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MIGRATION AND METABOLISM IN A TEMPERATE STREAM ECOSYSTEM¹

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Abstract. Fish migration, total stream metabolism, and phosphorus were studied in New Hope Creek, North Carolina, from April 1968 to June 1970. Upstream and downstream movement of fish was monitored using weirs with traps. Most of the 27 species had a consistent pattern of larger fish moving upstream and smaller fish moving downstream. Both upstream and downstream movements were greatest in the spring. For example, in the spring of 1969, a daily average of seven fish weighing a total of 1,081 g were caught moving upstream, and 17 fish weighing a total of 472 g were caught moving downstream. Although more moved downstream than up, the larger average size of the fish moving upstream resulted in a large transfer of fish mass upstream.

Diurnal oxygen series were run to measure the metabolism of the aquatic community. Gross photosynthesis at the principal sampling station ranged from 0.21 to almost 9 g O₂ m⁻² day⁻¹, and community respiration from 0.4 to 13 g O₂ m⁻² day⁻¹ (mean of 290 and 479 g O₂ m⁻² yr⁻¹). Both were highest in the spring. Area values of metabolism were often similar for different parts of the stream, but both production per volume and respiration per volume were always much larger near the headwaters than farther downstream. This was apparently due to the dilution effect of the deeper water downstream. Migration may allow populations to take advantage of such differences in productivity by maintaining young fish in areas of high productivity. Other effects of migration may include: prey control, recolonization of defaunated regions, genetic exchange, and mineral distribution.

An energy diagram was drawn comparing energies of insolation, leaf inputs, currents, total community respiration, fish populations, and migrations. About 1% of the total respiration of the stream was from fish populations, and over 1 year about 0.04% of the total energy used by the ecosystem was used for the process of migration. If it is assumed that upstream migration is necessary to maintain upstream stocks, which may be periodically decimated by droughts, each Calorie invested by a fish population in migration returns at least 25 Calories (kilocalories). Even without that assumption returns are 3-fold.

Analysis of phosphorus entering and leaving the watershed studied indicated that flows were very small relative to storages and that this generally undisturbed ecosystem is in approximate phosphorus balance. Upstream migrating fish were important in maintaining phosphorus reserves in the headwaters of New Hope Creek.

Animal migrations are a conspicuous and important phenomenon in many ecosystems of the world. One may ask the following questions about these movements: Why does migration exist? Specifically, what is the role of migration in the many and varied ecosystems in which it is found? Under what conditions do groups of animals that migrate have selective advantage over other groups that do not migrate? How much energy is required to migrate, and can energy be gained by migration? What effect does migration have on the ecosystem of which it is a component, and vice versa? What percentage of an ecosystem's energy budget is tied up in maintaining a migratory component? This study considers the above questions by analyzing migration as a functional component of a stream ecosystem. Seasonal patterns of metabolism and fish migration were measured in field studies in New Hope and Morgan creeks, Orange and Durham Counties, North Carolina, from April 1968 to June 1970. The results are considered in relation to other patterns of animal

migration and to some aspects of current ecological theory.

LITERATURE REVIEW

Migration may bring adult fish back to areas in which their ancestral eggs developed (Meek 1916), followed by a return migration of young. Heape (1931) lists three principal types of migration: alimetal, in response to food variations; climatic, in response to extremes in climate (particularly temperature), and gametic, in association with reproduction. Allee et al. (1949) state that an organism has but three choices when exposed to adversity: it may die, adjust, or migrate. Migration is considered a mechanism for removing the organism from unfavorable circumstances. The reason for return during more favorable circumstances is not as clearly spelled out.

Competition for food, principally as a result of reproductive excess, is suggested as the factor favoring the development of mechanisms for seasonal occupation of fluctuating environments (Mayr and Meise 1930). Students of S. C. Kendeigh (Siebert 1949, West 1960, Cox 1961, Zimmerman 1965)

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have undertaken a rigorous approach to this problem. They have found that migrations could improve the energy balance of birds in terms of calories gained by being in different places at different times.

Cox (1968) suggested divergent adaptation by both morphological and ethological means. Given interspecific or intergeneric competition, animals may broaden their niche by the exploitation, for example, of different food sources; or the exploitation of spatially different environments. There may be a limit to food niche divergence that can be sustained without the exploitation of new physical environments. Mechanisms and supporting data for this are discussed by Cox.

Odum and Hoskin (1958), Simmons and Hoese (1959), Hellier (1962), Odum and Wilson (1962), Copeland (1965), and Odum, Copeland, and McMahon (1969) emphasize how the very large spring primary production of Texas estuaries and similar regions is utilized by migrating animals, especially during their juvenile stages, and how the migratory patterns are such that maximum use is made of the pulse in energy availability in those ecosystems during the late spring. "Seasonal and diurnal migrations not only make possible occupation of regions which would be unfavorable in the absence of migration but also enable animals to maintain a higher average density and activity rate" (E. P. Odum 1959).

Margalef (1963, 1968) examined the reproductive migrations of animals in relation to the energetic characteristics of ecosystems. According to Margalef less "mature," or less organized, ecosystems are less efficient in their use of energy and support less biomass per unit of energy flow than do mature ecosystems. Thus there is an excess of available energy that may be exported or exploited. More mature systems with a great complexity of biological interactions, and resultant greater efficiency in energy use, produce no, or at least less, excess energy.

Margalef continues with the argument that those individual organisms that have developed behavior patterns leading to reproduction in less mature ecosystems have left behind more offspring and, therefore, are selected for. Even the seemingly enigmatic situation of eels and salmon can be explained in this way, he says, since the specific regions that both adult animals inhabit are more mature than the specific habitat of the larvae of the respective fish.

Certain models of migrating zooplankton imply that the energy saved by living one-half of the day in colder water, where metabolism is less, is greater than the energy used in the process of migration (McLaren 1963), and that migrations aid in the maximum exploitation of food resources (Kerfoot 1970). The energy saved or gained can then be used for growth and reproduction.

Possible selective advantages for fish migration in-

clude: dispersion of young, optimization of population density effects, regulation of numbers and maximization of environmental productivity usage (Northcote 1967). These perhaps may be summed up by considering migration as "an adaptation for abundance by making the most of a varied environment." (Harden Jones 1968). In reviewing possible causes for the evolutionary development of migration in fishes, Foster (1969) considers the possibilities of changes in food availability, climate, salinity, and topography over geologic time. The interaction of exploitation of new resources with the need for the adults or eggs to stay within certain physiological limits may have set the stage for the first fish migrations. This agrees with Meek's interpretation.

One common factor in all these previous studies is the role of migration in increasing the flow of energy, or decreasing the energy loss, to populations involved. Movements away from food-poor regions in the winter, as well as to seasonally energy-rich areas, can be considered in these terms. The energy cost of migration has been considered by Idler and Clemens (1959), McLaren (1963), Brett (1970), and Kerfoot (1970).

Migrations, ecosystems, and feedback loops

Many advantages or disadvantages accruing to a population from migration are relatively straightforward and obvious. Influences from the process of migration on an ecosystem that supports the migrants are less obvious but in several cases well documented. Odum (1967*b*, 1971) considers mineral distribution, population control, and information exchange the currency that is used in feedback loops to reinforce the selective patterns that feed energy to various components. Mutually reinforcing interactions of populations and ecosystems have selective advantages that are stronger than the exploitive use of one on the other. Resource sinks that develop without feedback loops are self-degrading since they weaken the supporting system that they depend upon.

A classic example exists in fisheries literature. Juday et al. (1932) observed that the Pacific salmon carcasses must be important in resupplying the nutrient-poor stream-lake ecosystems that constitute the nursery ground of several species of young salmon. Quantitative work on this was done by Donaldson (1967) and Krokhnin (1967), who demonstrated the vital role of adult salmon in bringing phosphorous to the headwaters. In years of heavy spawning runs the amount of this element brought to the headwaters by the fish equals or exceeds that supplied by all other sources. Growth and survival of juvenile salmon have been correlated with the availability of phosphorus (Parsons et al. 1970).

A similar situation, with Amazonian crocodile-like caimans acting as intermediaries in place of bears,

has been described by Fittkau (1970). With the tremendous importance of some trace elements now being recognized (Hutchinson 1957, Goldman 1969), possibilities do exist for migrations to control critical nutrients. Implicit in some of Odum's Texas Bay writings is the role of migration in supplying the bays with nutrients, energy links, genetic information, and the maintenance of community structure, biomass and energy flows.

Movements of fishes in streams

Nearly all studies of fish migration within fresh water have occurred with species that are associated with either lakes or the ocean. Only a small amount of the total information available concerns fish that spend all their time within one fresh-water stream. Some studies have found movement of stream fish to be important (Stefanich 1952, Brown 1961, Bjornn and Mallet 1964, Behmer 1964, Hunt 1964, Shetter 1968); other studies have found relatively minor migration in stream fish (Bangham and Bennington 1938, Scott 1949, Tate 1949, Allen 1951, Gerking 1959, Gunning and Schoop 1961). One possibility suggested for the contradictory findings between and within these studies has been supplied by Funk (1955), who suggested that many streams have both a mobile and sedentary population of each species. Heavy movements of fish in streams adjoining lakes are well documented, however (Shetter 1938, Raney and Webster 1942, Carbine and Shetter 1943, Warner 1959, Hartman, Northcote and Lindsey 1962, Niemuth 1967). These movements are generally spawning runs to streams, either above or below the lakes.

DESCRIPTION OF STUDY AREAS

New Hope Creek and Morgan Creek are small warm-water streams located in Orange, Durham, and Chatham counties Central North Carolina, (Fig. 1) within the Cape Fear watershed. The principal study area is located in the Korstian Division of Duke Forest between Chapel Hill and Durham. In this region New Hope Creek has a moderate gradient (4.0 m km^{-1}), a mean width of about 10 m, and an average depth of about 0.5 m. Rocky rapids alternate with large, deep pools, and much of the stream bottom is bedrock. The water is normally clear, although the stream becomes turbid during floods. Morgan Creek is similar but only about 5 m wide.

