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# NUMERICAL ANALYSIS OF POPULATION DYNAMICS OF NET-SPINNING CADDIS LARVAE AND SUBSTRATUM ADHESION DUE TO THEIR INHABITATION IN A COBBLE-BED RIVER WITH FEWER DISTURBANCES

BY

Takashi Tashiro

Post Doctoral Fellow, Aqua Restoration Research Center, Public Works Research Institute,
Kawashimakasada-machi, Kakamigahara, Gifu 501-6021, Japan

and

Tetsuro Tsujimoto

Professor, Department of Civil Engineering, Nagoya University,
Furo-cho, Chikusa-ku, Nagoya 464-8603, Japan

## SYNOPSIS

Net-spinning caddis larvae set up nests in the substrata of cobble-bed rivers. They are clearly abundant in the substratum with fewer disturbances and, moreover, cause ‘substratum adhesion’ which suppresses the flux of bed-load transport because of the binding of large amounts of bed-materials. We modelled the population dynamics of the net-spinning caddis larvae (*Stenopsyche* sp. and *Macrostemum radiatum*) by taking into account conventional knowledge about the caddis emigration, immigration and carrying capacity responding to various flow conditions and by considering the dynamics of the number of individuals and the individual growth. By combining the numerical simulations of the caddis population dynamics and the flow computation in a study reach with our experimental results about the substratum adhesion due to the caddis inhabitations, the temporal changes of actual substratum adhesion in a cobble river with fewer disturbances was calculated.

## INTRODUCTION

Net-spinning caddis larvae set up nests or retreats with particles of sand, gravel, and other materials in order to feed on suspended organic materials in water (e.g. Tanida (40)). In Japan, they often become predominant in lotic benthic communities (Nishimura et al. (29); Tsuda (47)). Tsuda and Gose (48) defined communities with these caddis abundances as a “climax” in the succession of lotic benthic communities, because the continuation of fewer disturbances was considered to favour these communities. They also hypothesized that the predominant species became Stenopsychidae via Hydropsychidae (both families belong to the category of net-spinning caddis) after a disturbance had occurred. However, frequent floods and spates caused by the seasonal precipitations usually control the diversity in lotic ecosystems of the monsoon regions, including Japan. Consequently, the intensity and frequency of disturbance significantly influences the aquatic organisms.

Recently, dams have been constructed in many rivers to control floods, to generate electric power and to provide potable water. Dams usually force flow and sediment continuity to deviate relative natural ones and, thus, so shortages of water and sediment supply occur to maintain geomorphic equilibrium in the downstream. Tsujimoto (49) reviewed the effects of dams on fluvial processes, especially reaches downstream of dams. He described the downstream effects of dams as riverbed degradation, armoring, drying of riparian zone (bars and floodplains), invasion of vegetation, and deposition of fine materials. In particular, channel armoring has been typically observed below dams all over the world as described by Livesey (23) and Parker (32), although this phenomenon could also occur without effects of dams, due to fluvial processes and the decrease of sediment supply (e.g. Dietrich et al. (7) and Parker (32)). Armoring has also been recognized as one of the physical factors leading to degeneration of lotic benthic communities (e.g. Tanida and Takemon (41)). Kitamura et al. (20) evaluated the decrease of disturbance frequency on the armored bed below a dam after construction and implied that the development of armoring with fewer disturbances caused changes in the lotic ecosystem, such as the bloom of filamentous attached algae and the decrease of specific fish catches. However, these biological effects are not described quantitatively in conventional works (Tanida and Takemon (41)).

Taking Tsuda and Gose's (48) hypothesis into consideration, net-spinning caddis larvae are predominant where there occurs armoring below dams. This view has been supported by the following studies. By investigating the Hydropsychid guilds above and below a dam, Camargo (4) observed that the biomass of these guilds was larger below the dam, while diversity was higher above the dam. Uchida (53) related the increased abundance of certain net-spinning caddis (*Stenopsyche sauteri* and *Macrostemum radiatum*) in benthic communities to dams by reviewing previous investigations before and after dam construction. Some researchers, meanwhile, have suggested that the abundance of specific net-spinners depends on the different feeding conditions in seston of flowing water. For example, Furuya (14) investigated the temporal increase of *Macrostemum radiatum* biomass below dams after dam construction and discussed the relationship between the caddis abundance and the drifting plankton in water, whereas Oswood (30) explored the spatial change in community structure of Hydropsychidae along a stream below a lake outlet in relation with the difference in food supply. These findings show that the characteristic abundance of specific net-spinning caddis larvae below dams occurs not only because of fewer disturbances, but also because of the food change in water.

Tanida (34) found the alterations of habitat conditions due to the inhabitation of net-spinning caddis larvae by considering Tsuda and Gose's (40) hypothesis. Their nets and retreats can reduce the habitat available to other benthos in the interstices of substratum (Tanida (40)), and also may influence the physical and geomorphic processes. Jones et al. (19) named organisms with such abilities 'ecosystem engineers'. Statzner et al. (38), Cardinale et al. (5) and Tashiro et al. (44) previously examined the effect of inhabitation of caddis larvae (Hydropsychidae or Stenopsychedae) on the critical shear stress of materials on the substratum, and considered net-spinning caddis larvae to be tn this category. Tashiro et al. (43 and 44) called this effect 'substratum adhesion', and suggested that it changes the amount of sediment load and produces the substratum with fewer disturbances. Furthermore, some of the previous experiments controlling nesting period and water temperature revealed the dependence of substratum adhesion on temperature variation (Tashiro et al. (44)), which suggests that substratum adhesion depends on climate variation. In these studies, their adhesive effects were also determined in indoor experimental flumes and even in the one or two life stages with latter instars larvae of the caddis. Life cycle of caddis is characterized by several distinct stages such as egg, larva, pupa and adult. Consequently, actual effects of the caddis inhabitations cannot be quantitatively estimated without taking into account population dynamics with seasonal and spatial variation.

