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Gastric evacuation in European seabass *Dicentrarchus labrax* (Linnaeus, 1758), forced-fed on commercial pellets

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ABSTRACT

The effects of meal size and body size on gastric evacuation rates were parameterised for European seabass *Dicentrarchus labrax* (Linnaeus, 1758). A total of three gastric evacuation experiments were performed on small (15.7±0.8 cm) and large (21.5±0.4) size fish forced-fed with meals of 0.5 and 1.5 g composed of commercial pellets. The stomach contents were then recovered by serial slaughtering the fish at predetermined post-prandial times. The surface-area dependent function adequately describes the gastric evacuation in European seabass independently of meal size. A power function of fish length *L* was then employed to evaluate the impact of body size, revealing its notable effect on gastric evacuation rates of European seabass.

Keywords: Aquaculture, Feeding regimes, General power function, Surface-area dependent

Introduction

Aquaculture is an important food production sector that has significantly contributed to global food security by meeting the growing demand for fish (Lem *et al.*, 2014; Kobayashi *et al.*, 2015). The growth of aquaculture can also ease the burden on capture fisheries by fulfilling the high demand for fish, reducing pressure on wild fish populations and decreasing fishing pressure (Ye and Beddington, 1996; Babu and Joshi, 2019). To meet the increasing global demand for fish sustainably, the aquaculture sector needs to adopt both existing and new technologies and use them innovatively (Ye and Beddington, 1996; Aas *et al.*, 2017; Alltech, 2017).

The automatic feeding system is a self-service technology that dispenses feed across a fish pond or cage at a predetermined time (Yeoh *et al.*, 2010; Molina and Espinoza, 2018). Several studies show that feeding fish at the return of appetite can ensure maximum feed intake and increase feed efficiency (Lee *et al.*, 2000; Riche *et al.*, 2004). The feed intake and the time required for appetite return are generally regulated by a complex combination of environmental, nutritional and physiological factors (Fletcher, 1984; Saravanan *et al.*, 2012; Andersen, 2022). Consequently, knowledge related to feed intake and time required for the return of appetite in fish under certain environmental conditions is a prerequisite for the optimised function of an automatic feeding system. The time needed for the return of appetite can be determined by the gastric evacuation rates of a fish (Riche *et al.*, 2004; Khan, 2022). Several factors such as temperature, dietary energy density, meal size and fish size have been reported to regulate the gastric evacuation rates (Seyhan, 1994; Khan and Seyhan, 2019; Andersen, 2022). Hence, gastric evacuation rates modelling needs to be parameterised under different environmental conditions for a possible determination of stomach fullness at a post-prandial time and stomach fullness at the return of appetite (Riche *et al.*, 2004; Bascinar *et al.*, 2017; Seyhan *et al.*, 2020).

The European seabass *Dicentrarchus labrax* (Linnaeus, 1758), is a primarily ocean-dwelling fish that was one of the first species to be commercially farmed in Europe (Vazquez and Munoz-Cueto, 2014). It was initially farmed in coastal lagoons and tidal reservoirs before mass production techniques were developed in the late 1960s (Vazquez and Munoz-Cueto, 2014). It is extensively farmed in the Mediterranean region (FEAP, 2015). Countries with the most significant farming operations for this species are Turkiye, Greece, Italy, Spain, Croatia and Egypt (Vazquez and Munoz-Cueto, 2014; Regnier and Bayramoglu, 2017). Turkiye's marine aquaculture industry is dominated by farming European seabass, which produced 155,151 t in 2021 (TUIK, 2022). This has enabled Turkiye to become the world's largest exporter of European seabass, with an annual export value of 355 million USD in 2020 and 467 million USD in 2021 (WWF, 2021; Sahin, 2022;

TUIK, 2022).The European seabass is popular for its plentiful and delightful taste and has earned the title "the superstar of the seas" (Hickman, 2008).

The primary objective of this study was to examine the pattern of gastric evacuation in force-fed European seabass. Additionally, the effects of two potential predictor variables, fish size and meal size, on the gastric evacuation rates of European seabass were also parameterised.

