———. 1961b. A study in insect multiparasitism, II. The mechanism and control of competition for the host. J. Exp. Biol. **38**: 605-628.

**Flanders, S. E.** 1948. A host-parasite community to demonstrate balance. Ecology **29**: 123.

———. 1958. The *Ephestia-Idechthis* ecosystem for illustrating population dynamics. Ecology **39**: 545-547.

**Nicholson, A. J., and Bailey, V. A.** 1935. The balance of animal populations. Part 1. Proc. Zool. Soc. London, Part 3: 551-598.

**Smith, H. S.** 1929. Multiple parasitism; its relation to the biological control of insect pests. Bull. ent. Res. **20**: 141-149.

# DIURNAL PERIODICITY IN THE DRIFT OF STREAM INVERTEBRATES[1]

THOMAS F. WATERS

*Department of Entomology and Economic Zoology, University of Minnesota, St. Paul*

## INTRODUCTION

Many aquatic animals exhibit diurnal periodicity in activity. In lakes the daily vertical migrations of crustaceans, rotifers, and the insect *Chaoborus* have been the subject of many studies (Bainbridge 1961, Pennak 1944, Berg 1937). Although similar phenomena might be expected in streams, little has been reported. Moon (1940), who studied the colonization by invertebrates of bottom materials set out in trays, reported greater activity at night than during the day in both a lake and a stream.

It is reasonable to postulate that changes in activity among stream organisms would be manifested in changes in the drift rate (defined as the quantity of organisms drifting downstream per unit time per unit of stream width), but published studies on drift either have not undertaken measurement of drift rates during hours of darkness or have not distinguished between night and daytime drift rates (Needham 1928, Lennon 1941, Dendy 1944, Müllor 1954, Waters 1961). However, Lennon (personal communication) observed in his study greater activity of stream insects at night and believed that in his 24-hour drift samples the immatures were collected mostly at night. Also, in a personal communication, G. R. Alexander, Michigan Department of Conservation, stated that in his drift studies (as yet unpublished), there appeared to be peaks in drift rate in the evening and again in early morning.

Prior to the present study, ecological investigations in the summer of 1959 included drift measurements out of an exclosure set into a stream bottom; much higher drift rates were observed at night than during daylight hours. Subsequent observations, both from an exclosure and in the open stream, confirmed the daily changes as regularly occurring events. The purpose of the present study was to document more intensively this phenomenon of diurnal periodicity in the drift rate.

I would like to express appreciation to Robert J. Knapp for his conscientious assistance in the field; to many students, especially George A. Swanson, for the extensive work of sorting and analyzing the samples in the laboratory; and to Roy C. Arnold on whose property the field work was conducted, and who generously offered his cooperation and facilities. The study was assisted by National Science Foundation research grant No. F 9935.

[1] Paper No. 4582 Scientific Journal Series, Minnesota Agricultural Experiment Station, St. Paul, Minnesota.

## METHODS

Drift rate was measured in a series of 24 hourly samples on each of the dates of August 19-20, 1959; October 24-25, 1959; February 20-21, 1960; and May 6-7, 1960, in Valley Creek, Washington County, Minnesota, a small, hardwater, spring brook containing brook trout (*Salvelinus fontinalis* [Mitchill]). The sampling location was in midstream near the downstream end of a riffle; at this site the stream width was 10 ft, the depth about 4 inches, surface velocity about 3 ft/sec, and the bottom material of cobbles and coarse gravel.

