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The Effect of Temperature on the Rate of Gastric Evacuation in Brook Trout *Salvelinus fontinalis* Fed on Commercial Pellets: Group-Feeding

Nadir Başçınar,[1,]* Nimet Selda Başçınar,[2] Kadir Seyhan[1] and Umar Khan[1]

[1]Department of Fisheries Technology Engineering, Faculty of Marine Sciences, Karadeniz Technical University, Trabzon, 61530, Turkey

[2]Central Fisheries Research Institute, Vali Adil Yazar Cad., No.14 Şana 61250 Yomra, Trabzon, Turkey

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Authors' Contributions

KS conceived and designed the project. NB performed the experimental work and analyzed the data with the help of NSB. UK wrote the manuscript.

Keywords

Brook trout, gastric evacuation, Group-feeding, Square-root model

ABSTRACT

The gastric evacuation rates (GER) of brook trout *Salvelinus fontinalis* were determined under three temperatures: 12, 15, and 20°C. A group of brook trout (ranging from 72—80 g) were fed on commercial pellets to apparent satiation and by means of serial slaughter their stomach contents were sampled with 3 h intervals until the first empty stomach was observed. The square-root model adequately described the gastric evacuation of brook trout by the current stomach content mass. The GER increased exponentially with temperature: $dS_t/dt = -0.0194e^{0.028T}$ (g h^{-1}), $r^2 = 0.91$, where T is temperature in °C. The effect of temperature on GER of brook trout was comparatively lower than other Salmonid species.

INTRODUCTION

Underfeeding of fish results in poor growth of fish and sometimes even fish death, whereas overfeeding of fish causes the degradation of water quality (*e.g.*, ammonia poisoning, low oxygen levels, low pH levels) and also decreases feed digestion efficiency and increases fecal production as well as the waste of expensive feed (Pennell and Barton, 1996; Culver and Castle, 2008; Daudpota *et al.*, 2016). Therefore, the quantification of daily rations for cultivated fish is necessary to cope with such situations.

The proper assessment of the feeding strategy and the daily food ration for cultivated fish requires the estimation of gastric evacuation rate (GER, the rate at which food passes from the stomach into the intestine). In ecological research, gastric evacuation (GE) experiments have received considerable attention and the relevance and importance of such studies are well recognized to quantify the food consumption rates of natural fish populations determining their impact on prey populations (Elliott and Persson, 1978; Bromley, 1994; dos Santos and Jobling, 1995; Seyhan and Grove, 1998). However, few studies have examined GER in fish fed commercial pellets similar to those used in aquaculture production (Windell, *et al*., 1972; Talbot and Higgins, 1983; Riche *et al*., 2004; Khan *et al*., 2016).

* Corresponding author: email: nbascinar@gmail.com
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Several studies have reported various factors influencing GER such as temperature, fish size, meal size, and energy content of the diet (Windell *et al*., 1972; Jobling *et al.*, 1977; Grove *et al*., 1978; Flowerdew and Grove, 1979; Jobling, 1980a, b; Persson, 1981, 1982; Holmgren *et al*., 1983; Seyhan, 1994; Andersen, 1999, 2001; Bernreuther *et al.*, 2009). Temperature appears to be the major factor regulating the GER and several studies have reported that GER increased with increasing temperature until upper temperature tolerance of the species is reached, after which the GER tends to decrease (Tyler, 1970; Bernreuther *et al*., 2009; Andersen, 2012). Generally the relationship between temperature and GER has been described by exponential model; confirmed by various studies (review by Bromley, 1994). The effect of temperature on GER have been shown with Q_{10} and in a variety of marine and freshwater species Q_{10} ranged from 2.2-4.3 which means that GER increases 2.2-4.3 for each 10°C increase in temperature.

The commonly used methods for estimating GER of fish are based on either serial retrieval of stomach content at time *t* by means of fish sacrifice (Medved, 1985; Lee, *et al*., 2000; Andersen, 2012; Khan *et al.*, 2016) or by using stomach lavage (Foster, 1977; Sweka *et al*., 2004; Stehlik *et al*., 2015), or by monitoring the movement of food through the gut of a fish by radiographic methods (Talbot and Higgins, 1983).

Brook trout *Salvelinus fontinalis* (Mitchill, 1814) is an endemic species in North America and artificially introduced to Europe, Asia, Africa, and South America (MacCrimmon and Campbell, 1969; Tzilkowski, 2005; Scharpf, 2011). In this study, GE experiments were performed on brook trout fed commercial pellets at three different temperatures: 12, 15, and 20°C. The stomach content of brook trout were sampled at 3 h intervals by means of fish dissection. The main objective of this study was to determine the pattern of GE of brook trout in group-feeding and to evaluate the influence of temperature on the GER of brook trout.