New Hope Creek is relatively unaffected by man's activities and has the biological characteristics of a diverse and healthy stream. Immature stages of mayflies, stoneflies, caddis flies, and many other insects are abundant in the riffles and the fish life is diverse. The North Carolina Division of Inland Fisheries has classified the creek as a "Robin-Warmouth" stream (Carnes, Davis, and Tatum 1964); however, fishing pressure is virtually nonexistent in the portion of the creek studied. Much of the watershed lies within the Duke forest and the rest runs through forested areas with an occasional farm. Very slight additions of domestic sewage enter from several sources near the headwaters. About 3.8 km below the lower limits of the study area, however, treated sewage from the city of Durham enters the creek. Very low oxygen (1.0 ppm) was occasionally found below the point of sewage addition, at station 8, during this study.

New Hope Creek is subject to extreme fluctuations in water levels. During the 2 years studied, summer water flows dropped to almost zero, although numerous large pools remained. Fall, winter, and spring floods were common and raised the water flow to as much as $8.1 \text{ m}^3 \text{ sec}^{-1}$ ($286 \text{ ft}^3 \text{ sec}^{-1}$). During these periods the stream overflowed its banks.

METHODS

The general plan for the study over a 27-month period included studies of upstream and downstream migration at four double-weir stations (4, 5, 6, and M; Fig. 1) and measurements of photosynthesis and respiration at seven stream stations (1, 2, 3, 4, 6, 7, 8; Fig. 1) using changes in oxygen concentration. Stations 2, 4, and 6 were sampled most frequently. The discharge at these stations is about 1:2:10 during normal spring levels. Stream width and depth profiles were taken at 50- or 100-m intervals for 1 or 2 km above these stations, and the results used for metabolic computations.

Total dissolved and suspended phosphorus and nitrogen in stream-water samples were analyzed colorimetrically on a Technicon Autoanalyzer (FWPCA,

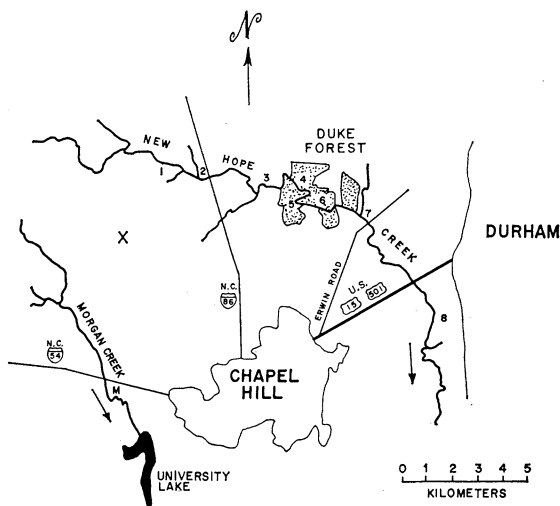


FIG. 1. Location of sampling stations on New Hope (1-8) and Morgan (M) creeks, central North Carolina. Arrows show direction of stream flow. An X marks the IBP site where subcanopy insolation was measured.

1969). Leaves being washed downstream were measured by removing and drying 24-hr accumulations on the fish weirs, or by subsampling for 15 min per day with a fish seine during flood levels.

Community oxygen metabolism studies

Entire ecosystems, like individual organisms, capture and use energy to maintain life. This process can be measured by determining the total amount of oxygen, or carbon dioxide, produced and consumed. Estimates of energy utilization can be made from measurement of metabolic gas usage, although knowledge of respiration quotients is necessary for accurate conversions (Brody 1945, Odum and Hoskin 1958, Rich 1970). In New Hope Creek oxygen was measured both by the azide modification of the Winkler method (American Public Health Association 1965) and with an automatic field temperature and oxygen recorder (Rustrak Model 192). Percentage saturation of the water was calculated from the oxygen solubility values of Churchill, Bucking-

ham, and Elmore (1962). Diffusion constants, necessary for accurate estimates of oxygen changes, were determined by three methods: the diurnal curve method (Odum 1956, Odum and Hoskins 1958), the stream morphology method (Churchill et al. 1962), and the dome method (Hall, Day, and Odum, in preparation). The diurnal curve method gave inconsistent and apparently erroneously high results and was not used for these studies. The reason for the high values by this method was that evening respiration was greater than morning respiration (Odum and Wilson 1962, Owens 1969). For these studies the stream morphology method, which was verified by the dome method, was used to determine the diffusion constant; this constant varied from day to day as the water level changed (Hall et al., in preparation).

The two-station analysis of metabolism, which is more accurate than the single-station method, was generally impractical on New Hope Creek because of the necessity of sampling at three to five locations

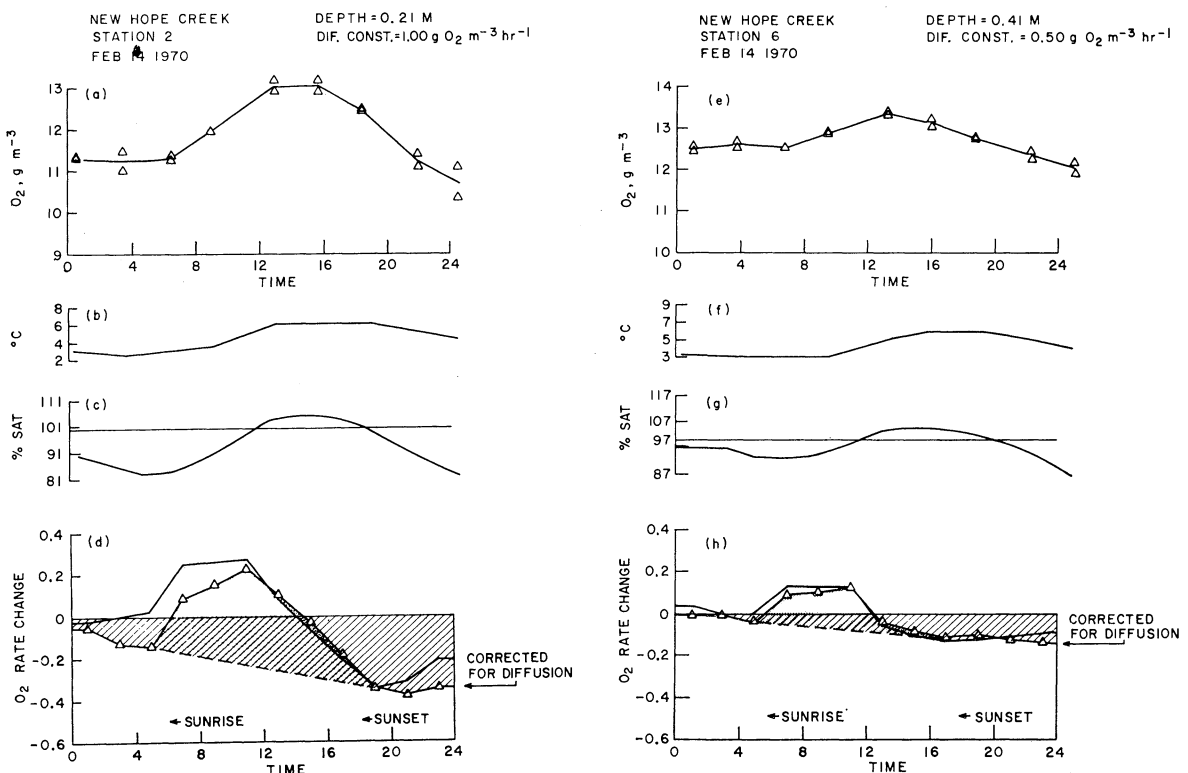


FIG. 2. A representative analysis of community metabolism for a single upstream station (2) in New Hope Creek. (a) Mean oxygen concentration based on Winkler determinations. Triangles represent single samples. (b) Temperature at 3-hr intervals. (c) Percentage saturation of the average of the two Winklers at the temperature of the sample. (d) The unmarked line is the rate of change of oxygen concentration in $\text{g m}^{-3} \text{hr}^{-1}$. The line with triangles depicts rates of change after correction for diffusion of oxygen across the air-water interface. The stippled area represents the gross photosynthesis of the water mass represented by these water samples. The crosshatched area is estimated gross community respiration. Planimetry is used to measure these areas, or a computer program may be used. The depth is average depth in meters for 1 hour's flow distance above sampling station. Figures 2e-2h represent a similar analysis on the same date at a downstream station where volume metabolism is less. Volume metabolism is corrected to area metabolism by multiplying by depth, $\text{g m}^{-3} = \text{ppm} = \text{mg ml}^{-1}$.

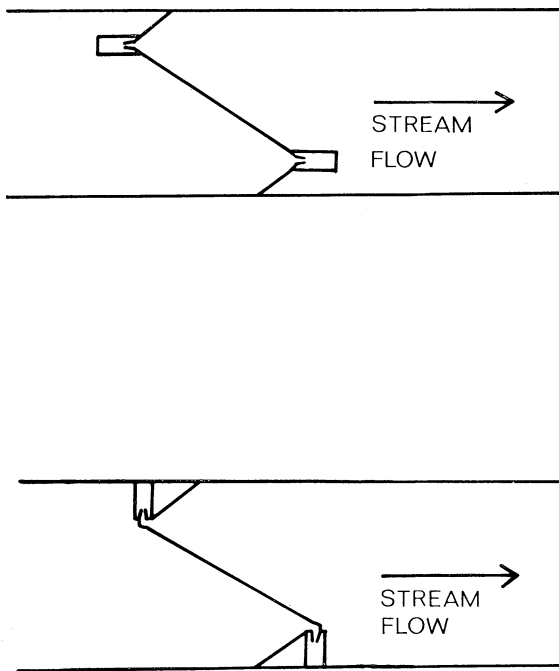


FIG. 3. Schematic diagram of fish sampling weirs and traps used for these studies. The upper diagram represents the normal trapping arrangement. The lower diagram represents the arrangement used for checking sampling bias. See text for explanation.

that were far apart. However, a two-station analysis on February 14, 1970, at both stations 2 and 6, indicated that in these short stretches of New Hope Creek, equivalent to the distance that water flows in 1 hr, the oxygen curve at one point is similar to that in another and the single-curve method could be used. The basic procedure in estimating stream metabolism by this method is to measure oxygen and temperature at one station every 2 or 3 hr. Sampling sites were chosen that were well mixed and showed no vertical oxygen stratification. The data are then plotted and graphically analyzed (Fig. 2). A sloping daytime respiration line was used (Odum and Wilson 1962). This is probably a representation of all daytime respiration except photorespiration. Calculations were done on an IBM system 360 model 70 computer linked with a Calcomp plotter. Computer calculations were periodically checked by hand throughout the study.