Population dynamics of lotic communities have been discussed by using some general hypotheses such as "the intermediate disturbance hypothesis (Connell (6))" and "the patch dynamics (Paine and Levin (31))". These hypotheses conceptualize that species diversity depends on external disturbances and interspecific interactions such as competition and prey-predator relationships in a community and is controlled by the magnitude of these factors. Furthermore, the former hypothesis predicts that species diversity is maximized under intermediate intensity and frequency of disturbance, and the latter concept argues that inferior species in competition could be sustained due to disturbed blank niches. There are some empirical evidence that supports the intermediate disturbance hypothesis (e.g. Townsend et al. (46)), but other research has not fully accepted this hypothesis (e.g. Lake (22) and McAuliffe (24)). Pringle et al. (33) conclude that the concepts of patch dynamics theory could be applied in streams and rivers, and Frid and Townsend (13) and Townsend (45) suggest that patterns of patch dynamics serve as a general organizing principle for running waters. Although community dynamics with the change in biota have been developed by many researchers in such a rather general way, the population dynamics of specific organisms in running waters have been rarely discussed. The population dynamics of net-spinning caddis have been only investigated by a few ecological researchers (Nishimura (27 and 28), Wills and Hendricks (58)). Numerical modeling has been the most effective method of understanding the dynamics of natural phenomena (e.g. Vehulst (54)). However, numerical modeling of these organisms has not been previously developed because of the insufficient knowledge of caddis population dynamics. Probabilistic simulations for benthic community dynamics recently carried out by Watanabe et al. (55 and 56) are the most developed models because they are reproducible. The objectives of the present study are to understand and to predict 'substratum adhesion' due to net-spinning caddis inhabitation. In particular, we simulate population dynamics of net-spinning caddis larvae by means of numerical modeling and limited previous knowledge and substratum adhesion due to their inhabitation by introducing the previous findings (Tashiro et al. (44)).

## METHODS AND MATERIALS

Field data on caddis larva population dynamics were collected to validate numerical modeling. The study area is located at the Yahagi River in Toyota City in the central region of Japan. The organisms investigated here, *Stenopsyche* sp. and *Macrostemum Radiatum*, were the biomass-dominant taxa of benthic invertebrates in the area during study period. Both are net-spinning caddis larvae that build nets and retreats with bed materials and usually inhabit the alluvial reach of Japanese rivers (e.g. Tanida (40)).

### *Field Investigation in the Yahagi River*

The main stem of the Yahagi River has a length of 117 km, and the catchment area is 1,830 km2. Fig. 1 shows the schematic image of the river basin and study area location. There are seven dams in the main stem. The Yahagi Dam is the largest one, located at river kilometer (Rkm) 80.0 and has multiple functions such as flood control, water resources development and providing environmental flow to the downstream area. Other dams are not large enough to regulate the discharge during flood events. The study area lies at Rkm 42.0 in the middle reach downstream of the Koshido Dam (at Rkm 45.8) in the northern part of Toyota City. Since the Yahagi Dam was constructed in 1971, the downstream substratum habitat has changed due to the regulation of flow and sediment (Uchida (53) and Kitamura et al. (20)). The middle reach of Yahagi River currently displays the characteristics of a cobble river with armoring.

The study reach was selected to include a reach with one continuous riffle-pool structure. A GPS (Global Positioning System) receiver and a leveling apparatus were used to carry out the investigation. Fig. 2 shows the contour of relative bed elevations referred to the instrument station in the investigated interval. The pool section was in the upper region, and the riffle section was in the lower region. Four quadrates (each 0.25m$^2$) were differently arranged in channel units such as rapids, riffles, shallows and pools of the reach to examine annual population dynamics of two kinds of caddis larvae (*Stenopsyche* sp. and *M. radiatum*) and characteristics of their habitat condition. We chose the location of these quadrates by considering the environmental properties such as the riffle-pool structure and the substratum conditions in the study reach.

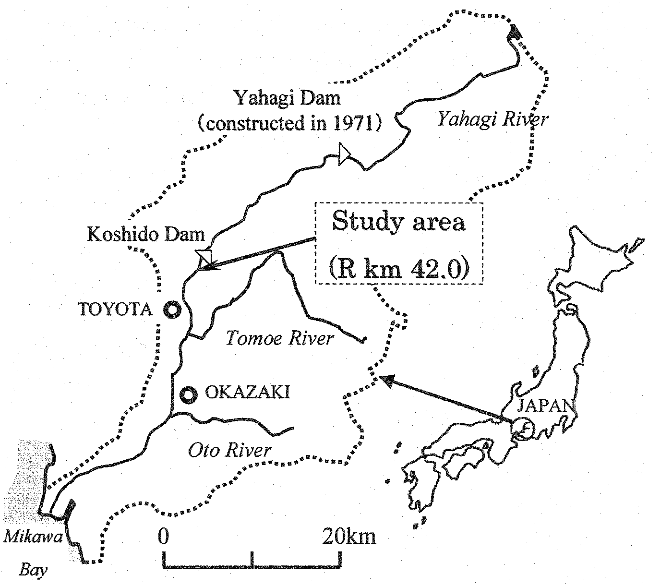

Fig. 1 Schematic image of study area location and Yahagi River overview

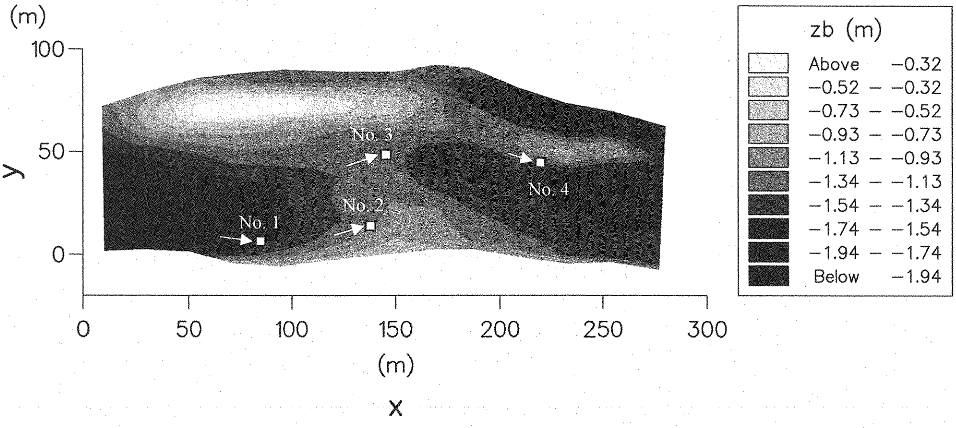

Fig. 2 Contour of the relative elevations of riverbed (zb) in the investigated reach
(The x and y axis are the longitudinal and transverse distance, respectively, and flow directions are indicated by the white arrows. Continuous data collection was conducted in the four numbered quadrates.)

