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ZOOLOGY

Effect of Flow Turbulence on Swimming Speed of Fish

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Abstract—The effect of flow turbulence on the swimming speed was studied in perch (*Perca fluviatilis*) with different body length. The critical flow rate was used as an index of fish swimming performance. The longer was the fish, the higher turbulence was required to decrease the critical flow rate. The mechanism of turbulence impact on fish locomotion relied on the vortex structure of the flow. The torque produced by hydrodynamic forces in a vortex favors fish overturn and loss of balance. Such effect of turbulence was observed when the sizes of the vortex and fish body were similar. The fish uses the pectoral fins to restore the balance, which increases their hydraulic resistance and, together with energy expenditure for spatial balance control, decreases the swimming speed.

Rheoreaction is the major behavioral response of fish in a stream. This inherited response consists in a tendency to swim against the current (Arnold, 1969; Pavlov, 1972, 1979). Movement is a component of nearly all behavioral responses of fish. The swimming speed is a common quantitative index of such reactions. At the same time, it permanently varies (pulsates) at each given point of water body. Such stream state is called turbulence. The nature of turbulence relies on formation and development of vortex systems in water flow. The indices of flow turbulence and its velocity are the main factors describing the hydrodynamic heterogeneity of fish environment.

Previous studies of fish behavior were commonly concerned with just one aspect of this heterogeneity—flow velocity. Even evaluations of fish swimming speed in a stream ignored turbulence. The first studies of the effect of turbulence on the functional indices of fish rheoreaction demonstrated that the threshold and critical flow rates decreased with turbulence (Pavlov *et al.*, 1982; Shtaf *et al.*, 1983).

In this work, the mechanism of turbulence impact on fish locomotion indices was explored with the assumption that balance loss is one of factors decreasing fish swimming performance under conditions of high turbulence with hydrodynamic forces arising in a vortex flow. Clearly, these forces should have different impacts on fish with different body length. The impact of flow turbulence on the critical flow rate of perch (*Perca fluviatilis*) individuals with different body length was studied.

MATERIALS AND METHODS

Experiments were conducted in a special hydrodynamic trough (Fig. 1) in the Volga River. The working region was a passage 120 cm in length and 8 cm in width limited by a special mesh. A device controlling turbulent properties of the flow was placed in the upstream part. River water was pumped to the trough at a constant flow rate of 3.7 l/s. The flow rate in the trough depended on the depth, which was controlled by a flat paddle in the downstream part of the trough.

The rate and turbulent properties of the flow were determined with a specially developed device including a velocity sensor and a signal converter/amplifier based on a single-chip processor (Pavlov and Lupandin, 1994). A microspinner with a fan diameter of 10 mm was used as the velocity sensor. This measuring complex allowed instant processing of data in the laboratory and field and controlling hydraulic conditions during experiments.

The flow rate variations were evaluated as turbulence number and scale (Grinval'd and Nikora, 1988). Turbulence number K, which describes the changes in instantaneous speed in time, was determined from equation:

$$K = \sigma / V_c,$$

where σ is standard pulsation or root-mean-square deviation of instantaneous speed from the time-average flow rate V_c.

A histogram of instantaneous speed frequency in a stream point within the averaging period (60 s) was used to illustrate the process of flow rate changes. The scale of turbulence (L), which describes the mean vortex size in a flow, was determined by one-dimensional time correlation of flow rate (Grinval'd and Nikora, 1988) using equation:

$$L = t_0^* V_c,$$

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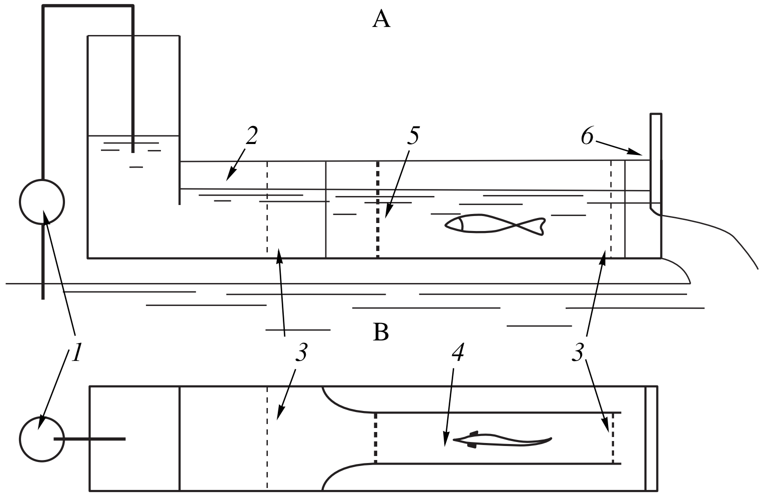