MATERIALS AND METHODS

Fish and experimental condition

Brook trout (ranging from 72-80 g) were provided by Sürmene Faculty of Marine Sciences in Trabzon, Turkey for each GE experiment (Table I). The acquired fish were stocked in holding tank (800 L) with aerated recirculating fresh water system and were fed with commercial pellets twice a day (protein, 44%; fat, 21%; fiber, 4%; ash 9%) for a month. The same batch of commercial pellets were used in all GE experiments.

GE experiments

The GE experiments were conducted when water temperature was 12, 15, and 20°C which were achieved at different times of the year. For each GE experiment, group of 100 fish were transferred into 450 L tank having recirculating water system and the oxygen saturation of the water was ensured by means of continuous air bubbling. Here in experimental tank, the fish were also fed twice a day with commercial pellets for 10 days before the experiments began.

Prior to the GE experiments, the acclimated group of fish in experimental tank were deprived of food for 72 h to ensure the complete emptying of the stomachs and then were fed on commercial pellets to apparent satiation. Three fish were removed at the end of feeding to determine the stomach content at time 0 (Table I) and then at each 3 h interval (*e.g.*, 3, 6, 9, 12 and so on until the first empty stomach observed) stomach contents were sampled from three fish. Removed fish were killed with an overdose of benzocaine (150-200 mg/L). Finally the stomachs were removed after measuring fish total length and weight and stomach contents were carefully transferred onto Petri dish and dried in Ecocell Drying Oven (Medcenter, Germany) at 60°C until constant weight. The dried stomach content (S_t) were weighted to the nearest 0·0001 g.

GE modeling

The best fit model to the GE data of brook trout was determined using following models similar to He and Wurtsbaugh (1993), Pääkkönen and Marjomäki (1997) and Sweka *et al.* (2004). This is an appropriate way of GE modelling where the initial meal ingested by each fish is unknown.

Linear model $\frac{dS_t}{dt} = -\rho t$ integrated:

$$S_t = a - \rho t \tag{1}$$

Square root model $\frac{dS_t}{dt} = -\rho\sqrt{t}$ integrated:

$$\sqrt{S_t} = \sqrt{a} \quad 0.5\rho t \tag{2}$$

Exponential model $\frac{dS_t}{dt} = -\rho t$ integrated:

$$S_t = ae^{-\rho x} \Rightarrow$$

$$\ln(S_t) = \ln(a) - \rho t \tag{3}$$

where S_t is the stomach content at time *t*, *a* is the intercept representing some sort of the mean ingested meal size S_0 and ρ rate parameter.

Model selection

The best fit model was selected by comparing the values of the adjusted r^2 and the residual sum of squares (*RSS*), and the one consistently providing higher value of adjusted r^2 and the lowest value of *RSS* was determined as best fit model.

After the determination of best fit model to the GE data of brook trout, the effect of temperatures on GER was then analyzed using exponential model.

RESULTS

In each experiment, fish were fed to apparent satiation. The maximum satiation amount was recorded at 15°C (Table I). In total three GE experiments, 128 fish were used to analyze their stomach content at time *t*. Out of these 128 stomachs only 6 stomachs were found to be empty, thus nearly all experimental fish were feeding actively which strongly indicates that they were facing very low-stress under experimental conditions. Moreover, fish were carefully removed for stomach content analysis at time *t* to avoid any disturbance into experimental tank.

Table I.- Basic data (mean) from gastric evacuation experiments on brook trout *Salvelinus fontinalis* fed on commercial pellets.

Exp. no.	Temperature (°C)	Length (cm)	Body mass (g)	*Meal size (g)	Obs. (*n*)
1	12	19.58 (0.06)	80.01 (0.21)	1.42 (0.08)	45
2	15	19.45 (0.04)	82.94 (0.13)	2.05 (0.29)	44
3	20	19.01 (0.04)	72.20 (0.12)	0.81 (0.27)	33

*Stomach contents recovered at time 0; standard deviation in parentheses.

Table II.- Estimates of the intercept *a* and rate parameter *ρ* in the square-root model: $\sqrt{S_t} = \sqrt{a} - 0.5\rho t$, linear model: $S_t = a - \rho t$, and exponential model: $\ln(S_t) = \ln(a) - \rho t$ from gastric evacuation data of brook trout *Salvelinus fontinalis* at different temperatures, standard deviation in parentheses.