Design of weirs and traps used for measuring fish movement

Weirs were variations of those used by Shetter (1938) and were placed in shallow riffle or small pool portions of the streams. "Hardware cloth" (wire screening 0.6 cm: ¼-inch mesh) was placed across the stream at an angle such that migrating fishes would be funneled into traps placed at either

side of the stream (Fig. 3, top). The lower 30 cm or so of the screening was bent at a 90° angle to the vertical and placed on the rock-cleared stream bottom. Rocks were then placed on the top of this screening, and the entire boundary of the screen and stream bottom was checked for holes through which fish might pass. This was modified in the summer of 1969 to prevent leaf accumulation on the upstream side of the hardware cloth weirs during high water. Steel electrical conduit pipes spaced at 0.9 cm intervals by plastic collars were used as recommended by Reimers (1966).

A fish-tight border between the lowermost pipe and the bottom of the stream was created by bending a ½-m-wide section of hardware cloth over the pipe and piling rocks on either side of this. The pipes were held in position by concrete-anchored wooden frames that allowed the pipes to be inserted and removed. Hardware cloth trap-entrance cones provided entrance to the actual traps.

The traps placed at either end of the weir consisted of frames of 2- by 2- by 66-cm or 2- by 2- by 132-cm pieces of aluminum covered with 0.6-cm wire cloth to form a rectangular trap. A cone was constructed at one end that fitted into a corresponding cone in the weir to form a tight fit that could be easily separated for fish removal. The other end of the trap contained a door to facilitate fish removal.

Each day the fish were removed from the traps and individually weighed. Smaller fish were marked by a fin clip distinctive for each station. Fish larger than about 80 g were tagged with individually numbered dart tags (Floy Tag and Manufacturing Company). The live fish were returned to the water about 50 m upstream or downstream from the weirs, in the direction they were moving.

Check on possible sampling bias.—The consistently greater catch in fish mass moving upstream compared to fish mass moving downstream raised the possibility of sampling bias—that fish enter the upstream trap more readily than the downstream trap. This was considered unlikely, as a certain additional amount of effort would have been needed by the fish to swim up into the trap, whereas a fish entering the downstream trap could drift passively with the current. However, this possibility was checked by a "sideways" trap arrangement, designed so that fish entering from either upstream or downstream would have to enter the actual trap perpendicular to the current (Fig. 3, bottom). In theory, if there were a substantial error introduced by the facing of the weirs this would become apparent by extreme variations from the expected ratio of fish moving upstream to fish moving downstream; however, on the 10 days that these traps were used, about the same weight ratio of upstream to downstream movement occurred as during normal sampling (1.82 vs. 2.02),

and no corrections of raw fish-movement data were made.

The trapping procedure used in this study is based on the assumption that it is much easier for a fish to swim into the traps than to swim out of them. The cone entrances make this seem intuitively true. However, this was checked by a series of 18 sets of experiments in which fish that were already caught in the traps were left in them for an additional 24 hr. Thus the rate of trap escape was measured.

A total of 132 various-sized fish weighing 10,364 g was placed in the traps. Of these, 36 fish weighing 2,517 g escaped over 24 hr. Since each fish normally trapped would have been in the traps an average of 12 hr (one-half the trapping-time interval) it was assumed that the escape rate for a normal day would be half of the 24-hr escape rate. (Casual observations and several direct checks indicated that fish moved about equally during different times of the day and night.) Correcting the escape rate to the mean 12-hr period gives an adjusted mean daily escape rate of 13.6% for numbers of fish and 12.3% for mass of fish. No important difference in escape rates for different traps was noted except that the smaller (66- by 66- by 132-cm) trap, when used to catch fish moving downstream, had a greater escape rate than other traps. This trap was replaced in February 1969 by a larger one from which virtually no fish escaped. Since the escape rates were not excessive, and since they were nearly identical for upstream and downstream, no corrections were made in data used for analysis. Stream migration was defined as what was found in the traps after each 24-hr set.

Sampling modifications during high waters.—New Hope Creek was subject to extreme flooding during the fall, winter, and spring months. The magnitude of some of the flows made any sampling of migration impossible; however, over the course of this project various sampling modifications were made to increase the level at which fish counts could be made. Initially the height of the weir was increased with additions of wire cloth. This reached a practical limit at a stage level of about 46 cm above zero flow, and even less during periods of heavy leaf flow. In February 1969, the principal sampling station was moved 100 m upstream to a wider portion of the stream so that a given increase in water flow would cause less increase in water height. These substations together are considered station 6. This change in site provided a means of sampling to a stage level of about 76 cm above zero flow, if leaf flow was small. During high waters a series of rock and wire supports were utilized to maintain the weir in an upright position. Removal of fish and general maintenance were performed two, three, or four times each day during flows that approached the limit of sampling. During the fall of 1969 the entrance cone pointing down-

TABLE 1. Fish captured in New Hope Creek and groupings used to simplify analysis

Analyzed as	Common name ^a	Scientific name ^a
B. crappie	Black crappie	<i>Pomoxis nigromaculatus</i> (LeSeur)
Bluegill	Bluegill	<i>Lepomis macrochirus</i> Rafinesque
B h. Chub	Bluehead chub	<i>Hybopsis leptocephalus</i> (Girard)
Bullhead	Flat bullhead	<i>Ictalurus platycephalus</i> (Girard)
	Snail bullhead	<i>Ictalurus brunneus</i> (Jordan)
Chubsucker	Creek chubsucker	<i>Erimyzon oblongus</i> (Mitchell)
Creek chub	Creek chub	<i>Semotilus atromaculatus</i> (Mitchell)
Darter	Johnny darter	<i>Etheostoma nigrum</i> Rafinesque
	Piedmont darter	<i>Percina crassa</i> (Jordan and Brayton)
H f. shiner	Highfin shiner	<i>Notropis altipinnis</i> (Cope)
Madtom	Margined madtom	<i>Noturus insignis</i> (Richardson)
Pickereel	Chain pickerel	<i>Esox niger</i> (Le Seur)
	Redfin pickerel	<i>Esox americanus</i> Gmelin
Redhorses	Smallfin redhorse	<i>Moxostoma robustum</i> (Cope)
	V-lip redhorse	<i>Moxostoma collapsum</i> (Cope)
Pirate perch	Pirate perch	<i>Aphrododerus sayanus</i> (Gilliams)
Pumpkinseed	Pumpkinseed	<i>Lepomis gibbosus</i> (Linnaeus)
R. sunfish	Redbreast sunfish	<i>Lepomis auritus</i> (Linnaeus)
Larger notropis	White shiner	<i>Notropis albeolus</i> Jordan
	Sandbar shiner	<i>Notropis scepclus</i> (Jordan and Gilbert)
W m. shiner	Whitmouth shiner	<i>Notropis alborus</i> Hubbs and Rancy
Others	American eel	<i>Anguilla rostrata</i> (LeSueur)
	Bowfin	<i>Amia calva</i> Linnaeus
	Gizzard shad	<i>Dorosoma cepedianum</i> (LeSueur)
	Green sunfish	<i>Lepomis cyanellus</i> Rafinesque
	Largemouth bass	<i>Micropterus salmoides</i> (Lacepede)
	Speckled killifish	<i>Fundulus rathbuni</i> Jordan and Meek

^aNomenclature used follows "A list of common and scientific names of Fishes from the United States and Canada," 1960. American Fisheries Society Publication No. 2 Waverly Press, Inc., Baltimore. 102 p.

stream was lined with a stiff, clear, plastic sheet so that clogging of this cone with leaves during high water would not occur.

The final major modification was the construction in August 1969 of the pipe weir previously discussed. This allowed sampling to a stage level of about 76 cm above zero flow, even during periods of moderately heavy leaf discharge. Sampling was impossible during higher stage levels; however, floods of this magnitude rarely occurred during periods of expected heavy migration.

Methodology of handling species and species groups for analysis.—Due to some uncertainties in taxonomy during the beginning of this study, and to the necessity of simplifying the large amounts of data for computer analysis, all organisms were placed into one of 21 taxonomic groups as listed in Table 1. All taxonomic groups of more than one species are listed below.

"Pickerels" included both chain pickerel (*Esox niger*) and redfin pickerel (*Esox americanus*), but the redfin pickerel was captured only as a rarity. Flat bullhead (*Ictalurus platycephalus*) has recently been subdivided into two species, *I. platycephalus* and *I. brunneus*. They are considered as one species for this study, although both are common in New Hope Creek. "Redhorses" include both v-lip redhorse (*Moxostoma collapsum*) and the smallfin redhorse (*Moxostoma robustum*). About two-thirds of the

redhorses captured were v-lip. The patterns of movement of the two species were not obviously different.

"Larger *Notropis*" included several species that were morphologically quite similar. The most abundant of these was the white shiner, *Notropis albeolus*, although the sandbar shiner, *Notropis scepticus*, and probably several other species, were also taken. "Darters" were generally Johnny darter, *Etheostoma nigrum*, although some Piedmont darters, *Percina crassa*, were also captured.

"Crayfish" included members of up to four species listed as being present in New Hope Creek (H. Hobbs, mimeographed checklist). No attempt was made to separate these into species. "Frogs" included several species, and "Turtles" included four species. "Others" included American eel, *Anguilla rostrata*; bowfin, *Amia calva*; gizzard shad, *Dorosoma cepedianum*; green sunfish, *Lepomis cyanellus*; largemouth bass, *Micropterus salmoides*; speckled killifish, *Fundulus rathbuni* and toads, snakes, wood ducks, muskrats, large bugs, and various other organisms. No more than 20 of any of these were captured with the exception of toads.

RESULTS

The most important findings of this study were the following: (1) The volume metabolism of New Hope Creek was inversely proportional to the depth. This meant that in the upstream, shallower reaches of the stream both gross primary production and community respiration were more concentrated than in downstream, deeper reaches, even though the areal metabolism was often similar. (2) Movements of stream fish were large and consistent, with heaviest migrations in the spring. On some days up to 20 kg of fish were captured moving upstream at one location. There was a general pattern of many small fish moving downstream and fewer, larger fish moving upstream, apparently to die and not return. This resulted in a large displacement of fish biomass upstream.