The investigation was carried out nine times from July 2002 to June 2003. Fig. 3 shows the daily change in water discharge and water temperature at the study area. To investigate the conditions of the habitat, we measured water depth and water velocity (with an electromagnetic current meter (KENEK VE10) at 60% depth) at the center of each quadrate. We also collected all of the benthic animals in each quadrate with a D-frame net (mesh size: 2 mm), and kept the samples in 5 % formalin solutions. The biomass and number of individuals for each benthic taxon were measured for each sample.

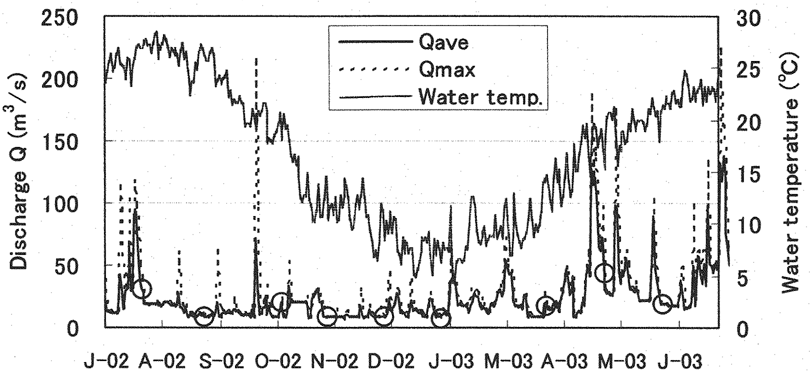

Fig. 3 Daily change in water discharge and temperature in the study area and period (The circles (○) indicate the days that the investigation was conducted. The data of the daily water discharge were provided by Chubu Electric Power Co. Inc., and the data of daily water temperature were predicted by Tsujimoto and Tashiro (51) with the correlation between observed water temperatures in the study area and the data of daily air temperatures in Toyota city at that time (Japan Meteorological Agency (18)).)

### *Numerical Modeling of Population Dynamics with Substratum Adhesion*

According to Velhulst (54), the growth rate and carrying capacity for the investigated population are needed in order to model population dynamics. Specifically, the growth of an organism depends on its nutrient composition and its physiological activity, while the carrying capacity is determined by surrounding conditions including physical, chemical and biological factors. In his review of modelling of the aquatic ecosystem in still water, Kusuda (21) formulated population dynamics of organisms with typical roles such as primary production and consumption in the ecosystem by considering these controlling factors. However, for stream benthic organisms, few studies of numerical modeling of their population dynamics have been conducted because they have complicated ecological conditions such as their physical habitat, their genetic physiology and their intraspecies or interspecies interactions. These conditions have been recognized as being significant factors in population dynamics by the many previous field studies and will be discussed later. Particularly, the hypothesis of 'drift paradox' or 'colonization cycle' (Müller (26)) is well-known for explaining typical population dynamics. This hypothesis suggests that aquatic insects often migrate upstream by flying in the adult stage after drifting downstream in the larval stage. Under such circumstances, we have introduced the concept of independently treating the changes in number of individuals and in individual growth of net-spinning caddis larvae for modeling their population dynamics (Tashiro et al. (43)). Although this concept is incomplete and has not been verified, it is a fact that the number of individuals and individual mass can express the changing standing crops of these net-spinning caddis larvae. The following equation simply expresses our concept:

$$X_c = N_c \times IM_c \tag{1}$$

where $X_c$ = the standing crop of caddis larvae ($g/m^2$); $N_c$ = the density ($individuals/m^2$); and $IM_C$ = individual mass (g). Additionally, the following differential equations are derived from 'logistic equation' dynamics (Velhulst (46)) suggested by Kusuda's (21) examples:

$$\begin{aligned}\frac{dN_c}{dt} &= \left(i_c - d_c\right)N_c - e_c N_c \frac{N_c}{K_c}\\ \frac{dIM_c}{dt} &= \left(\mu_c - r_c\right)IM_c\left(1 - \frac{IM_c}{IM_{c\max}}\right)\end{aligned} \tag{2}$$

where $i_c$ = the immigration rate of investigated caddis larva ($d^{-1}$); $d_c$ = the mortality rate ($d^{-1}$) ; $e_c$ = the emigration rate ($d^{-1}$); $K_c$ = the density of carrying capacity (individuals/$m^2$); $\mu_c$ = the anabolism rate ($d^{-1}$); $r_c$ = the respiration rate ($d^{-1}$); and $IM_{Cmax}$ = the maximized individual mass before becoming pupa (g). The density dependence effect on their dispersion examined by Glass and Bovjerg (16) and Statzner et al. (37) is added to the above equation. In this model, the conventional carrying capacity defined in Velhulst (54) is comparable to the product of $K_c$ and $IM_{Cmax}$. Essentially, this carrying capacity defined as $K_{Xc}$ (g/$m^2$) is expected to change dynamically according to the local and temporal environmental conditions. By adopting our approach to attached algae modeling (Tsujimoto and Tashiro (51)), $K_{Xc}$ also can be evaluated in relation to the physical environment factors such as flow velocity and water depth. The following equation, which is suggested by Tsujimoto and Tashiro (51), is utilized here:

$$K_{Xc} = X_{c\max}\sqrt{f_{K_{X_c}}(U) \times g_{K_{X_c}}(h)} \tag{3}$$

where $X_{cmax}$ = the potentially maximized standing crops (g/$m^2$); $f_{Kxc}$= the suitability index (0-1) of flow velocity; and $g_{Kxc}$ = the suitability index (0-1) of water depth. These suitability indices are determined by the field investigation (discussed later in Fig. 5). Maximum values of wet masses of standing crops observed in many regions and years in Japan (80.3 g/$m^2$ for *Stenopsyche* sp. and 82.9 g/$m^2$ for *M. radiatum* in Nishimura et al. (29)) are assumed to be equal at 80 g/$m^2$.