Exp	Square root model				Linear model				Exponential model			
#.	*a*	*ρ* (×10^{-2})	RSS	Adj. r^2	*a*	*ρ* (×10^{-2})	RSS	Adj. r^2	*a*	*ρ* (×10^{-2})	RSS	Adj. r^2
1	1.19	-2.6	0.067	0.923	1.32	-2.1	0.126	0.943	3.59	-4.8	1.814	0.855
	(0.03)	(0.2)			(0.04)	(0.1)			(0.16)	(0.5)		
2	1.25	-3.1	0.286	0.791	1.49	-2.6	1.096	0.733	4.54	-7.3	19.71	0.542
	(0.06)	(0.2)			(0.13)	(0.4)			(0.53)	(1.7)		
3	0.82	-3.3	0.141	0.712	0.65	-1.9	0.229	0.651	1.93	-2.8	0.654	0.604
	(0.07)	(0.3)			(0.09)	(0.4)			(0.14)	(0.7)		

RSS, residual sum of squares; Adj. r^2, adjusted r^2

GE pattern

Linear, square-root and exponential models were applied to the GE data to determine the best fit model. By comparing the value of adjusted r^2 and *RSS*, the square-root model consistently provided the best fit to the GE data of brook trout (Table II). According to adjusted r^2 and *RSS* values, the exponential model poorly described the evacuation of brook trout at all temperatures.

Temperature dependency of GER

The rate parameter (g h^{-1}) increased with increasing in temperature from a minimum of 0.026 (± 0.002 S.D) at 12°C to maximum of 0.033 (± 0.003) at 20°C (Fig. 2). The relationship between GER of brook trout and temperatures could be summarized by:

$$\frac{dS_t}{dt} = -0.0194e^{0.028\,T} (\mathrm{gh^{-1}}) \quad (4)$$

Using equation (4), the time requires for brook trout to evacuate certain portions of initial meal was estimated for different temperatures (Table III).

Table III.- Estimated time (h) required for different proportions of a meal to be evacuated from the stomach of brook trout *Salvelinus fontinalis.*

Temperature (°C)	Proportion of meal evacuated			
	5%	25%	50%	75%
12	2.3	12.1	26.4	45.1
15	2.1	11.1	24.3	41.5
20	1.8	9.6	21.1	36.0

DISCUSSION

The square-root model adequately described the GE of brook trout at all temperatures. This is in accordance with the result obtained by Khan *et al.* (2016) for individually maintained brook trout. In Khan *et al*. (2016) study, small and large sizes brook trout was fed a range of meal sizes (25%, 50% and 100% of satiation) composed of commercial pellets and revealed that GE of brook trout can be properly described independently of meal size by square-root model. In the present study, the apparent satiation amount of brook trout was different at different temperatures (Table I) and according to Khan *et al*. (2016) the GE of brook trout does not influence by meal size. Thus, in present study the GER is only influenced by temperature.

The square-root model has been observed to adequately describe the GE of different gadoids (*e.g.*, Jones, 1974; Temming and Herrmann, 2003), pikeperch *Stizostedion lucioperca* (Koed, 2001) and coho salmon *Oncorhynchus kisutch* (Andersen and Beyer, 2007). Likewise, Grove *et al*. (1985) fed turbot *Scophthalmus maximus* a range of meals composed of food pellets and revealed that square-root model properly described the GE of turbot.

Sweka *et al*. (2004) studied GE of brook trout fed a standard meal (3.7±0.09% of the fish total weight) composed of fly and beetle larvae at five different temperatures (*i.e*. 4.3, 9.1, 12.1, 15.6, and 17.0°C). Sweka *et al*. (2004) concluded that the GE of brook trout is best described by linear model except at 12.1 and 17.0°C where the square-root model gives a better fit to the data than linear model. They use mean square errors (*MSE*) to determine the best fit model to their data and the one consistently providing the lowest *MSE* values was determined to be the appropriate model. However, if the goodness of model fit in Sweka *et al*. (2004) is assessed using y-intercept values, it could be seen that rather than the linear model the square root model instead gives the best fit to the GE data of brook trout at four out of the five temperatures (except at 4.3°C where the linear model gives slightly better fit to the data compared to the square root model).