Fig. 1. Experimental arrangement; A, sectional view; B, top view; *1*, pump; *2*, trough; *3*, fish-limiting mesh; *4*, working region of the trough; *5*, turbulence source; *6*, control paddle.

where t_0 is the zero correlation time or the time interval when the coefficient of flow rate correlation decreases to zero.

Flow turbulence number was experimentally modulated by special devices. Low turbulence (0.03–0.06) was generated by a set of mesh cylinders of different diameter. Turbulence of 0.06–0.09 was generated by installing a 5 mm mesh at the trough entry. High turbulence was generated by a convergent–divergent screen with vertical plates; different positions of this screen generated hydraulic conditions with the turbulence number of 0.09–0.15.

Experiments were carried out on three size groups of perch: 30–60, 61–90, and 91–120 mm. Fish were caught 1 day before experiment and kept in special tanks without feeding. The data on experimental fish size and numbers are given in Table 1.

Experiments were conducted on single fish under illumination of 800–1000 lx at water temperature of 16–19°C. Cross black 1 cm-wide stripes were applied on white background of the trough walls and bottom each 10 cm to facilitate fish orientation.

Prior to the experiments, fish were placed to the trough and adapted to the experimental conditions. After 15 min in a 6–8 cm/s flow, the fish was exposed to a gradually increasing flow rate. At the moment when the fish stopped to resist the flow and was carried downstream, the speed was fixed, the measuring device was placed into the preceding position of the fish, and hydrodynamic parameters of the flow were recorded.

Table 1. Mean body length of experimental fish (l), its standard deviation (*SD*), and experimental fish number (*N*)

Index	Fish dimensional group, mm		
	30–60	61–90	91–120
l, mm	44.2	76.0	104.2
SD, mm	4.1	5.2	10.1
N, ind.	71	78	65

The experimental data were statistically evaluated using regression and variance analyses (Lakin, 1980).

RESULTS

Hydrodynamic properties at the moment of fish washing away by the flow where determined for each perch. This is illustrated with the histograms of instantaneous flow rates and correlation functions for three typical turbulence patterns (Fig. 2). These data indicate that the range of instantaneous speed variation ($V_{max} - V_{min}$) increased with the turbulence indices for the same mean flow rates. This range was several cm/s for the turbulence of $K = 0.042$, while it amounted to tens cm/s at $K = 0.140$; i.e., the range of flow rates to which fish are exposed in the flow increased with turbulence number. The intensity of turbulence also changed the pattern of the time dependence of the correlation coefficient of instantaneous speed, and consequently the scale of turbulence (Fig. 3). Overall data for all studied hydraulic conditions suggested the following relationship between the scale of turbulence and turbulence intensity:

$$L = 50.04K,$$

with the regression coefficient significant at $p < 0.01$.

Experiments on fish are shown in Fig. 4 as the relationships between the critical flow rate (V_c) per fish body length (l) and turbulence intensity for the three size groups. Later the normalized specific critical flow rates (V_c/l) were combined for the following turbulence number ranges: 0.03–0.06, 0.06–0.08, 0.08–0.10, 0.10–