Furthermore, most aquatic insects eclose outside of water because they have a short aerial life in their adult period for mating. Therefore, the population dynamics of benthic insects cannot be modeled without considering generation shift. In our modeling, Gose's (17) hypothesis is introduced to determine their eclosion date from aquatic living conditions. He founded that the eclosion date of *Stenopsyche marmorata* depended on the integrated water temperature during underwater inhabitation. The following equations are slightly adjusted for this model by converting Gose's (17) findings from monthly to daily values:

$$\begin{aligned}&\sum\left(T_W - 4\right) \geq 1650\left[{}^\circ\mathrm{C}\right] \quad (\textit{Stenopsyche}\ \text{sp.})\\ &\sum\left(T_W - 4\right) \geq 3650\left[{}^\circ\mathrm{C}\right] \quad (\textit{M. radiatum})\end{aligned} \tag{4}$$

where $T_W$ = the daily average water temperature (°C). Threshold values on the right-hand side of these formulas are estimated by employing Gose's finding for *Stenopsyche* sp. and taking into account the generation change in our field observation for *M. radiatum* (discussed later). He also noted that the eclosion happened under high temperature conditions (≥ 13 °C in water temperature) that meet the above criteria (Eqs. (4)). We applied this limitation not only to *Stenopsyche* sp., but also to *M. radiatum*.

At a fixed position, there are four controlling factors if mortality is disregarded: (a) emigration upstream, (b) drifting downstream (emigration), (c) crawling upstream (immigration) and (d) immigration downstream. Under the ideal equilibrium, emigration upstream equals drifts from upstream and drift downstream equals immigration upstream (Minshall and Petersen (25)). However, this assumption is not accepted because the benthic organism inhabitation varies in rivers and streams that have dynamic conditions due to the fluvial processes of flow and sediment regimes. Furthermore, Müller's (26) 'colonization cycle' hypothesis has been supported by some studies (e.g. Elliott (9), Gose (17), and Nishimura (27)), whereas other studies have examined the larval upstream migration (e.g. Elliot (10)), the effect of growth stage of specific net-spinning caddis larvae on their drift characteristics (Elliott (11) and Statzner et al. (37)), and the comparative drift characteristics of some species of stream invertebrate (Elliott (12) and Turner and Williams (52)). Particularly, Statzner et al. (37) and Turner and Williams (52) investigated the density dependence effect on drifting of some aquatic invertebrates. There are consequently a large variety of functions and studies of the dynamics of the numbers of individuals for benthic insects. These findings need to be organized for modeling of individual number dynamics, and more applicable quantitative data are required to understand these kinds of phenomena more clearly.

It is known that net-spinning caddis larvae drift downstream, which is a dominant factor in immigration and emigration (Elliott (9) and Nishimura (28)). Because this drifting might be passive motion, physical factors of flow field variation such as flow directions and velocity distribution are important. Also, emigration only depends on the local flow condition, whereas immigration depends not only on the local condition but also on the upstream and downstream conditions. Thus, we introduced the 'degree of horizontal flow concentration', originally defined in Tsujimoto et al. (50) and later revised in Tashiro et al. (42). The degree of flow concentration quantitatively expresses whether the flow discharge per unit width converges or diverges at a horizontal point with the surrounding discharge variation, and must be taken into account for immigration but not for emigration. With the term, $(1.0 + \alpha_i\,(\partial q/\partial s)\,/\,q)$ [m$^{-1}$] in Tashiro et al. (42), and the dimensionless critical shear stress ($\tau_*$), the immigration and emigration rates can be evaluated as follows:

$$i_c = f(\tau_*)\cdot\left(1.0+\alpha_i\left(\partial q/\partial s\right)/q\right) \quad \left(\alpha_i = 1.0[\mathrm{m}]\right) \tag{5}$$

$$e_c = f(\tau_*) \tag{6}$$

where $\alpha_i$ = coefficient for unit correction (m); $q$ = unit width flow discharge (m$^2$/s); $s$ = the distance of flow direction (m); and $f(\tau_*)$ = function of drifting effect (d$^{-1}$). Shimizu et al. (36) and Tashiro et al. (unpublished) conducted flume experiments to explore the impact of flushing on benthic invertebrates. The results of these previous experiments are shown in Fig. 4. According to the relationship between shear stress and washout rate in the left figure, $f(\tau_*)$ can be linearly estimated by using the least square method with threshold ($f(\tau_*) \leq 1.0$ [d$^{-1}$]) as shown in graph on the right side of the Fig. 4.

The mortality rates are difficult to evaluate because there are many factors which play a role in death in actual river and stream ecosystems. Detailed investigations of population dynamics such as Nishimura (27) and Wills and Hendricks (58) suggest that the mortality rates depend on the growth stages with changing life types and the surrounding physical environmental conditions included floods and spates. Furthermore, the number of individual mortality due to predation should be taken into account in order to model more natural phenomena including inter-species interaction. However, there are few findings on

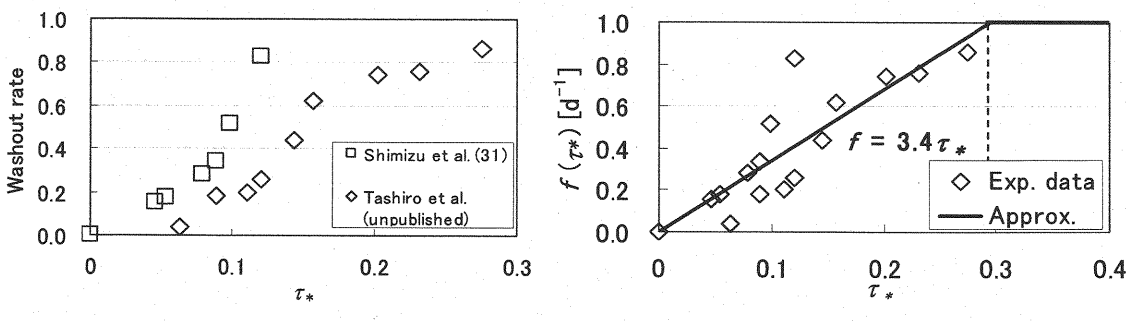

Fig.4 Relationship between shear stress and washout rate in experimental flumes
(Shimizu et al. (36) for *Hydropsyche orientaris* and Tashiro et al. (unpublished) for *M. radiatum*)