Drifting organisms were captured in a bag-like net, 1 $ft^2$ at the opening and about 3 ft long, similar to the nets designed by Alexander in Michigan in 1957 (personal communication). The material of the net was Nitex[2] with a mesh size of 471 microns, 39 meshes to the inch. Prior to the time of sampling, a wooden board was set in the stream flush with the stream bottom. Holes had been drilled in the board to receive iron rods that held the net in position by means of rings fastened to the net frame (Figure 1). The bottom edge of the net fitted closely to the board, preventing organisms from drifting underneath; the nets could be lifted from the rods and

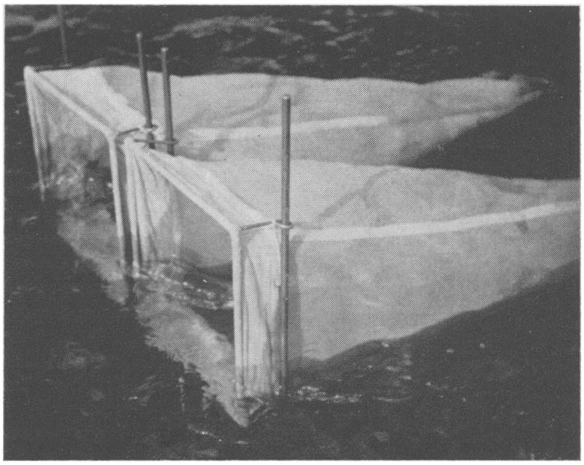

FIG. 1. Drift nets set in position for sampling.

[2] Trademark of Tobler, Ernst, and Traber, Inc., New York.

quickly replaced. Two nets were placed side by side to obtain concurrent samples; they were left in position for 1 hour and replaced with 2 others while the samples were being removed from the first 2. The sample, comprising the organisms and some debris, was rinsed from the net into an enamel pan, concentrated with a sieve, and stored in a jar with formalin. Air and water temperatures were recorded at hourly intervals.

In the laboratory the organisms were separated manually from the debris, sorted into taxonomic groups, and measured volumetrically by a liquid-displacement technique. The smallest quantities were measured to the nearest 0.01 cc in a section of glass pipette. Mean results, computed from the 2 samples, were expressed in cc/hr/ft of stream width, for each taxonomic group. Sex was not determined.

## Diurnal Changes in Drift Rate

### *Gammarus limnaeus* Smith

The crustacean, *Gammarus limnaeus,* was by far the most abundant organism by volume in the drift. It is an actively swimming animal, occurring commonly in almost all habitats in the stream. Drift rates are given for all 4 series in Figure 2, on which times of sunset and sunrise are also plotted. Usually the drift rate increased markedly about 1 hour after sunset, decreased during the night, and fell sharply to "normal" daytime low values at about sunrise. In the August series the principal drift rate increase was about 100-fold; the maximum mean was slightly over 11 cc, or about 4,000 individuals/hr/ft of width. In all 4 series the relationship to sunset and sunrise appeared to remain the same; the time of drift change followed the progression of sunset and sunrise with the seasons.

In the August and May series a 2nd peak in drift rate of *Gammarus* occurred during the night. This return to a higher rate may have been due to the sky's becoming overcast and the resultant occlusion of moonlight. In August, the sky was clear in evening with moonlight and was overcast at sunrise, but the exact time of occlusion was not recorded. In May, moonlight was occluded at midnight, just before the 2nd peak in drift rate occurred.

At 3 PM in the afternoon in the August series, a group of children was found playing the stream about 200 ft upstream from the sampling site. Although they were soon encouraged to leave, their disturbance caused a temporary increase of about 0.6 cc/hr in the drift rate of *Gammarus.* At 7 AM the following morning a heavy rain began, probably causing a slight increase in stream discharge; the drift rate increased about 0.5 cc/hr and remained above the normal daytime level until the end of the sampling period.

Large seasonal differences were apparent (note the difference in scale between the August-October and February-May graphs), with drift rates in summer being much higher than those in winter.

### *Baetis vagans* McDunnough

The mayfly, *Baetis vagans,* was the 2nd most important organism in the drift, being secondary to *Gammarus* in volume, but usually the most abundant in numbers. It too is an actively swimming form. The pattern of drift rate of *Baetis* throughout the daily period (Figure 3) was similar to that of *Gammarus.* The relation to times of sunset and sunrise was also similar to that of *Gammarus.* In August, the maximum mean drift rate was about 4.3 cc, or roughly 10,000 individuals/hr/ft of width, representing, as was the case with *Gammarus,* about a 100-fold increase over pre-sunset levels.