Materials and methods

Acquisition of fish

A total of 100 European seabass having different body sizes were acquired from the commercial fish farm, DOKABAS (Dogu Karadeniz Kultur Balıkcılıgı A.S) located in the Yomra, Trabzon, Turkiye. They were transferred to Surmene Faculty of Marine Sciences in Trabzon and stocked into two holding tanks to acclimate them to laboratory conditions under a 12L:12D photoperiod for the gastric evacuation experiments (Onder *et al.*, 2016; Khan, 2022). They were fed on commercial pellets obtained from Skretting (https://www.skretting.com/en-tr); having 44% protein, 18% lipid and 16% carbohydrate, for a month before transfer to experimental units (small tanks) with a capacity of 0.12 m^3 (120 l). Each experimental unit had a single fish for gastric evacuation experiments. Both holding tanks and experimental units were connected to a ventilated system with an equal seawater flow. The experimental units were siphoned daily to collect any remaining pellets (that were not consumed) and faeces. Fish behaving normally and appearing healthy were used in the gastric evacuation experiments.

Gastric evacuation experiments

Experimental fish were starved for a week to ensure that no food was left in their stomach before the follow-up experiment. Following Aas *et al.* (2017), we also intended to achieve equal feed intake in all fish and hence, they were fed a known amount of meal using force-feeding (Table 1). The fish were anesthetised using benzocaine before force-feeding (Gilderhus, 1990). Each fish was then forced-fed the experimental meal (pellets) following the procedure described by Nakatani (1962).

Fish were then sampled (after each ~3 h intervals), euthenised with an overdose of benzocaine and dissected to recover the stomach contents (S_t) into a petridish. Before dissection, each fish was measured to the nearest 0.1 cm total length and weighed to the nearest 0.01 g. The stomach contents were dried in an oven (Ecocell Drying Oven, MMM Medcenter, Germany) at 60°C until constant weight (Khan *et al.*, 2016).

Analysis of gastric evacuation data

The general power function was used to determine the pattern of feed evacuation from the stomach of European seabass. It was applied to combine data on estimated stomach contents S_t (g) at post-prandial time t (h):

$$\frac{dS_t}{dt} = -\rho S_t^{\alpha}, \quad \text{(1a)}$$

where ρ is the rate parameter constant ($g^{1-\alpha} h^{-1}$), which was expanded to account for the impact of fish total length L as:

$$\frac{dS_t}{dt} = -\rho_L L^{\lambda} S_t^{\alpha}, \quad \text{(1b)}$$

where, λ is the length exponent and α a power parameter that describes the course of gastric evacuation that would be exponential if α = 1, so-called surface-area dependent function if α = ⅔, square root function if α = ½ and linear if α = 0.

Equation (1b) was integrated over time t from the ingestion of the meal (t=0) to the total emptying of the meal:

$$S_t = S_0 (1-S_0^{(a-1)} \rho(1-a)t)^{1/(1-a)} + \varepsilon, \quad \text{(2)}$$

where, ε is an error term; similarly, equation (1b) was integrated.

The estimated value for the shape parameter α from the gastric evacuation data of European seabass was close to 2/3; hence, the so-called surface-area dependent function was used to describe the gastric evacuation of European seabass independently of meal size:

$$\frac{dS_t}{dt} = -\rho S_t^{2/3}, \quad \text{(3a)}$$

ρ was expanded as equation (1b) to account for the effect of body size:

$$\frac{dS_t}{dt} = -\rho_L L^{\lambda} S_t^{2/3}, \quad \text{(3b)}$$

This equation (3b) was also integrated over time t from ingestion (t = 0) to complete evacuation of meal:

Table 1. Basic data (mean±95% CI) from gastric evacuation experiments on *D. labrax* force-fed on commercial pellets

Experiment	Temp. (°C)	Length (cm)	Body mass (g)	Meal size (g)	No. of observations (n)
1	11	21.94±0.61	111.43±6.29	1.5	12
2	11	21.17±0.61	98.01±7.92	0.5	14
3	11	15.70±0.73	42.00±4.94	1.5	12

$$S_t = \left(S_0^{\frac{1}{3}} - \frac{1}{3}\rho_{LT} L^{\lambda} t\right)^3 + \varepsilon \quad (4)$$

The parameters of equations (2) and (4) were estimated by non-linear regression and the iterative Marquardt method (NLIN procedure) (Andersen, 1998) using SAS® OnDemand for Academics.

Results

The estimated value of α in the general power function was 0.67, with a 95% confidence interval of 0.31, which suggested that the surface-area dependent function adequately described the process of gastric evacuation in European seabass (Table 2). Furthermore, the length exponent λ estimated by the general power function was 0.89, with a 95% confidence interval of 0.62, suggesting a substantial impact of body size on the gastric evacuation rates of European seabass.