Table. 1 Conditions in storage experiments of caddis larvae in an experimental flume (Tashiro et al. (unpublished))

| | Case 1 | Case 2 | Case 3 |
|---|---|---|---|
| Taxa | *Stenopsyche* sp. | *M. radiatum* | *M. radiatum* |
| Collection date | 8-Oct-03 | 20-Oct-03 | 20-Nov-03 |
| Water temperature during collection (°C) | 17.4 | 17.1 | 14.0 |
| Initial date of experiment | 10-Oct-03 | 20-Oct-03 | 20-Nov-03 |
| Final date of experiment | 17-Oct-03 | 27-Oct-03 | 27-Nov-03 |
| Initial water temperature (°C) | 23.0 | 20.3 | 15.7 |
| Final water temperature (°C) | 19.3 | 19.8 | 12.7 |
| Initial number of individuals | 22 (each 2/unit) | 198 (each 18/unit) | 154 (each 14/unit) |
| Final number of individuals | 12 | 132 | 88 |
| Mortality rate ($d^{-1}$) | 0.065 | 0.048 | 0.060 |

food webs in river and stream ecology. We calculated the mortality rates obtained in an indoor flume for seven days (Tashiro et al. (unpublished)); the mortality rates are given as these values under feeding condition (0.06($d^{-1}$) for *Stenopsyche* sp.; and 0.05($d^{-1}$) for *M. radiatum*). There were 11 units made from 20 bricks (4.5 cm x 8.5 cm x 18.5 cm) and two kinds of sands (1 mm and 2 mm diameters) for nest building in an indoor flume (3.4 m length x 0.2 m width) under a stable discharge condition (1.5 l/s). The conditions of this experiment are shown in Table. 1.

On the other hand, anabolism and respiration rates related to individual growth could be relatively evaluated, because they are thought to depend on the interaction between physiological conditions and the surrounding environment. The anabolism rates are determined by the balance between feeding rates and excretion rates. The relationships between these factors related to the individual growth are shown as follows: (anabolism – respiration = net growth) and (anabolism = (feeding - excretion) x absorption). Specifically, because these net-spinning caddis larvae are recognized as filter feeders (e.g. Tanida (40)), it is important to determine the supply of food resources in running water. Alstad (1) and Georgian and Thorp (15) investigated the distributional patterns considering current velocity and filtration rate. Oswood (30) and Furuya (14) indicated that the change in distribution depended on the food quantity and quality in seston, whereas Benke and Wallace (3) observed variable absorption rates depending on types of food contents. Gose (17) also found a clear correlation between water temperature and the feeding rate of *Stenopsyche marmorata* by reviewing some previous studies. Roux et al. (34) studied the effects of changing water temperature on the respiration rates of some net-spinning caddis. The feeding and respiration rates can be modelled as long as reliable information for the filter feeders investigated is available, because there is enough dissolved oxygen under running water conditions. However, since feeding and excretion have not been studied, estimations of these parameters in this study are simplified using net growth rate (defined as $\varepsilon$ ($d^{-1}$)). Firstly, the initial wet mass for an individual is given as 0.01 (g) according to the average of all individuals without regard to quadrate difference. Then, the logistic curves (Eqs. (2)) are fit to the actually observed growth as follows: the net growth rates are 0.06 ($d^{-1}$) for *Stenopsyche* sp. and 0.025 ($d^{-1}$) for *M. radiatum*; and the final wet mass are simultaneously set at 0.35 (g) for the *Stenopsyche* sp. and 0.085 (g) for the *M. radiatum*. Although these values were directly estimated by means of the least square method with a logistic curve, the following findings served as useful references for these settings. Elliott (11) found the initial growth rate of similar caddis larvae (*Philopotamus montanus*) to be 0.06~0.075 ($d^{-1}$), and Nishimura (28) found the final wet mass of *Stenopsyche marmorata* to be 0.32~0.41 (g). Whereas there were few studies of *M. radiatum*, the data of slightly smaller caddis *Hydropsyche slossonae* in Virginia, U.S.A. showed a similar turnover rate (about one year) (in Wills and Hendricks (58)). This data ranged from 0.042 mg (for the egg before hatching) to 54.0 mg (for the mature larva) in wet mass by converting their dry mass data with Water's (57) method. Furthermore, it should be noted that our initial masses are much larger than the observed mass in these studies because only relatively large individuals were caught with a coarse mesh net in our investigation.

We previously evaluated the effects of the inhabitation of net-spinning caddis larvae on substratum adhesion (Tashiro et al. (44)). Specifically, the increase in critical shear stress of bed materials were calculated by employing the concept of Ashida et al. (2) with the one experiment for *Stenopsyche* sp. and only the other experiment for *M. radiatum* which could directly estimate the adhesive critical shear stress (Tashiro et al. (44)). They derived the following equation in order to estimate substratum adhesion due to cohesive material mixing:

$$\begin{aligned} \tau_{*cc} &= \tau_{*c}\left\{1+\frac{s_* A_2}{\mu_f A_3}\cdot\frac{f_c}{\rho(\sigma/\rho-1)gd_C}\right\} \quad (\textit{Stenopsyche}\ \text{sp.}) \\ \tau_{*cc} &= \tau_{*c}\left(1+\phi\eta N_c\right)\ \left[0.0\le\phi\eta N_c\le 2.0\right] \quad (\textit{M. radiatum}) \end{aligned} \qquad (7)$$

$$f_c = 0.15(t-15)T_W X_c \qquad (8)$$

where $\tau_{*cc}$ = the dimensionless critical shear stress of bed materials with cohesive materials; $\tau_{*c}$ = the dimensionless critical shear stress of bed materials without cohesive materials; $\mu_f$ = the coefficient of static friction (1.0); $A_2/A_3$ = the two or three dimensional shape coefficient of bed materials; $s_*$ = the surface area ratio of substratum adhesion (1.0 for exposed materials on substratum in this computation); $f_c$ = the adhesive strength of bed materials (N/m$^2$); $\sigma$ and $\rho$ = the density of bed materials and water; $g$ = gravitational acceleration; $d_C$ = the diameter of bed materials; $\phi$ = the proportionality constant (5.0) observed in the experiment of Tashiro et al. (44); and $\eta$ = the calibration coefficient (10.8) to convert the density from the overall quadrate to the interstice sandy substratum with exposed cobbles. This calibration was simply estimated as the interstice of thickly arranged circles on a flat surface. Also, Eq. (8) was determined in other experiments conducted by Tashiro et al. (44) and Nishimura (28) who studied the *Stenopsyche* sp. suspended life style in the early two weeks of life history. Therefore, the magnitudes of substratum adhesion could be predicted with the standing crops (or the density), water temperature and nest/retreat building period. Coarser materials such as cobbles were influenced by *Stenopsyche* sp., while finer materials such as sands were influenced by *M. radiatum*.