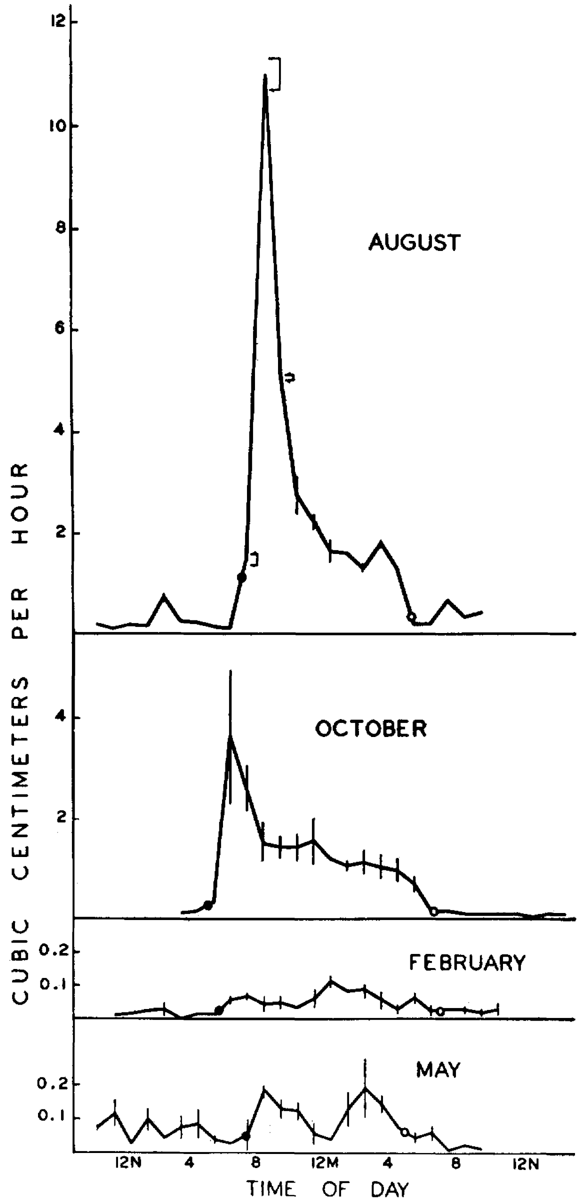


FIG. 2. Drift rate of *Gammarus limnaeus,* cc per hour per foot of stream width, mean of 2 samples per hour. Vertical lines and brackets represent range. Closed circles, sunset; open circles, sunrise.

In both the August and May series, a 2nd peak in drift rate of *Baetis* occurred during the night, similar to that of *Gammarus* and perhaps related to the occlusion of moonlight. In the August series, the effects of the children playing in the stream at 3 PM and the rainstorm at 7 AM were also apparent. The summer drift rate of *Baetis* was much higher than at other seasons (note difference in scales).

### *Glossosoma intermedium* (Klapálek)

Larvae of *Glossosoma intermedium* build small stone cases in which they move about over stones and other

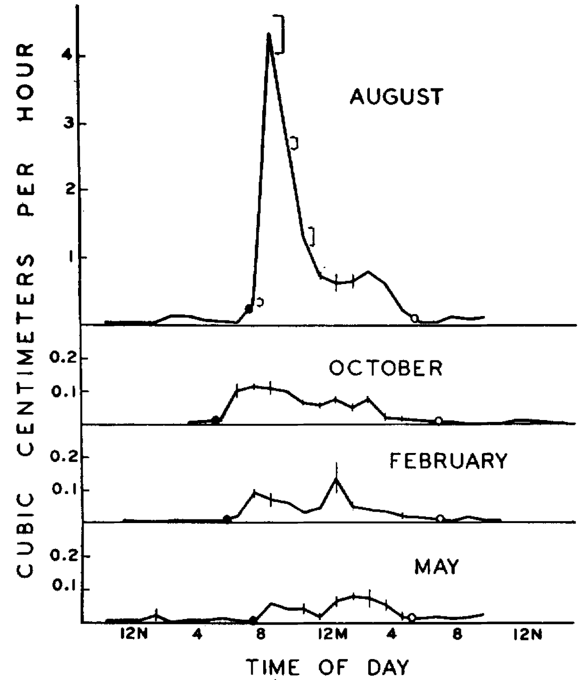


FIG. 3. Drift rate of *Baetis vagans*. For symbols see Fig. 2.