Based on the findings of the general power function, the surface-area dependent function was then applied to combined data on all European seabass and meal sizes to determine the effects of body and meal sizes. The length exponent λ estimated by the surface-area dependent function was 0.87, with a 95% confidence interval of 0.34 did not differ significantly from the value provided by the general power function (Student's t-test t_{74}= 0.0646; p>0.05).

The length exponent λ estimated from the combined data was fixed at 0.87 in equation (2) to determine the rates of gastric evacuation ρ_{LT} for individual gastric evacuation experiments. The estimated rate parameters from combined data, as well as individual gastric evacuation experiments, ranged between 0.00124 to 0.00142 and did not differ significantly (ANOVA; $F_{4,109}$ = 0.054; p = 0.764), which evinced no effect of meal size on the rate parameter constants of European seabass (Table 3).

Therefore, the gastric evacuation of European seabass fed commercial pellets described independently of meal size and could be summarised by:

$$\frac{dS_t}{dt} = -0.00129L^{0.87} S_t^{2/3} \text{ (g h}^{-1}\text{)} , \quad (5)$$

where *L* is the total fish length (cm), *T* is the temperature (°C) and *t* is time (h). This summarised model provided a curve line for each gastric evacuation experiment (Fig. 1).

Discussion

The shape parameter α of the general power function estimated from combined gastric evacuation data on all European seabass and meal sizes was 0.67, which suggests that the so-called surface-area dependent function is an appropriate gastric evacuation function for European seabass. This function has also effectively described the course of gastric evacuation in tilapia *Oreochromis niloticus* and sprat *Sprattus sprattus* (Riche *et al.,* 2004; Bernreuther *et al.,* 2009). These findings, however, are inconsistent with the results of Santull *et al.* (1993), Adamidou *et al.* (2009) and Nikolopoulou *et al.* (2011). The former used a linear function, whereas the latter studies used an exponential function to describe the gastric evacuation rate in European seabass. Contrarily, several studies have shown that the square root function is the most appropriate model for describing the pattern of food evacuation from the stomach in both farmed and wild fish, independently of meal size. This has been observed in several fish species including pikeperch *Stizostedion lucioperca* (Koed, 2001), brook trout *Salvelinus fontinalis* (Khan *et al.,* 2016; Seyhan *et al.,* 2020), brown trout *Salmo trutta* (Khan and Seyhan, 2021) and rainbow trout *Oncorhynchus mykiss* (Khan, 2022). Furthermore, Andersen and Beyer (2005) have provided a mechanistic approach to back up the square root function through a geometric abstraction of the stomach contents together with

Table 2. Summary statistics for parameter estimation of the general power function $\frac{dS_t}{dt} = -\rho_{LT} L^{\lambda} S_t^{\alpha*}$ to combine data on the gastric evacuation of meals force-fed to *D. labrax* [estimate ± 95% CI]

Experiment No.	α	λ	ρ_{LT}(×10^{-3})	Adjusted r^2	Observations (*n*)
1-3 combined	0.67±0.31	0.89±0.62	1.15±0.21	0.880	38
1-3 combined	0.67±0.30	0.89 (fixed)	1.15±0.13	0.880	38

**L*: Total fish length (cm); S_t : Stomach content mass (g) at post-prandial time *t* (h); α, δ, λ and ρ_{LT} : Parameters to be estimated

Table 3. Summary statistics for parameter estimation of the surface-dependent function $\frac{dS_t}{dt} = -\rho_{LT} L^{\lambda} S_t^{(2\text{-}3)}$ to combine data on the gastric evacuation of meals force-fed to *D. labrax* [Estimate±95% CI]

ExperimentNo.	λ	ρ_{LT}(×10^{-3})	Adjusted r^2	Observations (*n*)
1-3 combined	0.87±0.34	1.29±1.27	0.944	38
1-3 combined	0.87 (fixed)	1.28±00.10	0.944	38
1	0.87 (fixed)	1.24±0.14	0.909	12
2	0.87 (fixed)	1.42±0.13	0.926	14
3	0.87 (fixed)	1.29±0.14	0.925	12

**L*: Total fish length (cm); S_t: Stomach content mass (g) at post-prandial time *t* (h); α, δ, λ and ρ_{LT} : Parameters to be estimated