## RESULTS AND DISCUSSIONS

### *Field Investigation in the Yahagi River*

The biomass-dominant species were generally *Stenopsyche* sp. or *M. radiatum* throughout the study period in the study area riffle section, and also in the middle reach of the Yahagi River (Uchida (53)). Fig. 5 shows that the standing crops of net spinning caddis larvae are related to the velocity ($U$) and water depth ($h$) in the investigated four quadrates. Both of the species of caddis larvae generally inhabited areas with fast and shallow waters (velocity = 50~100 cm/s and depth = 20~60 cm), and with exposed cobbles on substratum. According to the relationship between the distribution of net-spinning caddis larvae and current velocity reviewed in Edington (8) and Tachet et al. (39), some of the other species show similar preference for the 10-120 cm/s velocity domain. The suitability indices (0-1) influenced by velocity and water depth were described by $f_{Kxc}$ and $g_{Kxc}$, which were assumed to have trapezoidal forms larger than the basic value of (0.5) with the most preferable value of (1.0) especially in the rapid and shallow conditions (=50~100 cm/s velocity and 20~60 cm depth) as shown in the data dispersion in Fig. 5. For a better understanding of these preferences, data should be collected in more variable flow conditions. Fig. 6 shows the annual change in the density and the average individual wet mass of each species for each quadrate. Growth processes were similar in all quadrates but No. 1. Although changes in the number of individuals varied, *M. radiatum* hatched one time, while *Stenopsyche* sp. hatched twice per year from spring to autumn. Gose (17) estimated that *Stenopsyche* sp. may hatch once or twice per year depending on the temperature of the water. Although this case also agreed with his finding, further investigations are needed for better accuracy. There were few caddis larvae observed in quadrate No. 1 located in pools with sandy substrata, whereas large numbers of *M. radiatum* individuals were observed in quadrate No. 4. Although Tanida (40) observed that *M. radiatum* larvae inhabit riffles with sandy substrata, the current study provides a counterexample to his observation. This figure also shows the logistic curves of individual mass change from our model. The lines were found to suitably replicate the investigation.

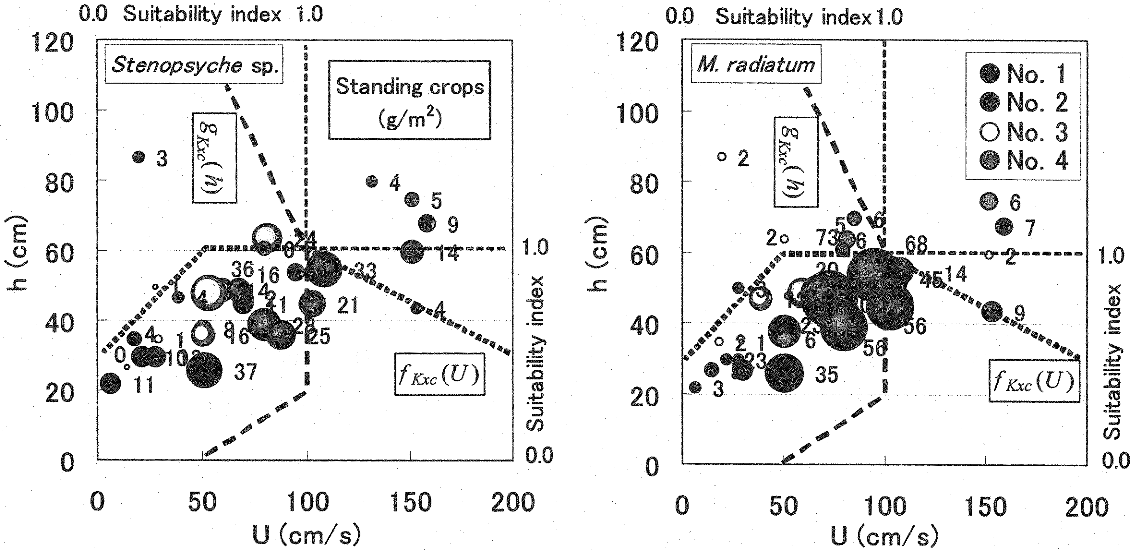

Fig. 5 Standing crops (g/m$^2$) of the net spinning caddis larvae (*Stenopsyche* sp. and *M. radiatum)* with the relationship between velocity ($U$) and water depth ($h$) investigated in the four quadrates ($f_{Kxc}/g_{Kxc}$, the suitability indices (0-1) influenced by velocity / water depth are also included)

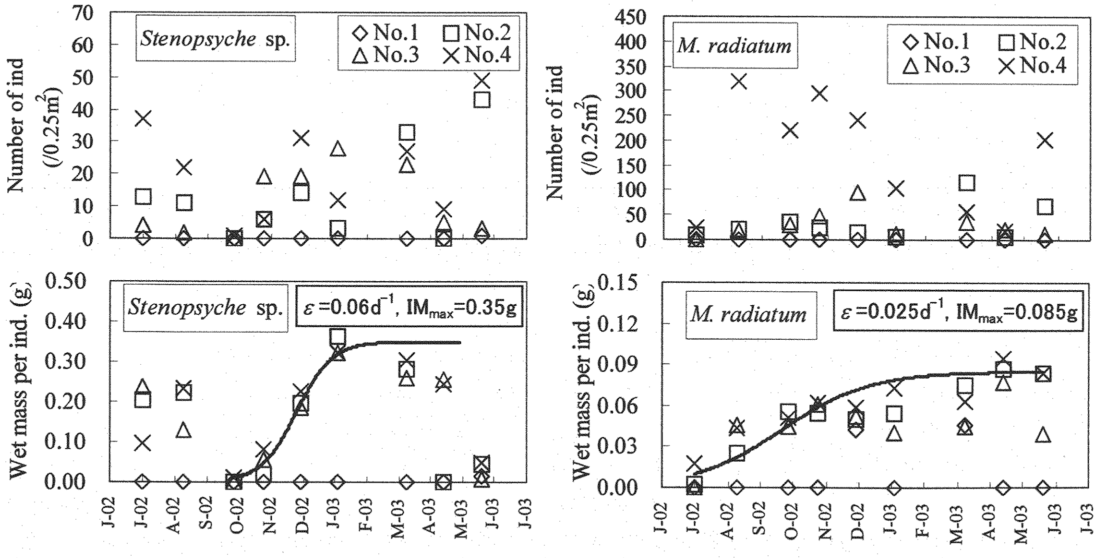

Fig. 6 Population dynamics of the net-spinning caddis larvae (*Stenopsyche* sp. and *M. radiatum)* in quadrates (upper: density (individuals/0.25m$^2$), lower: average individual wet mass (g))