substrates on the stream bottom where there is a fast current. A few larvae were found in the drift nets with their cases, probably the result of their having crawled directly into the net, but most were without their cases. Apparently the drifting larvae had voluntarily left their cases, perhaps to build larger ones or to seek new locations, and had been caught in the current.

The drift rate of *Glossosoma* was similar to those of the preceding 2 species in August and October (Figure 4), though it did not reach as great a magnitude in August. In August and October, the changes in drift rate were also closely related to sunset and sunrise. *Glossosoma* was present in the February drift samples only in small numbers and not at all in the May samples, though it was abundant on the stream bottom. The maximum mean drift rate in August was 0.34 cc, or about 350 individuals/hr/ft of width, approaching a 100-fold increase over pre-sunset levels.

A 2nd peak in drift rate of *Glossosoma* occurred in the August series, similar to those of *Gammarus* and *Baetis*. The children playing in the stream at 3 PM produced no effect; those individuals disturbed by the children probably kept within their relatively heavy cases and were deposited on the stream bottom a few feet below the area of disturbance, rather than drifting down to the sampling site as did lighter, unencased organisms. Probably for the same reason, the rainstorm at 7 AM did not produce a change in drift rate.

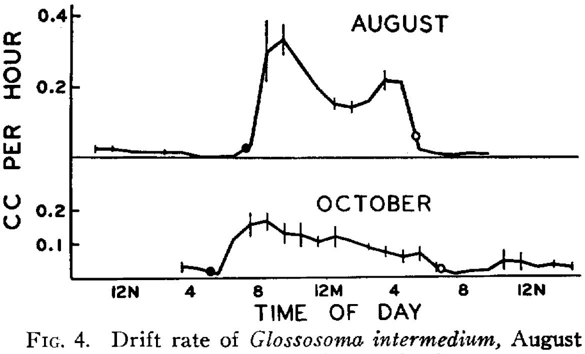


FIG. 4. Drift rate of *Glossosoma intermedium*, August and October series. For symbols see Fig. 2.

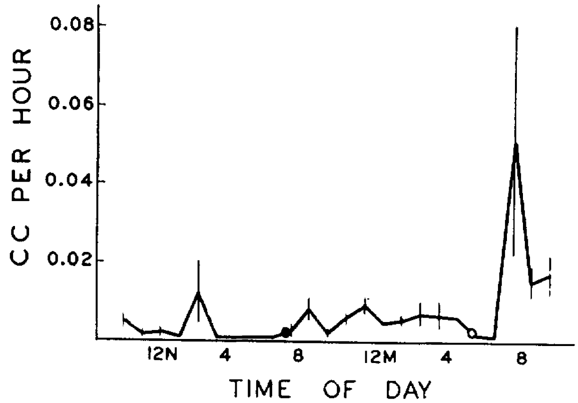


FIG. 5. Drift rate of *Dixa* sp., August series. For symbols see Fig. 2.

### *Dixa* sp.

Larvae of the dipterous genus, *Dixa*, were present in the drift in moderate quantities in August but only rarely at other seasons. The data presented in Figure 5 were obtained with counts and mean calculated volumes, rather than by the volumetric analysis of each sample, since quantities were low and all individuals were of similar size. A slightly higher mean rate of drift appeared between the times of sunset and sunrise, although the phenomenon was not as conclusively demonstrated as with other species. The effect of the children playing in the stream of 3 PM was apparent, but the effect of the rainstorm at 7 AM was pronounced, increasing the mean drift rate about 50-fold. Since this organism is associated with the surface film at stream edges and in wet areas above the surface near the water's edge, it seems reasonable that a sudden, heavy rain would have this effect of increasing the rate of drift.