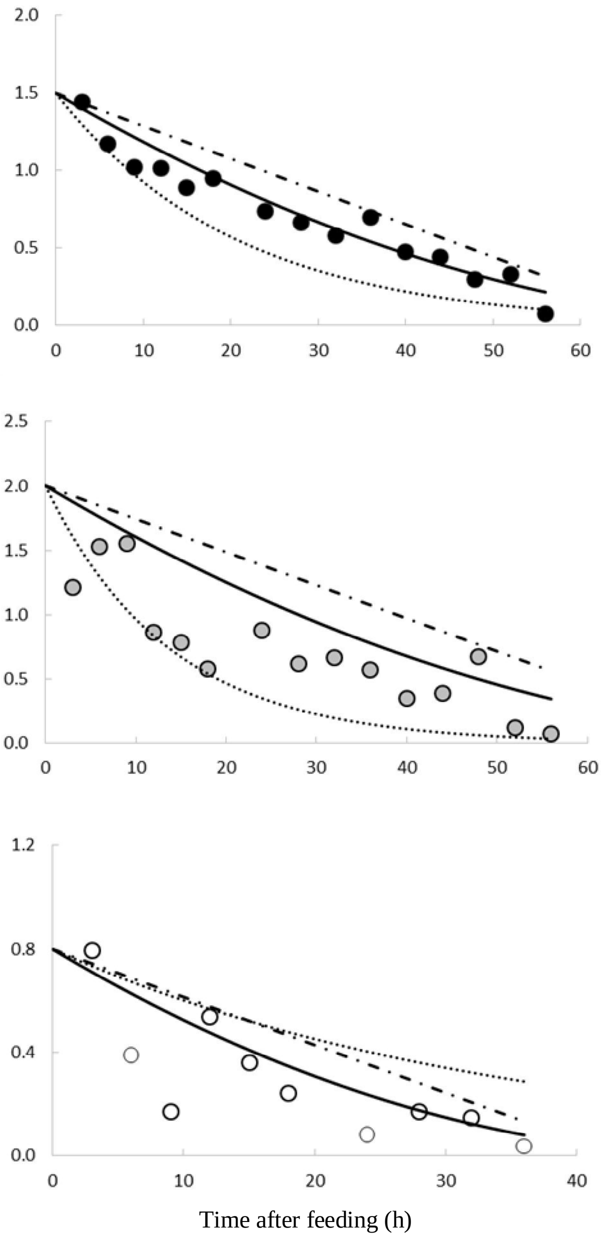

Fig 1. Gastric evacuation of brook trout *Salvelinus fontinalis* at three different temperatures: 12°C (●), 15°C (●), and 20°C (○) each with three curve lines: square root (——), linear (– · – · –) and exponential (·········).

The temperature coefficient in equation (4) [δ = 0.028] indicates that GER increases 1.32 times for each 10°C increase in temperature [$Q_{10}=e^{10}\delta$]. In Sweka *et al.* (2004) study, the Q_{10} values between 4.3 and 9.1°C (calculated from the rate parameter obtained through linear and square root function) ranged from 6—7 which is too high and unrealistic. It might be due to the short starvation period (5 days) provided to brook trout at 4.3°C. According to the estimated rate parameter, at this temperature brook trout would take at least 7 days to completely evacuate the last meal before the start of the GE experiment. As regards other studies on salmonid species, Amundsen and Klemetsen (1988) found the value of δ = 0.12 for a closely related salmonid Arctic charr *Salvelinus alpinus*, which corresponds to a Q_{10} of 3.3. Elliott (1972) found the value of δ = 0.112 for brown trout *Salmo trutta* fed invertebrate prey, which corresponds to a Q_{10} of 3.06. Similar values (δ = 0.113: Q_{10} of 3.10) were obtained by Jensen and Berg (1993) for brown trout fed pellets. However, He and Wurtsbaugh (1993) have estimated a low temperature effect (δ = 0.073: Q_{10} of 2.1) in brown trout than Elliott (1972) and Jensen and Berg (1993). Seyhan (1994) studied the GER in Whiting *Merlangius merlangus* under temperatures 10, 13 and 18°C and reported remarkably very low effect of temperature on GER in Whiting which correspond to a Q_{10} of 0.14. The value of δ in a variety of marine and freshwater species ranged from 0.081 to 0.145 (Bromley, 1994) which corresponds to a Q_{10} ranged from 2.2–4.3.

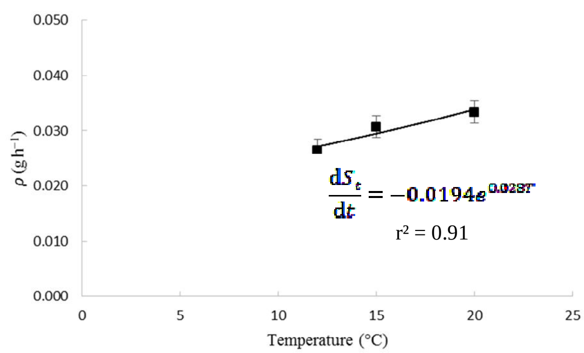

Fig 2. The relationship between ρ (rate parameter estimates by square root model) of brook trout *Salvelinus fontinalis* and temperature was determined by exponential equation. Error bars indicate S.D.

CONCLUSIONS

In conclusion, the present study finds that GE of brook trout under group-feeding could also be properly described by the square-root model similar to individually maintained brook trout (Khan *et al*., 2016). There might be an optimum temperature after which the GER of brook trout may tend to decrease (Sweka *et al.*, 2004). However such trend has not been observed in present study following group-feeding instaed of indvidually maintained fish. This study should add a confidence in the application of GE results obtained from individually maintained fish to group of fish, and vice versa. The result of such studies could be used by fish culturist to properly quantify the daily rations of cultivated brook trout at certain temperature to avoid the waste expensive feed.

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Statement of conflict of interest

Authors have declared no conflict of interest.

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