### *Numerical Simulations of Population Dynamics and Substratum Adhesion*

Two series of numerical simulations were carried out in the investigated reach (Fig. 2) by using the 2D flow computation with the NH2D model (Nagoya Hydraulics two-dimensional flow computation model) in Tsujimoto and Tashiro (51) and the population dynamics model. After the daily flow fields were continuously computed according to the daily discharge variation in Fig. 3, the following equations derived from Eqs. (2) were solved on a daily basis:

$$\begin{aligned} N_C(t+\Delta t) &= \frac{N_C(t)\cdot \exp \alpha_c \Delta t}{\beta_c N_C(t)\cdot(\exp \alpha_c \Delta t - 1) + 1} \\ IM_C(t+\Delta t) &= \frac{IM_C(t)\cdot IM_{C\max}}{IM_C(t) + \left(IM_{C\max} - IM_C(t)\right)\cdot \exp \varepsilon_c \Delta t} \end{aligned} \tag{9}$$

where $\Delta t$ = a finite time interval; $\alpha_c = i_c - d_c$; $\beta_c = e_c / \alpha K_c$; and $\varepsilon_c$ = net growth rates, $\mu_c - r_c$. The simulations started on Oct. 16, 2002 for *Stenopsyche* sp., and on Jul. 23, 2002 for *M. radiatum* corresponding to their life cycle in our observation. In the initial condition (at $t = 0$), the individual masses ($IM_c(0)$) were all set to 0.01 (g) as noted above, and both species populations ($N_c(0)$) started at 5000 (individuals / m$^2$) in the local substratum condition with exposed coarse materials. The exact number could not be counted in our field investigation since a coarse sampling net was used. Nishimura (27 and 28) estimated approximately 5000 eggs (/m$^2$) for *Stenopsyche* sp. and Wills and Hendricks (58) counted approximately 10000 eggs (/m$^2$) for *H. slossonae*.

Fig. 7 shows population dynamics simulations and the validations of the investigated net-spinning caddis larvae in the quadrates. The field observations were not suitably replicated because there are many gaps between the calculations and the observations in the early stages of life. The calculated number of individuals varied somewhat, especially in the early life stages as compared to previous investigations carried out by Nishimura (27) and Wills and Hendricks (58). This was due to the method of data collection (above mentioned) and the uncertainty of estimating depletion of individuals. All of the controlling factors of individual mortality were assumed to be easily expressed in this model. This result shows evidence of the complexity of population dynamics, especially in the dynamics of number of individuals in running waters. The following studies supported this implication. Schlosser (35) found that filter feeder colonization depends on life-history attributes, and Wills and Hendricks (58) demonstrated that the reduction rates are varied in their life histories. Moreover, density-dependent effects on mortality rates should be considered for future models by referring to the findings of Glass and Bovjerg (16). However, the calculation results (except for early life stages) could generally describe the difference in magnitude among standing crops of the four quadrates.

Fig. 8 shows the increased dimensionless critical shear stress due to caddis inhabitation with the population dynamics simulations in quadrates. Although *Stenopsyche* sp. could bind substratum materials more strongly than *M. radiatum*, the substantial adhesion effect on sandy substratum with *M. radiatum* in interstices among coarser materials was founded to be larger than on stony substratum with *Stenopsyche* sp. because these series of shear stress were calculated by removing dimensional effects with bed material diameters. Also, the sandy adhesions broadly kept high magnitudes, as shown in Fig. 8. The population of *M. radiatum* was large enough to influence the sandy substratum adhesion in the study area. However, the ecology of early life stages has not yet sufficiently been understood, except for some information about *Stenopsyche* sp. in which Nishimura (28) observed that caddis larvae require about two weeks to creating their nests after incubation. Though the current results for *Stenopsyche* sp. support his findings, the adhesion effects simulated during the early life stages should be treated cautiously. Furthermore, residual effects of the former generation after eclosion were not treated in these simulations. Thus, there are a number of unresolved problems in understanding the dynamics of substratum adhesion. At present, significant effects of substratum adhesion that were quantitatively explored and dynamically estimated in this paper exist in the Yahagi River. Tsujimoto and Tashiro (51) suggested that adhesion due to the net-spinning caddis inhabitation was one of the controlling factors of substratum disturbance when they studied the dynamics of attached filamentous algae. We reexamined