### *Hesperocorixa* sp.

An adult bug, *Hesperocorixa*, was found in the August samples, but not at other seasons (Figure 6). No individuals were found in the drift samples until after sunset, when there was a maximum mean drift rate of about 0.25 cc, or 30 individuals/hr/ft of width, persisting for 2 hours. During the rest of the night, few *Hesperocorixa* appeared in the drift samples, and shortly after sunrise they disappeared once more. Since this organism was

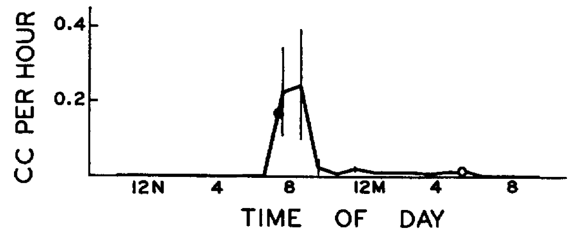


FIG. 6. Drift rate of *Hesperocorixa* sp., August series. For symbols see Fig. 2.

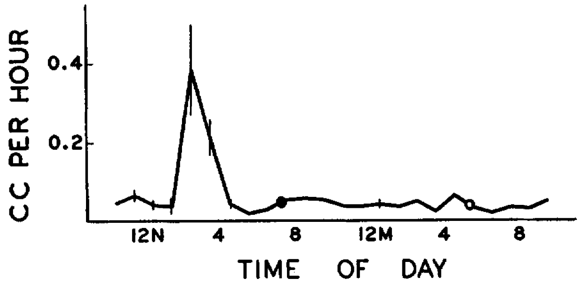


FIG. 7. Drift rate of *Simulium* sp., August series. For symbols see Fig. 2.

not normally found in the stream in the sampling site vicinity, its occurrence in the drift probably was the result of an evening flight originating elsewhere.

### *Simulium* sp.

Larvae of the blackfly, *Simulium,* appeared regularly in the drift during the August series (Figure 7). There seemed to be no difference in drift between night and day, and very little effect due to the rainstorm at 7 A.M. But the response to the children playing in the stream was pronounced, being about a 10-fold increase. Since this organism is light and unencased, but, in contrast to the other more vagile species, remains firmly attached to submerged rocks and other substrates in fast water, it seems reasonable that it would not exhibit diurnal changes in activity, nor that a rainstorm resulting in a slightly higher stream discharge would alter its drift; however, a physical disturbance that caused the larvae to be brushed off their substrates would increase the drift rate considerably.

### *Other organisms*

Among other organisms present in the vicinity of the sampling site were those that were abundant but not susceptible to drifting, and those present only in small quantities. In the first group were a snail and another stone-encased caddisfly, *Limnephilus,* very abundant in the stream, but virtually absent from the drift samples.

The group of species present in small quantities on the stream bottom as well as in the drift, included *Asellus,* the aquatic isopod; chironomids; tipulids; the caddisfly, *Hydropsyche;* several beetles; large bugs of the families Nepidae and Belostomatidae; *Hydracarina,* the water mite; and oligochaetes. Several species of copepods, known to be present in slack-water areas and water-cress beds, were observed irregularly in the drift, but valid data on their drift rate could not be obtained by the sampling method used.

## Discussion

Higher drift rates at night were probably due to greater activity of the invertebrates; apparently at the proper time after sunset the animals left their places of protection and concealment, swam or otherwise moved about more freely, and were swept downstream by the current. Changes in drift rate were related to times of sunset and sunrise, although a time lag of about 1 hour appeared between sunset and the onset of the principal increase in drift rate, which was precipitate and occurred in full darkness. Sky conditions (overcast or clear) seemed to have no effect on the time of the principal increase. In almost all cases, the decrease occurring just before sunrise was a sharp drop, indicating that the organisms' reattachment to the substrate was an active response to conditions of changing light.