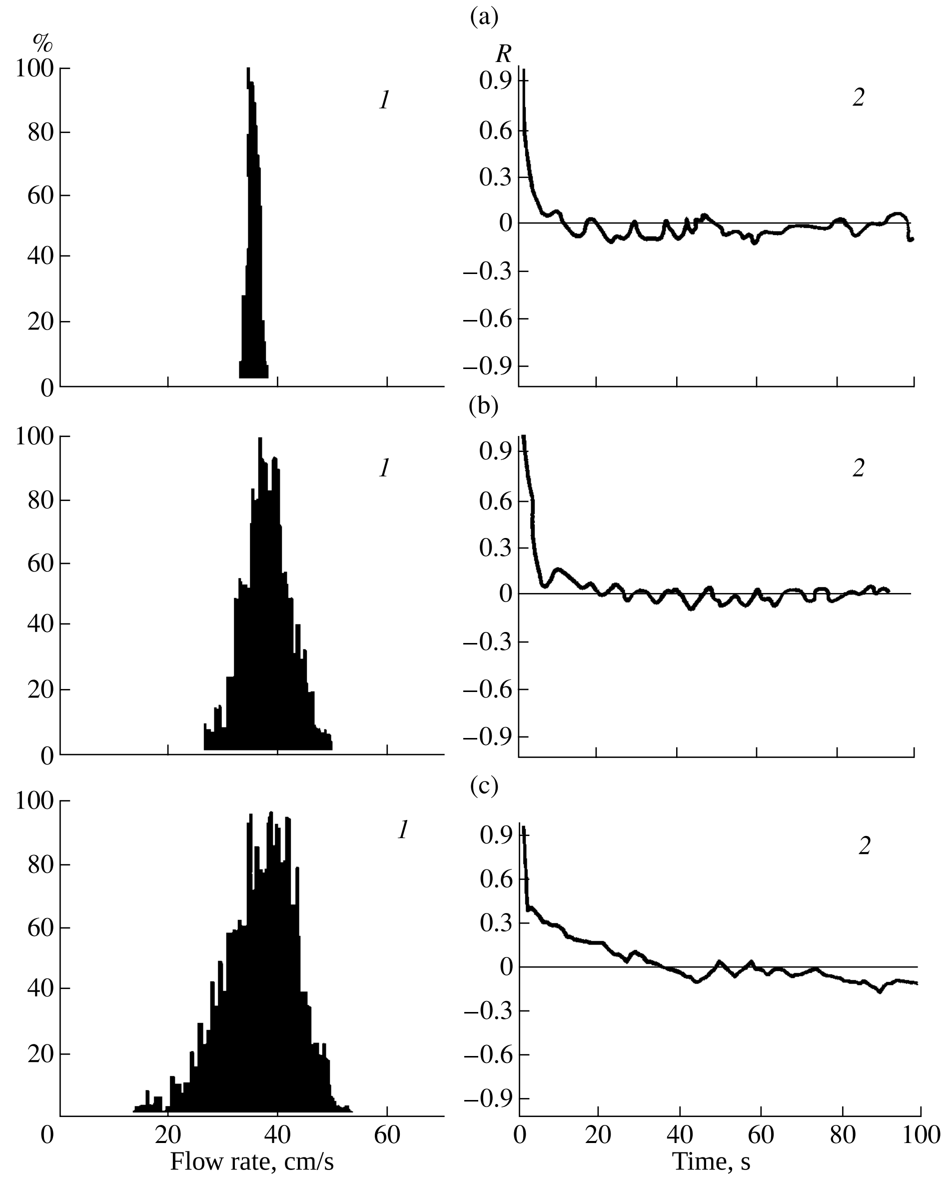

Fig. 2. Histogram of the flow rate (*1*) and the coefficient of rate correlation (*2*) for different turbulence numbers (K); (a) K = 0.042; (b) K = 0.064; (c) K = 0.14.

0.12, and 0.12–0.15. The mean critical flow rates were also calculated for these intervals (Table 2).

Single-factor analysis of variance was used to reveal the differences in these rates. Calculations demonstrated that the intensity of flow turbulence significantly influenced the critical flow rate and this influence was different for fish with different body length.

Four homogeneous groups of critical flow rates could be recognized in 40–60 mm perches. These groups significantly differed (p <0.05) within the considered turbulence range. The data obtained for fish with a longer body could be divided into two homogeneous groups: critical flow rates at low and high turbulence. At the same time, the first group included three turbulence intervals for 61–90 mm perches and four such intervals for 91–120 mm perches. The differences in critical flow rates were observed in 61–90 mm fish for turbulence numbers over 0.10, while in longer fish (91–120 mm) this threshold increased to 0.12.

Hence, the longer was fish body, the higher turbulence was required to affect the critical flow rate. Statistical analysis allowed us to interpret the experimental data as plots shown in Fig. 4. These data indicate that fish swimming speed decreased when turbulence reached certain critical numbers. These thresholds depended on fish body length—the longer was the fish, the higher was the threshold turbulence number.