Stream metabolism

The annual gross photosynthesis at station 6, which was the most heavily sampled, was 290 g O₂ m⁻² yr⁻¹ (640 g O₂ m⁻³ yr⁻¹). Community respiration at the same station was 479 g O₂ m⁻² yr⁻¹ (1,030 g O₂ m⁻³ yr⁻¹). Both photosynthesis and respiration were least in the winter (Fig. 4). Primary production increased as the season progressed, reaching a peak in March and April when light striking the surface was also maximal. Shading of the surface by the forest canopy reduced insolation at the stream surface after late March. Respiration followed a pattern similar to photosynthesis but had a secondary pulse in October. Extremely high values of respiration were associated with either high photosynthesis,

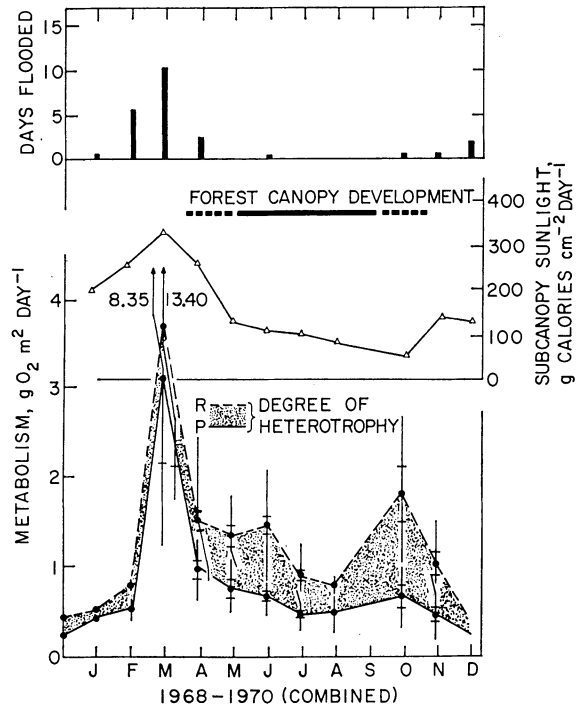


FIG. 4. Annual areal oxygen metabolism and some associated phenomena at station 6. The upper graph represents the mean number of days per month of heavy floods, defined as at least 76 cm above the level of zero stream flow. The middle graph gives mean monthly subcanopy insolation determined on days on which stream metabolism was also measured. Included is an approximate representation of the forest-canopy shading effect. The lower graph is the annual oxygen gross photosynthesis and gross community respiration based on 60 diurnal analyses over 27 months. Points represent mean monthly values, vertical bars are the range of values, and horizontal bars are 1 standard error above and below the mean.

or with low water levels and large leaf inputs in late summer and fall. The very highest values of photosynthesis and respiration were associated with a small flood in March, although metabolic measurements were not normally taken during periods of flooding.

New Hope Creek exhibits an annual variation in the ratio of photosynthesis to respiration (Fig. 4). The stream as a whole is nearly autotrophic in the winter and early spring, and becomes increasingly heterotrophic during the summer and fall. Only rarely, on a few days in March and April, was the stream producing as much energy as it was using.

The more shallow regions of New Hope Creek invariably had greater daily oxygen changes than deeper regions (Fig. 2). Since Winkler or electrode oxygen values are measurements of volume relationships of oxygen to the aqueous solute (mg or ml liter⁻¹, or g m⁻³), this means the volume metabolism was greater in the shallower regions of the stream. Volume metabolism is converted to areal

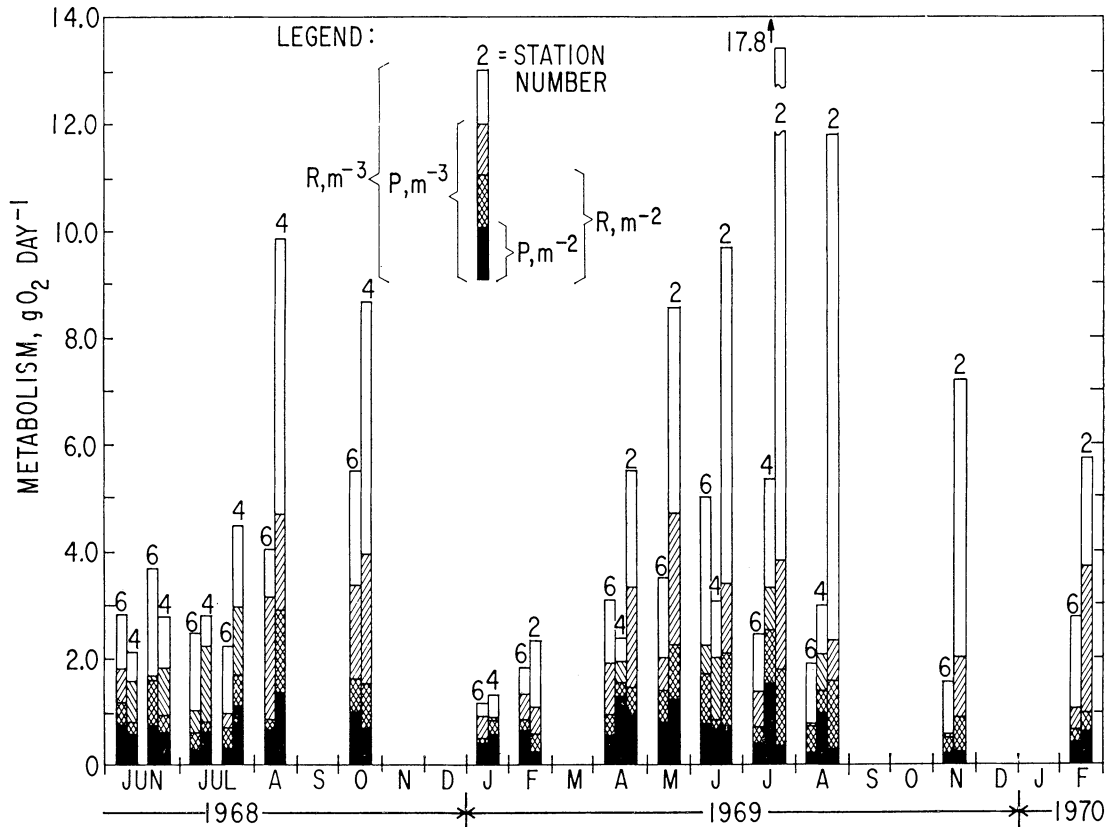


FIG. 5. Seasonal and geographical relation of area and volume gross metabolism in New Hope Creek. This graph is difficult to fully understand and the reader who is not directly interested in stream metabolism is referred back to Fig. 2(d) and 2(h) for a more easily understood representation of the phenomena of greater volume metabolism in shallower waters. In Fig. 5 each group of two or three bars represents area and volume metabolism on the same day at different stations. Station 2 is farthest upstream, station 6 is farthest downstream, and station 4 is intermediate. It is important to read each value from the top of the respective solid, right-slanted, left-slanted, or clear box to the base of the graph. On some days, for example, the first sampling date at station 6, production per volume is greater than respiration per area; on others, such as at station 4 on the same date, the converse is true. Thus it is important to read each bar carefully.

metabolism (g m^{-3} to g m^{-2}) by multiplying by the mean depth of each reach, thus the shallower, more metabolically active regions tend to have areal metabolism often similar to deeper, but less metabolically active regions (Fig. 5). Station 2, which was one-half to one-third the depth of station 6, depending on season, has, on the average, 2.25 times greater volume photosynthesis, and 3.23 times greater volume respiration than station 6. Areal photosynthesis, however, was only 1.06 greater, and areal respiration 1.34 times greater at the upstream station. Thus the areal values of stream metabolism are more similar than the volume values, although metabolism was greatest upstream for all ways expressed.

The relation is also manifest as the stream becomes shallower during the summer. At stations 2 and 4, from May through August, the areal metabolism is relatively constant, but the volume metabolism becomes much greater. Station 6 shows this

in 1968 but not in 1969. The intermediate station 4 is seemingly anomalous. It was lower in volume metabolism than either station in the spring, but higher than station 6 in the summer. This situation is caused by the peculiar morphology of that region. The sampling station is located in a long shallow pool a few hundred meters downstream from the deepest and longest pool in the entire study area. Thus the oxygen content measured at station 4 is the integral of the effects in the shallow and the deep stretches. During the summer the flow is much slower, or even absent, and therefore, the average depth influencing the metabolism is much less. The relatively high areal metabolism at this station during the summer may be a reflection of a possibly high estimate of depth. This potential error is not present at the other stations since the depth profiles were much more uniform. Other stations (1, 3, and 7), which were sampled less frequently, also had volume me-

tabolism that is inversely related to depth. Station 1, which is very shallow, had a diurnal range in oxygen even greater than station 2 on the one day it was sampled.

Fish movements

Analysis of total movement at principal sampling station.—During the 27 months (799 days) of this study, fish movement at station 6 was sampled on 455 days. During this period 6,034 fish and other organisms were captured in the traps at the principal sampling station, 2,655 moving upstream and 3,379 moving downstream, for a daily average of 5.8 organisms moving upstream and 7.4 moving downstream. The total mass (live weight) of the organisms captured at station 6 moving upstream was 187,927 g and moving downstream, 93,092 g, for a daily unweighted average of 411 g and 204 g, respectively. Fish alone accounted for 170,229 g moving upstream, 47,964 g moving downstream, and 73% of the total number of all the organisms captured.

Thus for this study, 1.27 times more organisms were captured moving downstream than upstream, and 2.02 times more mass of organisms was captured moving upstream. Although more animals moved down than up, the larger size of those moving up contributed to a net movement of mass upstream. A number of very large snapping turtles moving downstream contributed heavily to the difference between the total mass of fishes moving downstream and the total mass of all organisms. For fish alone, 3.58 times more mass was sampled moving upstream than downstream.

Of the 6,034 fish and other organisms captured at

the principal sampling station, 417, or 6.9%, were marked from previous captures (6.7% moving upstream, 7.1% moving downstream). This very low recapture rate indicated either that, in general, the fish were migrating and “home range” (Gerking 1959) movements were not being intercepted, or that the fish became very trap shy after one encounter.

Figure 6 summarizes by month the movements of all organisms captured at station 6, the principal sampling station. The maximum number and weight of organisms captured was in the spring months of the 3 years sampled. The greatest mass moving was consistently in March and April, and the greatest number of animals moving was in April, May, and June. Movement was much less during low water in the late summer and during the winter months. The seasonal pattern of movements was quite similar from one year to the next, although movements in 1969 were greater than movements during 1968 or 1970.