That the principal peak was not caused by physical disturbance was confirmed by the observation of increases at identical times from exclosures which prevented all disturbance such as that by mammals, fish, or drift from upstream. Nor did it appear that the 2nd peak occurring in the August and May series was the result of physical disturbance; *Simulium,* which responded markedly under conditions of known physical disturbance (children playing), showed no increase during the night at the time of the peaks in other species, while *Glossosoma,* one of those showing 2 peaks in the August series, did not respond to the known physical disturbance at all. It is suggested that the 2nd peak in drift rate was the result of a real period of increased activity perhaps caused by the occlusion of moonlight on those nights when the moon had been shining but was occluded by clouds, an event that did occur during the August and May series. In the October series the moon rose in late evening in a sky that remained clear all night, and no 2nd peak occurred in the drift rate of any species. The occurrence of the 2nd peak still may only have been the result of normal variation; but its constancy for 2 samples, for all 3 strictly aquatic species which showed the principal peak, and for both dates when moonlight became occluded during the night, at least suggest that it was not. The magnitude of the nocturnal drift rate may be, in part, a function of moonlight; Beeton (1960) observed a depression of the vertical migration of *Mysis relicta* due to moonlight.

Neither absolute temperature nor rate of temperature change appeared to affect the time of increase, but temperature may affect the magnitude of the nocturnal drift rate; Lennon (1941) reported increased drift upon a rise in water temperature. Temperatures of Valley Creek waters vary little through the day; for example, the range of water temperature in the August series was only from 57°F to 64°F, despite a maximum air temperature of 90°F. In February, water temperatures varied only from 37°F to 41°F. Although water temperatures were usually decreasing at the time the principal peak in drift rate occurred, the rate of temperature fall was approximately the same from before sunset to early morning.

Moon (1940) pointed out that the greater nocturnal activity that he observed among lake and stream insects was not connected with the stage of development, as might be supposed. In the present study also all stages and sizes were well represented in the drift, for insects as well as *Gammarus,* indicating that the high drift rates at night were not merely the result of pre-emergence activity.

The active, free-swimming animals, such as *Baetis* and *Gammarus,* exhibited the greatest diurnal fluctuations in drift rate although the encased caddisfly, *Glossosoma,* also participated apparently by leaving its case at night. The seasonal differences in night drift rates were large, the drift in the summer being relatively great. Since it has been indicated in a previous paper that drift rate is a function of production rate (Waters 1961), the seasonal difference in drift rate may correspond to a similar seasonal difference in production rate.

The basic response in these stream organisms to changing light conditions may be the same as that in zooplankters exhibiting diurnal vertical migrations, but ecologically the effect must be completely different. In lakes and oceans the movements of zooplankters are true migrations; the animals travel upward toward the surface and later return to the original water level. In streams, the organisms are transported downstream not to return; the effect is thus removal.

Both Dendy (1944) and Müller (1954) pointed out that the downstream drift of invertebrates is a normal characteristic of streams even in the absence of floods, and therefore is an ecologically significant phenomenon. But they were both remarking on daytime drift rates; if the daily mean rate of drift, including night values, is considered, the impact of the drift phenomenon must be considered tremendously greater. In Valley Creek, it should be emphasized that the night drift rates, particularly in the summer, were extremely high; the maximum rates included several thousands of organisms per hour for *Gammarus* and *Baetis*. The total daily drift over an area of 1 $ft^2$, for example, was many times the standing crop on that area, causing, potentially at least, an extremely rapid turnover in the resident populations of certain species. (Standing crop in Valley Creek riffles, all species combined, was probably about 1.5 $cc/ft^2$ (Waters 1961).) Such high rates of drift, representing removal from upstream areas, must be balanced by production rates much higher than may have been previously supposed.

The relationship of high nocturnal drift rates to the feeding behavior of stream fishes, although unknown at present, should prove highly interesting; in a lake, for example, the feeding habits of white bass were correlated with the diurnal migrations of daphnids (McNaught and Hasler 1961).