Turbulence scales were determined in comparison with fish body length from the obtained critical turbu-

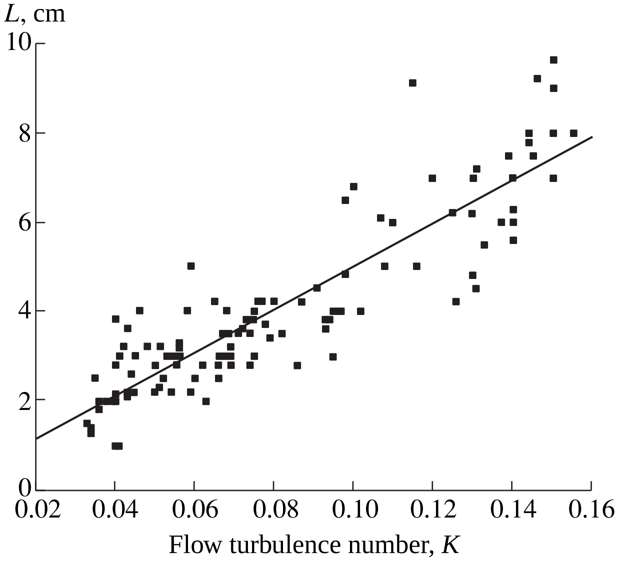

Fig. 3. Changes in turbulent scale (L) as a function of turbulence number (K).

lence numbers. Regression analysis demonstrated their intimate linear relationship ($p = 0.0015$):

$$L = 0.66l,$$

where l is fish body length.

Hence, fish swimming performance started to decrease when the turbulence scale, which describes the hydraulic vortex size, exceeded 2/3 of fish body length.

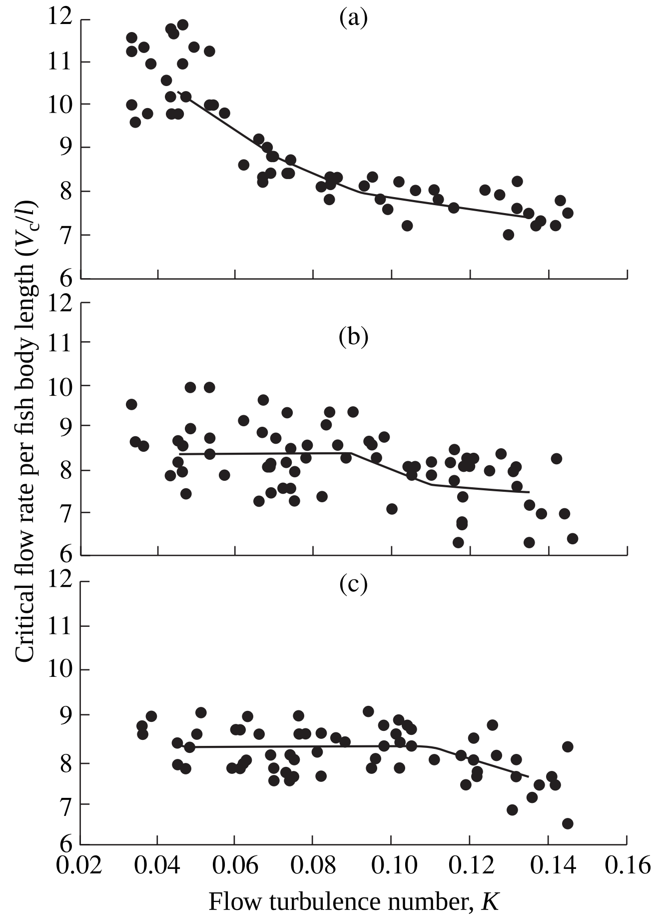

Fig. 4. Changes in the critical flow rate per fish body length (V_c/l) as a function of turbulence number (K); (a) 30–60 mm fish; (b) 61–90 mm fish; (c) 91–120 mm fish.

