates higher and lower than field or modelled estimates for Fleming Creek have been observed (Stevenson, unpublished data).

Among other assumptions, the model assumed that the relationship between immigration rates could be related to abundances on substrates by a half-saturation constant. Thus, immigration rates increased asymptotically not linearly with abundances on substrates. Immigration could have been related mathematically to the number of algae on substrates in a variety of ways. An asymptotic relationship was chosen because of a combination of factors. The most rapid enhancement of immigration was expected during early stages of colonization as films of adsorbed organic molecules and bacterial secretions developed rapidly, considerably faster than algal accumulations. The rate of immigration enhancement from attached algae, debris, and other organisms interrupting flow should decrease because the proportion of the surface where currents were interrupted by organisms would decrease as additional organisms colonize the substrate. Assume, for example, that the area of the surface around an attached organism, where currents are altered and immigration is enhanced, is a fraction of a circle (a) around it. The circle has the radius of the organism (r) plus a constant distance (c) around the organism (r + c). The area affected around organisms, $a(\Pi(r+c)^2 - \Pi r^2)$, is greater than one-fourth the area around four organisms, $a(\Pi(2r+c)^2 - \Pi(2r)^2)$. Eventually, interruption of flow, and concommittently, related immigration rates, would decrease as areas of substrate affected by aggregates of organisms and debris started to overlap. However, high immigration rates would probably continue to be sustained as drifting algae became entangled in the overgrowth of stalked and filamentous forms. Although immigration rates are not directly and realistically related asymptotically to abundances of algae on substrates, it was judged to be the simplest and most accurate way to generate the immigration pattern hypothesized for colonization. Relating immigration rates to abundances of diatoms on substrates by using a half-saturation constant was judged practical and informative.

Violation of model assumptions could cause overestimation of maximum immigration rates. If emigration and nutrient competition were density-dependent, then maximum growth rates may have been underestimated with data from the last 16 days of colonization. There was some evidence for and against negative density-dependent interactions. If the negative effects of emigration and/or nutrient competition developed before day 16, maximum growth rates and abundance on day 16 would have been underestimated. Abundance on day 16 was underestimated during modelling. However, similarity of estimates of growth rates between days 16 and 24 and rates between days 24 and 32 indicated that growth rates did not decrease during colonization (Stevenson, 1984). If density-dependent emigration or growth inhibition occurred, growth rates calculated for the period between days 16 and 24, when abundances were low, should be greater than the growth rate between days 24 and 32, when abundances were higher. So the assumptions that emigration and density-dependent growth were not important in his habitat seem justifiable.

Violation of other assumptions could cause underestimation of maximum immigration rates. Low model predictions of abundances on day 16 could be explained by overestimating growth rates and underestimating maximum immigration rates. This would have also enhanced early accumulation rates, slowed late accumulation rates, and produced an almost perfect fit between model predictions and observed accumulation patterns. It has been shown that immigration accounts for about 15% and 5% of the accumulation on days 16 and 24, respectively when immigration and growth rates are close to those in this study (Stevenson, 1981). Thus, it seems likely that a modest overestimation of growth rates and underestimation of maximum immigration rates is the best founded explanation for predictions of low abundances on day 16.

The accuracy of estimating immigration and growth rates with the modelling and field procedures used can be judged by comparing model predictions and actual accumulation patterns and comparing model estimates and independent field estimates of maximum immigration rates. Despite slight differences, the fit between modelled and actual colonization was good. Therefore, modelled estimates of immigration and growth rates must have been accurate enough to be informative, and errors due to density-dependent interactions were probably not important in this habitat. It is difficult to judge whether modelling or field estimates of immigration were most accurate. Field estimates of immigration were probably less accurate than modelled estimates because immigration samples were only collected on the first day of colonization. In addition, simulated flow interruption, which enhanced immigration greatly (Stevenson, 1983), did not cover the entire substrate as would occur during colonization. Thus, low field estimates can be explained and high modelled estimates of immigration are within immigration rates that have been measured with field procedures in other habitats. Further evaluation of the accuracy of the modelling and field procedures for estimating immigration and growth will require use of more controlled field procedures.

ACKNOWLEDGEMENTS

I would like to thank Mrs. Leah Kohn, Administrative Assistant, Department of Biology, University of Louisville, for editing and preparing this manuscript. Reviews by Kyle Hoagland and two anonymous reviewers were also helpful.

REFERENCES

Bothwell, M.L., 1983. All-weather troughs for periphyton studies. Water Res., 17: 1735-1741.

Hamilton, P.B. and Duthie, H.C., 1984. Periphyton colonization of rock surfaces in a boreal forest stream studied by scanning electron microscopy and track autoradiography. J. Phycol., 20: 525-532.

Hoagland, K.D., 1983. Short-term standing crop and diversity of periphytic diatoms in an eutrophic reservoir. J. Phycol., 19: 30-38.

Hoagland, K.D., Roemer, S.C., and Rosowski, J.R., 1982. Colonization and community structure of two periphyton assemblages, with emphasis on the diatoms (Bacillariophyceae). Amer. J. Bot., 69: 188-213.

Hudon, C. and Bourget, E., 1981. Initial colonization of artificial substrate: community development and structure studied by scanning electron microscopy. Can. J. Fish. Aquat. Sci., 38: 1371-1384.

Hudon, C. and Bourget, E., 1983. The effect of light on the vertical structure of epibenthic diatom communities. Bot. Mar., 26: 317-330.

Ivlev, V.S., 1933. Ein Versuch zur experimentellen Erforschung der Okologie der Wasserbioconosen. Arch. Hydrobiol., 25: 177-191.

Korte, V.L. and Blinn, D.W., 1983. Diatom colonization on artificial substrata in pool and riffle zones studied by light and scanning electron microscopy. J. Phycol., 19: 332-341.

Lamberti, G.A. and Resh, V.H., 1983. Stream periphyton and insect herbivores: an experimental study of grazing by a caddisfly population. Ecology, 64: 1124-1135.

Pielou, E.C., 1977. Mathematical Ecology. John Wiley & Sons, Inc. New York. 385 pp.

Stevenson, R.J., 1981. Microphytobenthos accumulation and current. Ph.D. Dissertation. The University of Michigan, Ann Arbor, Michigan, USA, 172 pp.

Stevenson, R.J. 1983. Effects of current and conditions simulating autogenically changing microhabitats on benthic diatom immigration. Ecology, 64: 1514-1524.

Stevenson, R.J., 1984. How currents on different sides of substrates in streams affect mechanisms of benthic algal accumulation. Internat. Revue ges. Hydrobiol., 69: 241-262.

Stevenson, R. J., (in press). Mathematical model of epilithic diatom accumulation. In: M. Ricard (Editor), Proceedings of the VIIIth International Symposium of Recent and Fossil Diatoms.

Stevenson, R.J. and Stoermer, E.F., 1981. Quantitative differences between benthic algal communities along a depth gradient in Lake Michigan. J. Phycol., 17: 29-36.

Sumner, W. T. and McIntire, C.D., 1982. Grazer-periphyton interactions in laboratory streams. Arch. Hydrobiol., 93: 135-157.

Zar, J.H., 1974. Biostatistical Analysis. Prentice-Hall, Inc. Englewood Cliffs, New Jersey, USA. 620 pp.