## Summary

Diurnally recurring changes in the drift rate (defined as the quantity of organisms drifting downstream per unit time per unit stream width) of several species of invertebrate organisms were observed in a small Minnesota stream. These changes usually were a precipitate increase in drift rate about 1 hour after sunset, a decrease through the night, and a sharp return to daytime low values at about sunrise. In some cases, a 2nd peak in drift rate occurred during the night, possibly being related to the occlusion of moonlight. Active, free-swimming species, the crustacean *Gammarus limnaeus* Smith and the mayfly *Baetis vagans* McDunnough, exhibited these changes most strongly. *Glossosoma intermedium* (Klapálek), a stone-encased caddisfly, exhibited similar changes in drift rate but was present in the drift without its case. Data on the dipteran *Dixa,* though inconclusive, also suggested a slight increase in drift rate at night. An adult bug, *Hesperocorixa,* exhibited high drift rates in early night, apparently the result of an evening flight originating elsewhere. *Simulium* was common in the drift but exhibited no diurnal periodicity. A snail and another stone-encased caddisfly, *Limnephilus,* though abundant in the stream, appeared only rarely in the drift. For all species, drift rates were much higher in summer than in winter.

## References

**Bainbridge, R.** 1961. Migrations, p. 431-463. *In:* Talbot H. Waterman (ed.), Physiology of Crustacea. Vol. II: Sense Organs, Integration, and Behavior. New York: Academic Press.

**Beeton, A. M.** 1960. The vertical migration of *Mysis relicta* in lakes Huron and Michigan. J. Fish. Res. Bd. Canada **17**: 517-539.

**Berg, K.** 1937. Contributions to the biology of *Corethra* Meigen (*Chaoborus* Lichtenstein). Det Kgl. Danske Vidensk. Selskab., Biol. Medd. **13**(11): 1-101.

**Dendy, J. S.** 1944. The fate of animals in stream drift when carried into lakes. Ecol. Monographs **14**: 333-357.

**Lennon, R. E.** 1941. Drift-borne organisms in Pond Brook, Passaconaway, N. H., Univ. N. H. Extension Serv., Contr. No. 2, Biol. Inst.

**McNaught, D. C. and A. D. Hasler.** 1961. Surface schooling and feeding behavior in the white bass, *Roccus chrysops* (Rafinesque), in Lake Mendota. Limnol. Oceanogr. **6**: 53-60.

**Moon, H. P.** 1940. An investigation of the movements of fresh-water invertebrate faunas. J. Animal Ecol. **9**: 76-83.

**Müller, K.** 1954. Investigations on the organic drift in North Swedish streams. Rept. Inst. Freshwater Res. Drottningholm **35**: 133-148.

**Needham, P. R.** 1928. A quantitative study of the fish food supply in selected areas. N. Y. Cons. Dept., Suppl. to 17th Ann. Report, p. 192-206.

**Pennak, R. W.** 1944. Diurnal movements of zooplankton organisms in some Colorado mountain lakes. Ecology **25**: 387-403.

**Waters, T. F.** 1961. Standing crop and drift of stream bottom organisms. Ecology **42**: 532-538.

---

# REMARKS ON THE TAXONOMY AND INTERTIDAL DISTRIBUTION OF *LITTORINA* IN THE SAN JUAN ARCHIPELAGO, WASHINGTON

Emil K. Urban
*Department of Zoology, University of Wisconsin, Madison*

One of the most abundant forms in the intertidal area of the San Juan Islands is the snail, *Littorina*. This animal occurs on the shore from the level of mean low tide to the highest levels of the intertidal zone. Some individuals are exposed to air for only short periods of time in each tidal cycle; others are almost continuously exposed and may sometimes receive water only from the spray of waves at times of high tide. In this paper, the species of *Littorina* that occur in the San Juan Archipelago are described and one phase of their ecology, their vertical intertidal distribution, is discussed. Areas studied in the San Juan Islands (San Juan County, Washington) were the rocky intertidal areas of Marvista and False Bay, Cactus Islands, Parker Reef, and the shore in front of the Friday Harbor Laboratories. For comparison, the open coast at Point Renfrew, Vancouver