During the spring, summer, and fall any substantial rise in water level was invariably accompanied by increased fish migration, particularly upstream. The largest fish movements, however, were during normal water levels in early April 1969. There was apparently little or no fish movement regardless of water level when the water temperature was below about 7°C. There was also no indication that small fish were necessarily swept downstream by flood waters as occurred in Valley Creek, Minnesota (Elwood and Waters 1969), although sometimes they would move downstream during periods of high water.

Many more very small fish may move downstream than were measured in this study, since the mesh size on the weir and traps was large enough to let any fish smaller than 1 or 2 g pass through. Plankton nets hung in the current on 6 separate days during periods of heavy migration of larger fish caught only one small darter. More extensive sampling could possibly give very different results. On May 15, 1970, leaves plastered on the side of the downstream trap formed a barrier in which was observed a school of about 250 tiny (1.3-cm) fish. Complete identification was impossible but they appeared to be some species of *Notropis*. How often this occurs when the movement is not observed is a matter for another study.

When the upstream stations were sampled simultaneously with station 6 a movement of total mass at least as great as at the downstream station was observed. Upstream movement of mass was again generally greater than downstream movement. (Table 2). Thus there was no diminution in movement toward the headwaters, although the few recaptures of marked fish between stations indicated that movement may have been by displacement or “leapfrog-

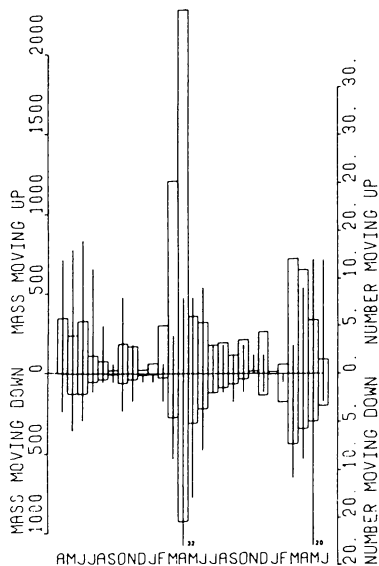


FIG. 6. Average daily migration by month. Mass is in grams moving per day. Numbers are represented by lines and mass by bars.

TABLE 2. Summary of trap catches at stations 4 and 5, New Hope Creek, compared with values for station 6 (principal station) during the same period, and summaries for Morgan Creek

Date sampled	Location	Number moving up	Number moving down	Mass moving up (g)	Mass moving down (g)
1968					
June 5–Sept. 2	Stations 4 and 5 ^a	782	not sampled	18,725	–
	Station 6	567	165	9,034	4,732
1968					
Oct. 22–31	Station 5	57	39	1,422	1,381
	Station 6	61	33	1,772	824
1969					
May 6–June 8 (26 days)	Station 4	161	190	12,205	4,417
	Station 6	207	364	7,843	6,585
1968					
Sept. 29–Oct. 4	Morgan Creek	24	26	666	556
November 4–8	Morgan Creek	11	12	297	448
1969					
April 6–25	Morgan Creek	66 ^b	33	2160	849
June 11–17	Morgan Creek	214	119	2652	1207
Aug. 6–12	Morgan Creek	44	38	2523	1655
1970					
Mar. 15–21	Morgan Creek	26	51	214	605
Total	Morgan Creek	375	269	7659	5320

^aStation 4 sampled June 5–28, 1968. Station 5 sampled on 23 days from July 29 to September 23, 1968.

^bApril 15 fish not included in totals because only upstream trap was functional.

ging” rather than by long movements of individual fish. However, Carpenter (1967) in a study of a nearby stream in North Carolina, Little River, found many adult redbreast sunfish, one of the important fish of this study, making upstream journeys of at least 1–8 miles during the spring.

Fish sampling at station 2 was not possible because of time and property limitations. Local sports fishermen interfered with sampling at Morgan Creek during the spring and almost no sampling was accomplished there during periods of expected large migration. Nevertheless, on the 38 days sampled, a greater mass of fish was captured moving upstream than downstream, although this was not nearly as pronounced as for New Hope Creek (Table 2).

Net contribution of migration to headwaters and turnover rate.—During this study an estimated 119,400 g of fish and other animals moved each year into the region above station 6, and 56,700 g moved out of this area. A net movement into this area of 62,700 g occurred. There is approximately $1.6 \cdot 10^5 \text{ m}^2$ of stream above station 6 as determined by field measurements and topographic maps. Therefore, over this 1-year period there was a net addition of 0.39 g animals m^{-2} of water. This is about 14% of the estimated fish standing crop for a portion of New Hope Creek between stations 7 and 8, of 2.78 g m^{-2} (Carnes et al. 1964). Summing the mass of animals leaving this area and the mass of animals

TABLE 3. Minimum, maximum, total, and average mass in grams and total number of each species or group sampled at station 6, New Hope Creek

Species	Minimum weight	Maximum weight	Total number	Total weight	Average weight
Black crappie	1	210	64	4,457.5	69.6
Bluegill sunfish	1	194	266	1,869.5	7.0
Bluehead chub	1	80	404	4,204.6	10.4
Flat bullhead	1	689	203	14,416.2	71.0
Creek chubsucker	1	345	202	4,544.0	22.4
Creekchub	1	84	72	798.5	11.0
Darter	1	4	109	161.0	1.4
Highfin shiner	1	7	139	270.5	1.9
Margined madtom	1	32	120	1,107.6	9.2
Pickereel	1	738	217	13,394.5	61.7
Pirate perch	1	12	81	309.0	3.8
Pumpkinseed sunfish	1	287	120	1,982.0	16.5
Redhorses	1	1,363	328	150,799.7	459.7
Redbreast sunfish	1	167	394	15,299.5	38.8
White shiner	1	35	543	3,612.9	6.6
Whitemouth shiner	1	6	868	960.5	1.1
Crayfish	1	44	446	5,242.0	11.7
Frogs	1	500	88	5,359.7	6.0
Turtles	6	4,000	62	35,679.7	575.4

entering the area gives 176,100 g, or 1.1 g m^{-2} of animals (about 0.8 g m^{-2} of fish alone) involved in migrating to or from the area. This is 40% of the estimated standing crop of fish in that region.

If eliminated, the standing crop of a part of New Hope Creek would, according to these figures, be replaced in 3.7 years by upstream migration alone, in 7.9 years by downstream migration alone, or in 2.5 years by movement from above and below.

Analysis by species

The maximum, minimum, and average weight, as well as the total number and mass, of the more important species encountered at the principal sampling station are given in Table 3. V-lip and smallfin redhorses together were, by far, the most important in terms of mass. Turtles, redbreast sunfish, flat bullheads, and chain pickereel also contributed heavily to the total mass. Frogs (including tadpoles), whitemouth shiners, white shiners, crayfish, bluehead chub, and redbreast sunfish were most frequently encountered.

There was a tendency in nearly all fish species for larger individuals to move upstream and for smaller individuals to move downstream. This was particularly evident for black crappies, bluegill sunfish, flat bullheads, creek chubsuckers, pumpkinseed sunfish, redhorses, white shiners, and redbreast sunfish. Creekchubs and darters showed no particular pattern, highfin shiners and whitemouth shiners had greater upstream movement for all measured sizes, margined madtoms and pirate perches of all sizes moved downstream more than up. All larger species showed the large fish upstream–small fish downstream pattern. An analysis is presented in Fig. 7 of several impor-

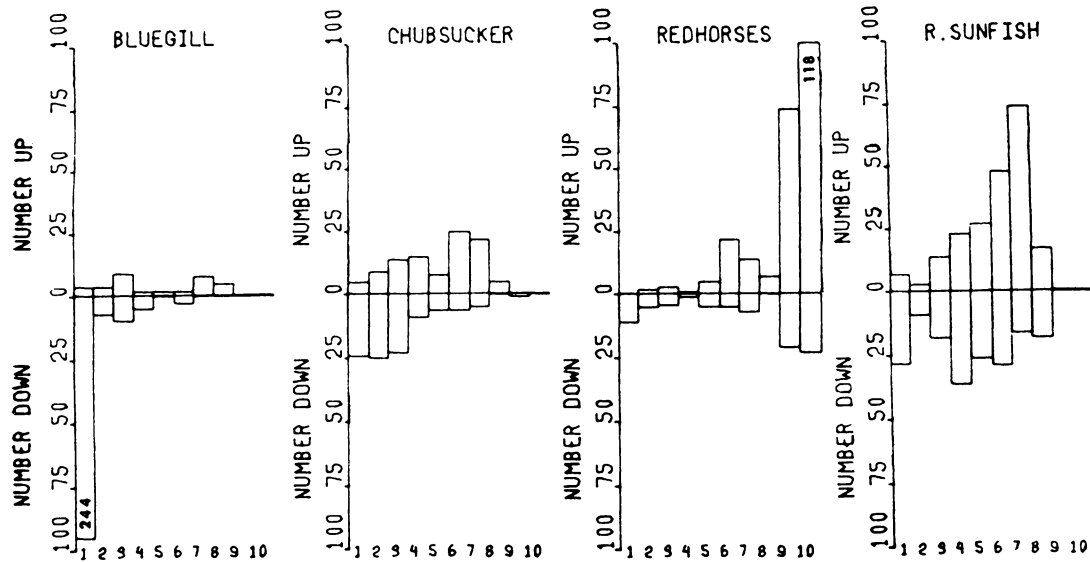


FIG. 7. The movement of several important fish species in New Hope Creek. The vertical axis shows numbers of fish, for the entire study, captured moving upstream and downstream. The horizontal axis shows size interval groupings as follows: 1 = 1 g or less, 2 = 2 g, 3 = 3-5 g, 4 = 6-10 g, 5 = 11-20 g, 6 = 21-50 g, 7 = 51-100 g, 8 = 101-200 g, 9 = 201-500 g, 10 = 501 or more g. The larger fish, in general, moved upstream and the smaller fish, in general, moved downstream.

tant fish species by size interval and by upstream or downstream movement at the principal sampling station for the entire sampling period. Smaller crayfish were captured moving downstream more frequently than up. Larger crayfish moved in both directions about equally. Turtles of all sizes were caught moving downstream more often than up. Many tadpoles and adult toads were captured moving, or being swept, downstream in the spring.