DISCUSSION

The obtained data confirmed the working assumption about the factors of decreased fish swimming speed in a turbulent flow. The critical flow rate proved to decrease as flow turbulence increased. At the same time, the ranges of fish length corresponded to particular threshold turbulence number, after which this rate started to decrease. The longer was fish body, the higher turbulence was required to decrease the studied rheoreaction index. The relationship between the critical turbulence number and its scale indicate that the vortex action is of the factor decreasing fish swimming performance. Such decrease was observed when vortex size exceeded 2/3 of fish body length.

Table 2. Normalized critical flow rate (V_c/l) and its standard deviation for different ranges of turbulence number (K) and fish dimensional groups

K range	Fish dimensional group, mm		
	30–60	61–90	91–120
0.03–0.06	10.30 ± 0.90	8.64 ± 1.04	8.31 ± 0.47
0.06–0.08	8.65 ± 0.39	8.26 ± 0.71	8.11 ± 0.62
0.08–0.10	7.91 ± 0.48	8.36 ± 0.56	8.28 ± 0.59
0.10–0.12	7.73 ± 0.39	7.69 ± 0.66	8.25 ± 0.66
0.12–0.15	7.65 ± 0.44	7.56 ± 0.66	7.60 ± 0.71

Initially Pavlov *et al.* (1982) proposed that the decreased fish swimming rate in turbulent flow is due to high kinetic energy resulting from the pulsation components of flow rate. High energy of the turbulent flow was considered as a factor complicating fish movement in it, which should decrease the functional indices of their rheoreaction.

Later Pavlov *et al.* (1994) experimentally demonstrated that fish (gudgeon *Gobio gobio*) started to lose its balance at lower flow rates as turbulence increased. Accordingly, additional energy expenditures of fish for balance control in turbulent flow were proposed as the factor decreasing the critical flow rate.

Let us consider the mechanism of the turbulence impact on fish. Turbulent flow has a complex vortex structure with various vortex formations of different shape and size (Loitsyanskii, 1987). In terms of size, small-scale and large-scale vortex systems are recog-

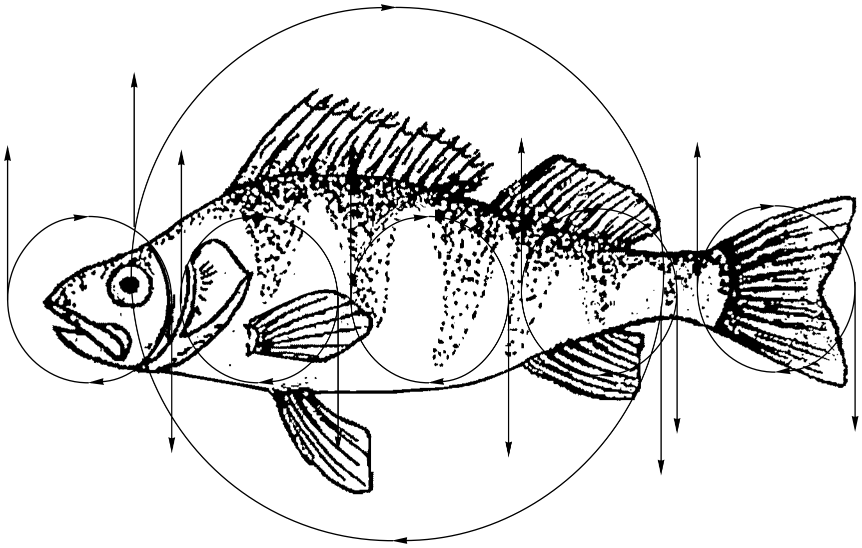

Fig. 5. Histogram of forces exerted on a fish at different vortex size.

nized. Turbulent diffusion induces dissociation of large vortexes into smaller ones. Fish meet such vortex systems in a turbulent flow.

In nature, these vortexes have different orientation in the water flow space. In our experiments with a narrow trough and even flow rate distribution across it, the vortex impact in the horizontal plane can be neglected. Accordingly, below we consider a planar problem with vortex development in the vertical plane of water stream.

The mean vortex size is commonly described by the scale of turbulence. In this work, a higher turbulence number corresponded to a higher turbulence scale (Fig. 3), and hence, to a higher vortex size. Apparently, vortex size is crucial for the balance of fish swimming in turbulent flow. The decrease of the critical flow rate for fish with different body length is observed only in a certain range of the turbulence scale. The larger is an individual, the larger vortex is required to decrease this rate.