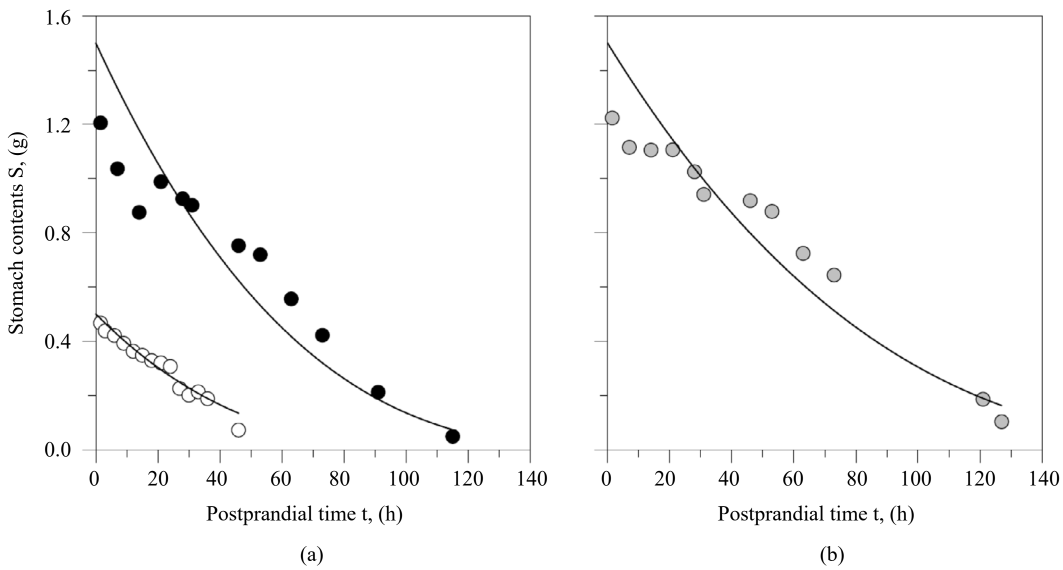

Fig. 1. Gastric evacuation of *D. labrax*, force-fed on commercial pellets, (a) Large fish and (b) Small fish. The curve lines were provided by $S_t = S_0^{1/3} - \frac{1}{3}\ 0.00129L^{0.87}$ (g h^{-1}), where S_t is the current stomach contents mass (g) and *t* is time (h)

some underlying assumptions to provide a mechanistic so-called cylinder model that can predict evacuation of the contents irrespectively of the composition of the contents and the prehistory of the food intake. In their abstraction, the meal is digested by peeling off layers, decreasing the thickness of the cylinder without affecting its ends, where the layer that is peeled off the cylinder depends on the resistance of the prey to the digestive processes and the prey energy density. The rate of peeling off the mass of the total stomach contents is always the same length as the stomach. If the stomach content is significantly heterogeneous in composition (resistance to digestion or energy density), the mechanistic cylinder model may need to be expanded, according to Andersen *et al.* (2016). Thus, it might be expected that the square root function would also perform better if European seabass is fed voluntarily instead of force-feeding.

The estimated length exponent λ of European seabass from the combined data was 0.87, with a 95% confidence interval of 0.34, which is consistent with the findings of Dossantos and Jobling (1995) and Temming and Herrmann (2003) for Atlantic cod, Koed (2001) for pikeperch. Furthermore, a similar length exponent λ has been estimated for rainbow trout (Khan, 2022). Though, a substantially higher impact of body size on gastric evacuation rates have been recorded for several fish species such as whiting *Merlangius merlangus*; saithe *Pollachius virens*; haddock *Melanogrammus aeglefinus*; Atlantic cod *Gadus morhua* and brook trout (Jones, 1974; Andersen, 1999, 2001, 2012), that ranged between 1.30 to 1.44.

This study found a substantial effect of body size on the gastric evacuation rates of European seabass observed using the surface-area dependent function. The gastric evacuation of European seabass can be determined independently of meal size by $dS_t / dt = -0.00129L^{0.87}\ S_t^{2/3}$ (g h^{-1}). The gastric evacuation rates model developed in this study can be applied to determine the stomach fullness of force-fed European seabass at post-prandial times. It should be noted that several studies have indicated that force-feeding may impair the process of gastric evacuation in fish (Windell, 1965; Swenson and Smith, 1973; Behrens *et al.*, 2011). Thus, the model is specifically designed for European seabass that is force-fed on commercial pellets. Force-feeding may also influence the suitability of the square root function to accurately describe the course of gastric evacuation in European seabass. Therefore, future investigations should explore how different feeding strategies, such as volunteer feeding *vs* force-feeding of fish, impact the fitness of the gastric evacuation function for *e.g.* the square root function.

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