The greatest movement for all taxonomic groupings, both in mass and numbers, occurred in the spring months (March, April, May, and June). There were in some fish, such as bullheads, continued, though smaller, movements throughout the summer; and for chain pickerel a secondary series of movements in the fall. The pattern for most fish was repeated from year to year. The centrarchids were almost never encountered during the colder months. More detailed analyses of the patterns for each species are available from the author.

Records were kept of signs of reproductive activity for the fish sampled. These signs included: breeding tubercles, seasonally bright colors, and the actual discharge of eggs or milt. Over 100 fish were encountered in unquestionable breeding condition, and many hundreds more which probably were. Signs of breeding condition were only noted in the spring, and were always associated with the heaviest movements of that species. Fish in obviously ripe condition were taken almost invariably moving upstream, and spent fish always were taken moving downstream. From these observations it is assumed that upstream migra-

tions for the purpose of spawning are taken by all larger fish species in New Hope Creek. It is not known how many individual fish spawn without migrating upstream.

Physical and chemical results

During normal spring conditions the average depth, based on approximately 100 individual measurements at each station, for 1 hour's flow time above each respective sampling station, was 0.27, 0.83, and 0.50 m, respectively, for stations 2, 4, and 6. These measurements included pools and riffles about equally in each stretch. Casual observations coupled with these measurements suggested that, in general, average depths were less than 1/4 m above station 2 and greater than 1/2 m below station 6, and in the vicinity of 1 m or more below station 8.

Stream discharge varied from 0 during the drought of August-October 1968 to about $7 \cdot 10^5$ m³ day⁻¹ during winter floods. The estimated total discharge, as determined from daily stage levels correlated with discharge estimates, for the year from June 14, 1968, to June 13, 1969, was estimated as $1.23 \cdot 10^7$ m³.

The minimum temperature recorded in New Hope Creek was 0°C during January 1969 and 1970. A maximum temperature of 28°C was recorded on July 21, 1969. The largest fish migration occurred when spring temperatures were about 12°-18°C.

Measured daily leaf discharge at the Concrete Bridge station varied from zero to about 825,000 g. The log of leaf mass discharged per day was linearly proportional to water stage. Estimated annual leaf

discharge for the year June 14, 1968, to June 13, 1969, was $2.6 \cdot 10^6$ g dry weight, and most of the discharge occurred during a few major floods.

The intensity of light striking the surface of New Hope Creek was measured on a completely cloudless day (Sept. 26, 1969) at 100-m intervals for 1 km above stations 2 and 6. The results indicate that when the leaf canopy is full, insolation at the water surface of both stations is similar, with about 10% of the supercanopy solar energy entering both aquatic ecosystems. The results at station 2 may be biased by one very large value that was not representative for that stretch. Thus differences in metabolism between the two stations does not appear to be due to differences in insolation.

Total phosphorus dissolved and suspended in the water ranged from not detectable (less than 0.005 ppm, or mg l^{-1}) to 0.26 ppm. Most values were in the range of 0.02–0.10 ppm and the average for 79 samples was 0.05 ppm. No seasonal trend was evident and samples often varied widely from one sampling date to the next. Nor was there any consistent relation between river discharge and phosphorus concentrations. Therefore, the mean value was used for computations of total phosphorus discharge.

Total nitrogen dissolved and suspended in the water ranged from 0.20 ppm to 6.16 ppm, although the latter was the only value above 1 ppm and may have represented an insect in the sample. The mean for all 20 samples was 0.74 ppm.

DISCUSSION

I assume that since animal migrations exist, they have a net positive selective advantage for those populations involved. I further assume that the movements observed in New Hope Creek are similar in function, if not in magnitude, to the more spectacular migrations of, for example, salmon and waterfowl. My hypothesis, although others have also stated this, is that migration and reproduction are coupled to optimize the use of energy resources. In New Hope Creek, for example, my analysis indicates that upstream migration results in a net energy gain for the populations involved. This energy balance hypothesis should be considered one plausible and, perhaps, conceptually aesthetic explanation for migration. It is not necessarily evolutionary cause and effect. A more rigorous analyses must include detailed food chain studies interrelated with fish population density determinations (Warren, 1970).

This study of migration and metabolism of the New Hope Creek stream system allows the two to be related so we may infer some of the roles which migration may play in stream metabolism and the ways in which migrations may take advantage of ecological programs of life support. These compar-

isons may be made by examining the seasonal timing of events, the spatial distributions, the nutrients processed, and the energy involvements of each part.

Patterns of metabolism

New Hope Creek has a sharp peak in primary production in the early spring (Fig. 4). This peak is associated with a similar peak in respiration that continues high throughout the summer and early fall. Therefore, as the season progresses, the stream becomes increasingly dependent upon outside sources of energy or energy storages, or both. This greater respiration than production of energy constitutes a condition of heterotrophy, a condition often characteristic of woodland streams that are dependent on allochthonous detritus for some or a great deal of their energy supply (Hynes 1969). Hoskin (1959) found similar patterns in other streams of North Carolina. The principal supply of this detritus to New Hope Creek is probably riparian leaf fall from the surrounding forest. Other sources of externally supplied energy may be forest insects dropping into the stream, organic runoff, and several minor sources of domestic pollution that exist near the headwaters. The greater areal respiration upstream is probably due to increased leaf fall per area in the narrower stream.

Dilution of energy resources with depth.—Many previous investigators have found an inverse correlation between depth and the primary and secondary productivity of waters. For example, this has been found in the sea (Steeman Nielson 1957) and in the Sacramento–San Joaquin estuaries (Bailey 1967). Lake Michigan, with very low oxygen changes in each cubic meter nevertheless had very high metabolism in the total water column under each square meter of surface because the euphotic zone in this clear lake is large (Manny and Hall 1969). Data from large boreal lakes in Canada indicate that the areal production of net plankton, benthos, and fish is inversely proportional to the depth of the lakes (Rawson 1952, 1960). Demersal oceanic fisheries tend to be concentrated on relatively shallow banks and nearshore areas (Bigelow and Welsh 1924), and oceanic benthic biomass shows a negative correlation with depth (Hela and Laevastu 1961). A number of studies have shown that primary productivity and fish productivity are positively correlated (Nelson 1958, Hellier 1962, Hall, Cooper, and Werner 1970), and that organic energy additions can increase fish production (Warren et al. 1964).

In New Hope Creek, with generally similar metabolism per unit area, increase in water depth between stations diminished the concentration of metabolism per unit volume. It may be reasoned that food resources for fish were also diluted and that greater energy expenditure is required per food calorie gained, due

to searching. If so, the shallow zones should have had more concentrated food for young fish. In addition, the amount of energy available to benthic plants is less in deeper regions because of light extinction with depth. In New Hope Creek there were two manifestations of this change in water depth. These are changes from the deeper, downstream areas to the more shallow upstream regions, and changes at any one place as the water level drops during the summer. Much of the energy that enters a system is similar no matter what the depth, for both light and leaf litter enter a stream on a square-meter basis. Thus the total energy to support organisms may not change much with depth. It is, however, more concentrated, and perhaps more available to food chains in shallow water. This effect during summer low waters may be partially offset by a lessening of the total light-energy input to the stream as the total water-surface area becomes smaller.

Seasonal variations in metabolism.—Both photosynthesis and community respiration in New Hope Creek varied seasonally with a spring maximum and a secondary peak in the fall (Fig. 4 and 5). The possible causes include seasonal variations in solar energy, nutrients, temperature, and water-level changes.

Daily records of insolation under a deciduous forest canopy kept at the International Biological Program Site (Fig. 1 and 4) showed seasonal patterns of insolation with a peak in early spring that corresponds with the peak of observed values of gross primary production (Fig. 4 and 5). The peak of photosynthesis in March rather than in June was apparently due to the shading effect of overhead trees, which leaf during the middle of April. A second, smaller peak in primary production in the fall may have been related to an increase in light after leaf fall. Neither total phosphorus nor any of the important forms of nitrogen showed any consistent seasonal variation that was correlated with seasonal variations in metabolism.

Seasonal community respiration at station 6 (Fig. 4) showed two peaks, one during the high solar-energy input in the spring and one during fall low waters. Therefore, apparently neither the primary production nor respiration was principally controlled by temperature, which had maximum values in late summer. There were indications of increased metabolism during floods, perhaps due to the stimulatory effect of additional stirring energies, or additions of organics in runoff, but there were insufficient data to generalize on this point.

Patterns of fish movements and relation to metabolic patterns

The annual peak in fish movements is closely correlated with the annual peaks in gross photosynthesis, community respiration, and the end of winter

floods (Fig. 4 and 7). These may reflect selective pressures on the fish to schedule their own time of high energy usage or needs with the time of maximum total energy potentially available in the environment. Storage and lag processes in the stream may smooth out the pulse in food availability at second and third trophic levels into the season when the young fish are ready to tap the food chains. The continuing high levels of respiration after the pulse in primary production indicate sustained biological activity in summer and fall.

It is assumed that the total energy available to a population, or an ecosystem, for growth, reproduction, and evolution is equal to the incident energy times a coefficient of usage minus that energy needed for physiological adjustment to stress. The generally upstream movement of larger fish and generally downstream movement of smaller fish observed in this study raises some interesting questions about these energy relations for a population of animals. The upstream movements are obviously tied in with reproduction, which implies that there may be selective value in bringing the potential progeny upstream. One advantage would be in distributing the genetic stock over the stream. The very small fish with large surface-to-volume ratios affecting friction cannot swim upstream against the current, but the large ones can and do, and the small ones can and do move downstream with the current. Thus, the upstream migrations of the adults may be necessary to provide agents for stock maintenance and gene dispersal. Also, since the spring and summer pulse in energy available per volume at the upstream station is considerably greater than the pulse at the downstream station (Fig. 5), it would be more advantageous to have the more rapidly growing small stages located upstream.

The large number of juvenile fish moving downstream in spring indicates a dispersal of many fish after spending 1 year, raising the question of why the fish move back downstream. This may be an adaptation to prevent population pressures between the new-year class of juveniles and other fish upstream which increase their activities as the water warms. Because of geometric adaptation to rocks, currents, and microenvironments, large fish may experience less stress in the deeper waters. Hellier (1962) found small fish moving to deeper waters as they grow.