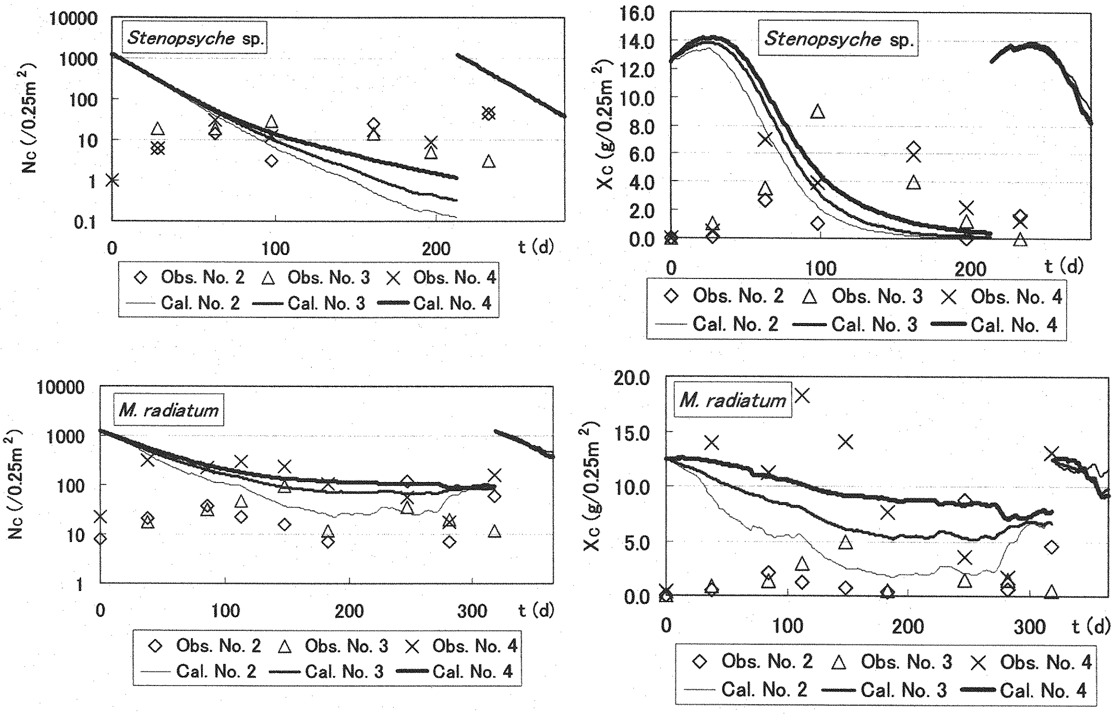

Fig. 7 Population dynamics simulations and the validations of the investigated net-spinning caddis larvae (*Stenopsyche* sp. and *M. radiatum)* in the quadrates

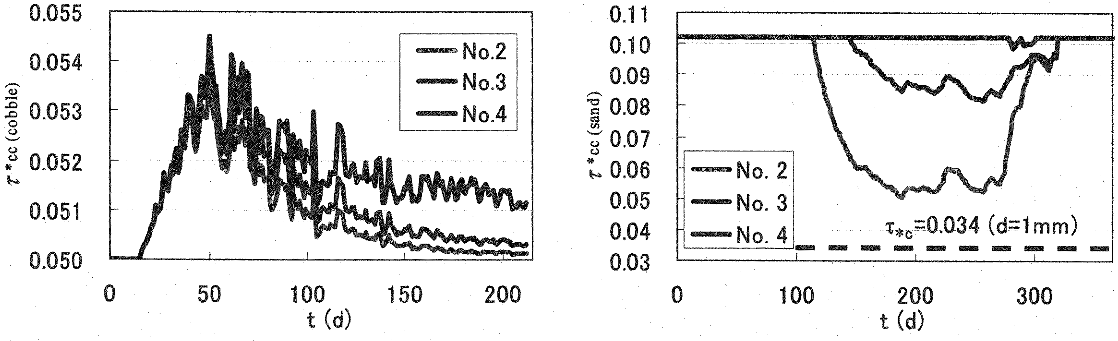

Fig. 8 Substratum adhesion dynamics due to the inhabitations of investigated net-spinning caddis larvae (*Stenopsyche* sp. and *M. radiatum)* in the quadrates

the increases in critical shear stress due to adhesion that partly supported their suggestion. According to these results, the frequency and magnitude of disturbances due to fluvial sediment load could be much fewer and smaller than those estimated by Kitamura et al. (20) using only abiotic factors. Furthermore, these findings may be effective tools in understanding the degeneration of benthic ecosystems such as those below dams.

## CONCLUSIONS

In the present study, we modelled the population dynamics of two kinds of net-spinning caddis larvae in a cobble-bed river, and simulated the dynamics of these caddis populations and substratum adhesion. For the modeling of their population dynamics, the processes of individual growth and changes in density were treated using 'logistic equations' (Verhulst (54)). The changes in density were estimated using local hydraulic conditions, while individual growth was estimated using observation data. Furthermore, previous studies of the controlling factors of net-spinning caddis larvae dynamics were reviewed. Significant effects of substratum adhesion existed in the Yahagi River, and these effects were quantitatively evaluated and dynamically estimated in spite of many unresolved problems. This study suggest that the frequency and magnitude of disturbances may be much fewer and smaller than previously estimated (e.g. Kitamura et al. (20)) using only abiotic and physical environment factors.

Flow and material regimes in rivers and streams have been recently recognized as important factors that play a role in river ecosystems. This substratum adhesion could influence the material regimes by controlling sediment load. Thus, in order to manage environment conditions of rivers and streams, substratum adhesion due to caddis larvae should be considered. The present study should provide new ideas for future fluvial management. However, few studies have been conducted to examine 'ecosystem engineers' (Jones et al. (19)), including net-spinning caddis larvae, for concrete modeling and discussion. Therefore, we are trying to take two approaches: technical development for easy monitoring of multiple fields and improvement of modelling for a better understanding of phenomena in related to ecosystems.

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## APPENDIX – NOTATION

The following symbols are used in this paper:

$A_2, A_3$ = two and three dimensional shape coefficient of bed materials, respectively;

$d_c$ = mortality rates of caddis larvae;

$d_C$ = diameter of bed materials;

$e_c$ = emigration rates of investigated caddis larvae;

$f_c$ = adhesive strength of bed materials;

$f_{Kxc}, g_{Kxc}$ = suitability indices of flow velocity and water depth of caddis larvae, respectively;

$f(\tau_*)$ = function of drifting effect of investigated caddis larvae;

$g$ = gravitational acceleration;

$i_c$ = immigration rates of caddis larvae;

$IM_c$ = individual mass of caddis larvae;

$IM_{cmax}$ = maximum individual mass of caddis larvae before becoming pupae;

$K_c$ = carrying capacity of caddis larvae;

$N_c$ = number of caddis larvae individuals;

$q$ = unit width flow discharge;

$r_c$ = respiration rates of caddis larvae;

$s$ = distance in flow direction;

$s_*$ = surface area ratio of substratum adhesion;

$T_W$ = daily average water temperature;

$X_c$ = standing crops of caddis larvae;

$X_{cmax}$ = maximum potential standing crop of caddis larvae;

$\alpha_c, \beta_c, \varepsilon_c$ = $i_c - d_c$, $e_c / \alpha K_c$, and net growth rates of caddis larvae ($\mu_C$ - $r_C$) in Eq. (9), respectively;

$\alpha_i$ = coefficient for unit correction in Eq. (5);

$\Delta t$ = a finite time interval for population dynamics simulation of caddis larvae;

$\phi$, $\eta$ = proportionality constant (5.0) and calibration coefficient (10.8) in Eq. (8), respectively;

$\mu_c$ = anabolism rates of caddis larvae;

$\mu_f$ = coefficient of static friction;

$\rho$, $\sigma$ = the density of water and bed materials; and

$\tau_*$, $\tau_{*cc}$, $\tau_{*c}$ = dimensionless shear stress and critical shear stress of bed materials with and without adhesion.

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