The vortex structure of turbulence is described by the torque of hydrodynamic forces in a rotating vortex and this torque increases from the vortex center to the periphery. Clearly, if vortex is much smaller than fish, the moments of force are evenly distributed along its body and cannot affect its balance. If the sizes of vortex and fish are close, hydrodynamic forces of rotating vortex introduce a torque, which tries to overturn the fish and to affect its balance. Schematic impact of hydrodynamic forces in rotating vortexes of different size on a fish is shown in Fig. 5.

Visual observations demonstrated dorsoventral oscillatory movements of the fish in a high turbulence zone at flow rates close to the critical point. Such movements are clearly due to the impact of the hydrodynamic torque of the vortex.

Decreased critical flow rates were observed for fish with different body length within a turbulence range corresponding to certain vortex size. This was due to the loss of fish's balance. They spread their pectoral fins to stabilize the body in the stream, which sharply increases the hydraulic resistance of their body and consequently decreases the swimming speed. Our previous studies (Lupandin *et al.*, 1999) of roach inertial movement after a jerk indirectly confirm these suggestions. For instance, flow rate pulsations proved to affect the pattern of fish movement. The higher was the flow turbulence, the earlier in the inertial phase of the jerk the fish spread its pectoral fins to stabilize body position.

Note that turbulence is a widespread natural form of viscous fluid movement resulting from water mixing and vortex formation. In addition to large vortexes, streams contain numerous small ones, which fill up the whole water space. Fish behavior in such environment largely depends on the impact of turbulent flow. Hence, turbulence is a factor of environmental heterogeneity of great importance for fish ecology.

Turbulence is emphasized in the context of the feeding ecology of marine larval fish (Dower *et al.*, 1997). However, it can have an even greater significance for fish living in rivers with a much more diverse hydraulic structure of the stream. Our research interests include the problem of turbulence impact on the ecology and behavior of river fishes.

Previously we demonstrated that fish can distinguish different degrees of flow turbulence and select them depending on species ecology, individual motivation, and physiological state (Pavlov *et al.*, 2000). For instance, fishes of different ecological groups select streams with different turbulence (Pavlov and Lupandin, 1994). Fishes of the rheophilic complex, chub (*Leuciscus cephalus* (L.)) and grayling (*Thymallus thymallus* (L.)), prefer streams with high turbulence, which is not the case for limnophilic crucian carp (*Carassius carassius* (L.)) and eurybiontic perch (*Perca fluviatilis* (L.)) preferring streams with low flow rate pulsations. Roach fry (*Rutilus rutilus* (L.)) caught in a river prefer a more turbulent flow as compared to those from a storage reservoir with no pronounced stream (Skorobogatov *et al.*, 1996). Satiated and hungry fish of the same species also demonstrate different attitude to turbulence: they start to prefer turbulence with hunger (Lupandin and Pavlov, 1996). A more efficient fish feeding in turbulent flow conditions underlies such selection, which is also confirmed by other studies (Pavlov, 1979; MacKenzie and Leggett, 1991; MacKenzie *et al.*, 1994; Landny *et al.*, 1995).

Moreover, turbulence considerably affects fish locomotion. High flow turbulence was shown to increase fish rheoreaction sensitivity and to decrease the critical flow rate as well as the cruising speed for different fish species and ages (Pavlov *et al.*, 1982, 1994, 2000; Shtaf *et al.*, 1983; Skorobogatov *et al.*, 1996; Lupandin *et al.*, 1999). Thus, high turbulence decreases the range of flow rates that allow fish rheoreaction, and hence their keeping in the corresponding water flow regions.

CONCLUSIONS

Flow turbulence, being a factor of hydrodynamic heterogeneity of fish environment, has an impact on their behavior. This impact is largely mediated by changed fish swimming speed. Particular flow turbulence conditions decrease the locomotion indices of their rheoreaction. Moreover, the longer is the fish body length, the higher turbulence is required to decrease the critical flow rate. This mechanism is primarily related to the impact of the vortex structure of turbulence on fish. The vortex affects the fish balance and the torque generated by the hydrodynamic forces favors fish overturn. In order to stabilize their position, the fish spreads its pectoral fins, which increases their hydraulic resistance and consequently decreases the swimming speed.

ACKNOWLEDGMENTS

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