Another possibility was considered by Margalef (1963, 1968), who commented on the movement of animals as they grow older from the highly productive regions of juvenile growth to more stable environments. Downstream regions in New Hope Creek may be, to a fish at least, more stable, since they are not subject to the extreme diurnal variations in oxygen that occur in the upstream, more metabolically

active regions during the low-water stages of summer drought (Hall 1969). In addition, the deep pools in the downstream regions provide insurance against complete annihilation during extreme droughts. There may be a trade-off of high productivity versus a more stable environment that is best utilized by sending armies of young to the highly productive regions to get a quick start in life, followed by dispersal of those that survive to more stable regions. A single small fish is more expendable than a larger one since there are many more of the former and an ecosystem has invested less of its energy resources in it.

Comparisons of energy budgets

Consider next the energy budgets of the stream, its metabolism, the fish, and their migrations. To relate energy budgets of the fish to that of other parts of the system it is convenient to express work processes in their caloric form, since energy is a common denominator for all processes. Many of these estimates are far from precise, but their orders-of-magnitude differences give the estimates realism for comparative studies.

The physical potential energy released per day in turbulence (E) in a cubic meter of water flowing downhill between station 2 and station 6 can be calculated as equations that follow:

$$E \text{ in kg-m m}^{-3} = (\text{mass in kg}) (\text{acceleration due to gravity in m sec}^{-2}) (\text{difference in height in m}).$$

$$E \text{ in Cal m}^{-3} = (10^3) (9.8) (45.7) (2.34 \cdot 10^{-3} \text{ Cal kg-m}^{-1}).$$

$$E \text{ in Cal m}^{-3} = 1,040 \text{ Cal m}^{-3}.$$

For the year a mean time of about 1 day was required for water to flow from station 2 to station 6; therefore the physical power dissipation is 1,040 Cal m⁻³ day⁻¹, or about 350 Cal m⁻² day⁻¹. The energy of sun insolation reaching New Hope Creek through the canopy, measured at the nearby IBP site (Fig. 1) was about 4,200 Cal m⁻³ day⁻¹, on the average, depending upon the depth of the water. Thus the solar energy input is about four times the water current contribution.

Estimates of the energies involved in the leaf detritus budget of the creek indicate that considerably more leaf energy is used *in situ* than is transported downstream (Fig. 8). Leaf fall input was estimated as 476 g m⁻² yr⁻¹, or 5.85 Cal m⁻² day⁻¹ (Garret, personal communication). This would be a minimum estimate since there is probably some blow-in from adjoining banks. Fisher and Likens (1972) found that 1.2 times as much leaf mass fell into Hubbard Brook as fell on adjoining forest floors. Since New Hope Creek is larger than this stream, and since it flows through a sheltered small valley where there

was rarely noticeable wind, the leaf-fall data for the forest floor of Garret is probably a reasonable, if low, estimate.

According to the oxygen studies of community metabolism, about two-thirds of the energy used at station 2, and one-half of the energy used at station 6, must be supplied from allochthonous sources. The leaf-fall estimates indicate that at least that much energy is supplied from this source. In fact, the close agreement between caloric estimates, from oxygen respiration, of allochthonous detritus input (18.1 and 3.74) and measured leaf-fall energy input (20.8 and 11.7) make it tempting to assume that this is a complete energy budget (Fig. 8). However, more rigorous research would be necessary to justify complete faith in the leaf-budget numbers. Less canopy overhang downstream may have given an overestimate (11.7) for leaf input, and actual *in situ* measurements would perhaps agree more closely with oxygen estimates.

Energy of biological metabolism.—The mean biological respiration in the same cubic meter of water flowing through the same zone over the entire year was about 2.85 g oxygen used per cubic meter per day (Fig. 4–5). Since about 3.5 Cal are released per gram of oxygen metabolized (Brody 1945), a total of about 10.0 Cal of energy were used in respiration per day. Thus the system receives about 100 times more energy from the work of currents and 400 times more energy from insolation, than from autochthonous and allochthonous organic fuels.

A rough figure for the use of oxygen by fish under normal conditions is about 100 ml (0.143 g) O₂ hr⁻¹ kg⁻¹ (Brown 1961, Brett 1965, Brett and Sutherland 1965). This is quite variable with temperature and activity rates but is probably close to mean values for New Hope Creek. There are about 18 g fish m⁻³ in New Hope Creek (Carnes et al. 1964) which would use (0.143 g O₂) (365 days) (24 hr) (18 · 10⁻³ kg), or 23 g O₂ m⁻³ year⁻¹. This is approximately equivalent to 0.22 Cal m⁻³ day⁻¹.

Energy used by migrating fish.—There are at least three different ways to measure the energy used by migrating animals such as fish: (1) One may calculate the total work expended against frictional forces, or that used in moving the organisms against gravity, or both. (2) One may convert the additional oxygen used during migration to caloric values. Considerable data exist on oxygen use by fish during different levels of activity and estimates have been made for use during migration (Brett 1970). These figures are about 100 ml O₂ kg⁻¹ hr⁻¹ at low levels of activity and about twice this during migrations. (3) One may weigh fish and analyze them for different food reserves at the beginning and end of their movements. This type of work has been done for orga-

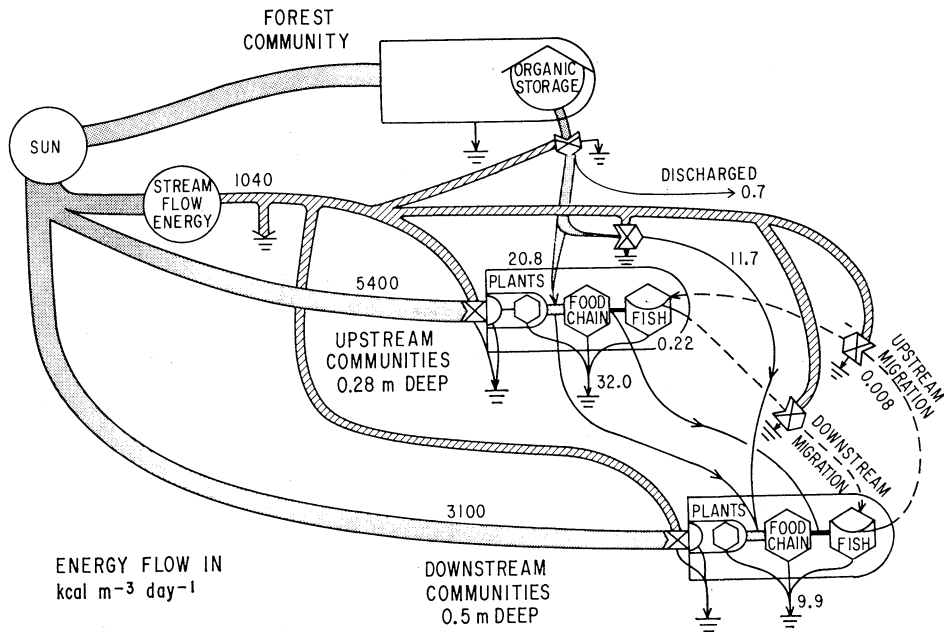


FIG. 8. Energy-flow diagram for upstream and downstream communities of New Hope Creek. Metabolism is in Cal m⁻³ day⁻¹, as volume differences in metabolism is suggested as an important factor. Energy enters the system either directly as solar energy, which passes through the food chain, as leaf litter, or as stream-flow energy which aids in the distribution of resources and dispersal of wastes. Upstream migration requires additional energy to overcome this flow. Symbols are those of Odum (1967a, 1967b, 1971). Circles represent energy sources and darts energy (heat) sinks. Bullet-shaped modules represent plant or plant-animal-microbial communities. Hexagons represent animal populations of interest. The six-sided figures with included multiplying symbol are work gates, or places where one energy flow may influence another, often larger flow. In general energy flows are from the upper left to lower right, and the width of the energy-transfer lines is only roughly proportional to their magnitude.

nisms that do not feed during their migrations, such as salmon (Idler and Clemens 1959) and some birds (Caldwell, Odum, and Marshall 1963).

The second method was used for these estimates. An additional 100 ml O₂ kg⁻¹ hr⁻¹ was allotted as the cost of migration. This is probably a high estimate. Multiplying this by the annual biomass moving upstream past station 6 (120 kg) by the period of major movements (3 months or 2200 hr) gives a high total energy cost of 1.32 · 10⁵ Cal for the entire watershed above station 6, or 2.8 cal m⁻³ year⁻¹. This is about 4% of the estimated fish metabolism and about 0.04% of the annual metabolism of the entire ecosystem. If it is assumed that the upstream migration is necessary to maintain the stocks of fish in the upstream portion of the stream that periodically dries up, this energy used for migration has a multiplying effect of at least 25. That is, for every calorie spent in migration, that population would gain at least 25. Another analysis, oversimplified because it does not take into account density-dependent factors, indicates that a New Hope Creek fish, assumed to be at the third trophic level, would gain 0.021 cal m⁻³ year⁻¹ by living upstream, compared

with a cost of 0.008 cal m⁻³ to get there. The larger absolute increase in energy availability during the spring pulse upstream makes seasonal exploitation of this resource worthwhile even including density-dependent effects. By any of these analyses, migration is a worthwhile investment of a population's energy resources. Shorter migrations would gain less energy, but also cost less. Energy relations are summarized in Fig. 8.

Possible adaptive values of migrations in New Hope Creek

Various possibilities exist for the selective advantage of tying together various sections of the stream by animal migration: (1) Already discussed is the role of migration in the reproduction and dispersal of juvenile stages of the species. (2) Various areas of the stream may become devoid of fish due to natural disasters, such as drought, summer low oxygen, severe predation, and so forth. Migration provides a steady source of recolonizers that can occupy empty habitats. (3) The migration and reproduction system allows a population to be maintained in a current. Any downstream drift may be compensated

for by migration. (4) Predators moving through the stream tend to feed most heavily in areas with large numbers of prey species, and thus tend to control possible excessive increases in these species. (5) The contribution of minerals to upstream regions by migrating animals is discussed elsewhere in this section. (6) According to Levins (1964) migration has selective value in permitting sufficient interchange between populations so that local adaptation for short-range environmental fluctuations will not become a very important factor which would reduce the overall fitness of the gene pool. However, this does not reduce the adaptability of the population as a whole to widespread changes in environment. This may be a factor in the selection of species fitness in streams such as New Hope Creek in that the fitness of the gene pool as a whole is maintained and not wasted on nonselective adaptation to short-term local events, such as stress during exceptional drought. (7) Olfactory cues may be transmitted downstream from upstream.

Interaction of yield and organization.—New Hope Creek, like many other complex systems, can be arbitrarily divided into a subsystem exporting energy and another subsystem receiving this energy, and in return supplying certain organizational or other services to the exploited system in a feedback loop. Examples of this relation would be: A prey “donating” a certain percentage of its energy resources to predators in exchange for population regulation; flowers providing bees with energy in return for pollination services; and farms supplying cities with food and receiving in exchange fertilizers, farm machinery, and social services.

Such a system can be defined in New Hope Creek. The upper regions of the stream export food energy to downstream regions and receive in return genetic information resources, populations of higher trophic levels to utilize seasonal energy pulses, population control, repopulation when necessary, and minerals. All of the above are concentrated biological control agents and are effective in relatively small amounts.

Margalef (1963, 1968; see also Deevey 1969 and Cox 1970) has considered the energy-information exchange between two systems or subsystems in some detail. A downstream system that has greater organization (which Margalef calls “mature”) may be more efficient in its use of energy. An upstream, less organized system (which Margalef calls “immature”) may not have the structural and organizational framework for using energy as efficiently as the more mature system, and as a result often loses much of its energy to export or exploitation. If the more organized system is able to utilize this energy lost by less organized systems it, in a certain sense, exploits the less organized system. In return, the more organized system gives up information to the less ma-

ture one, aiding it in becoming more efficient in its own use of energy, and increasing its organization.

Although New Hope Creek is readily divisible into two segments, the upstream one supplying energy to the downstream one, and the downstream one supplying genetic information to the upstream one, further agreement with Margalef’s theory is not substantiated. The indices of maturity should, according to Margalef, be higher in the downstream region and lower in the upstream region. This was not borne out by investigations. The upstream region had higher volume production (1,440 vs. 640 $\text{g m}^{-3} \text{ year}^{-1}$) and a lower ratio of production to respiration (0.4 vs. 0.6), indicating that the biomass supported per unit of photosynthesis was greater. Studies of pigment ratios (Motten and Hall, in press) showed slightly greater D_{430}/D_{665} for both pools and riffles in the upstream regions of New Hope Creek in opposition to Margalef’s theory, although edaphic factors may have swamped intra-stream patterns. Thus, the energy-information interchange theory may have validity apart from any consideration of relative “maturity.” (See also Fisher and Likens, 1972)

Some other animal migrations and environmental energy patterns

Migration in New Hope Creek may be an example of a widespread phenomenon. A number of examples of migration to regions of high productivity for reproduction were considered in the introduction, for example, the work of Odum and others in Texas Bays. Other examples would be summer migration of many birds to arctic areas for reproduction during the high energy input of very long daylight periods, ungulate and hominoid movements in savannas as water-limited production rises and falls, and the heavy utilization of rich estuarine and nearshore regions by small salmon, particularly chums and pinks. Further analyses of present salmon migration patterns and energy availability patterns, as well as post-Pleistocene opening of niches and evolution of lakes containing sockeye salmon, may be fruitful areas for additional research. We are currently considering general estuarine patterns more closely (Woodwell, Rich and Hall; Goodyear and Hall, in preparation).

New Hope Creek watershed annual phosphorus budget

Fish migration upstream may partially offset the downstream transport of minerals. It is important in the mineral budgets of salmon lakes in Alaska (Donaldson 1967) and in Russia (Krokhin 1967); and in New Hope Creek, the relatively large mass of fish moving upstream apparently also contributes to the mineral balance. Some data on the phosphorus

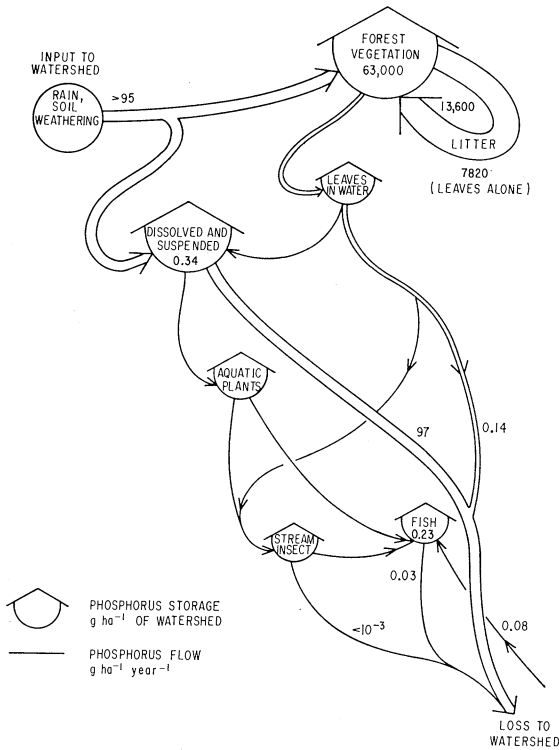


FIG. 9. Some phosphorus storages and flows for New Hope Creek and surrounding watershed, based on studies from June 14, 1968, to June 13, 1969, and on literature values.

budget for the watershed of New Hope Creek are summarized in Fig. 9. These data, like some of the energy data, are not precise, but again the orders-of-magnitude difference between various compartments and flows gives a good picture of the most important components for phosphorus in this watershed.

Measurements were made from June 14, 1968, to June 13, 1969, of phosphorus flows in the water, in leaves, and in fish. The results indicated that phosphorus discharged in suspension or solution in water was the most important factor in the movement of that element. Less than 0.2% of that amount is lost in leaf discharge and even less than that as fish and other animals moving downstream. The amount of phosphorus brought upstream by fish was about one-half of that lost by leaf discharge and less than 0.1% of that lost by stream discharge. Therefore, on an annual basis, the contribution of phosphorus to the headwaters by fish was small.

Some studies have suggested that upstream movements of invertebrates may help or entirely compensate for the downstream drift (Ball and Hooper 1963, Minckley 1964, Hughes 1970). Others have emphasized the loss in drift. Insect drift was not formally sampled in New Hope Creek; however, casual observations and several 24-hr plankton net drift samples indicated that insect biomass in the

drift was small compared to leaves. Maximum possible values were estimated from data recorded by Waters (1965) and Anderson and Lehmkuhl (1968) and these were adjusted to the volume of discharge of New Hope Creek.

Even assuming 10 catastrophic floods per year of the magnitude of the largest recorded in New Hope Creek, only about 0.2 of 1% of the mass of leaves lost would be lost as insect drift. Thus phosphorus loss by insect drift was considered small. Bedload transportation during floods was neglected, but may be a source of error. Settling effects in large pools make this unlikely.

Some numbers used in Fig. 9 were calculated from literature values as follows: The watershed has about 6,800 ha above station 6 as determined from topographic maps. Phosphorus added in rainfall was calculated as about $1 \cdot 10^{-8}$ parts P in rainfall (Donaldson 1967, Cooper 1969, Weibel 1969, Pearson and Fisher 1971) times 10^4 m² ha⁻¹ times 0.95 m rainfall for that 1-year period (U.S. Weather Bureau, Raleigh-Durham Airport, N.C.), or about 95 g p ha⁻¹. About 20% of the rain falling on the watershed was discharged in the stream.

Annual cycling of phosphorus through leaf development and fall was obtained for deciduous forest in Duke Forest (N. Garrett, personal communication). Using conversions from Gosz, Likens, and Bormann (1970) and Rodin and Bazilevich (1965), this represents about 7,820 g P ha⁻¹ year⁻¹ for leaf litter and approximately 13,600 g P ha⁻¹ for total litter.

Standing crop of phosphorus for fish was estimated from stream sampling data done by the North Carolina Wildlife Resources Commission (Carnes et al. 1964). Their value of 28 kg ha⁻¹ (1,758 g for 0.154 acres with a depth of 0.5 ft) was multiplied by the approximate phosphorus content of fish (0.35%—Vinogradov 1953, Donaldson 1967).

Total phosphorus in the total organic standing crop of Duke Forest was approximated by averaging values for 14 pine and mixed deciduous regions of the world given in Rodin and Bazilevich (1965). A mean value of 63 kg P ha⁻¹ was used, as the watershed of New Hope Creek is about one-half deciduous and one-half pine (anonymous map supplied by the Duke University School of Forestry). The loss of phosphorus by New Hope Creek (97 g ha⁻¹) compared to the standing crop is small, and may be entirely replaced by amounts added in rainfall alone. This loss of phosphorus from Duke Forest by New Hope Creek is about the same as values from other studies reported in Rodin and Bazilevich (1965). This compares with a general loss of from 0.9 to 21 kg ha⁻¹ year⁻¹ for Ca, Mg, K, and Na for four studies summarized by Likens et al. (1967). Standing crops of phosphorus in fish is an important reservoir during summer low-water flows and migration

may be important in the mineral budget by maintaining this reservoir.

ADDENDUM: RESOURCE MANAGEMENT IMPLICATIONS

Since differences between daytime and predawn oxygen values are often greater than 3 mg ml⁻¹, any oxygen-monitoring program should emphasize predawn sampling. These day-night differences are exaggerated in more shallow regions as a result of concentrated metabolism. Therefore shallow regions, either during summer low water or in head waters, are particularly vulnerable to oxygen-depleting pollution and need particular protection.

Stream obstructions may reduce the potential for fisheries yield of a stream. The patterns of movements observed may optimize the fishes' use of their environment and increase the yield to man of food or sport fish. Areas of localized pollution may be more detrimental to the fish of a stream than just those in the immediate area as many fish move upstream or downstream in the spring. For this reason particular attention should be paid to water quality in March–April–May. Predictions for the recolonization of regions defaunated by pollution, such as happened in mid-North Carolina on several occasions during the summer of 1970, can be made from the New Hope Creek data. Under similar conditions about 2.5 years would be required to repopulate an area by migration. These estimates may be helpful in the economic assessment of a fish kill. Finally the balanced phosphorus budget of Duke Forest indicates the value of natural ecosystems for maintaining our mineral stocks where we want them and keeping excessive nutrients out of watercourses where they may cause undesirable eutrophication (Likens et al. 1970).

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