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Research Article

Effects of Temperature on the Gastric Evacuation Rate and Maintenance Ration of Adult Pointhead Flounder *Cleisthenes pinetorum*

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We investigated the gastric evacuation rate (GER) and maintenance ration (MR) for the adult pointhead flounder *Cleisthenes pinetorum* (77–421 g) at 4°C, 9°C, and 14°C which reflect the bottom, middle, and surface temperatures of their habitat in early summer. GERs were obtained from gravimetric experiments with 34 flounders fed juvenile walleye pollock *Gadus chalcogrammus* as prey. A 169-day feeding experiment for 67 pointhead flounders fed krill *Thysanoessa inermis* was undertaken to measure MR. The effects of a 10°C temperature increase (Q_{10}) on the GER and the MR were 6.55 and 2.04, respectively, indicating that the effect of temperature was greater on GER than on MR. As a result, the differences between the GER and MR, indicating the maximum amount of food ingestible for growth, were 2.8 and 30.7 $\text{cal}\cdot\text{g}^{-1}\ \text{day}^{-1}$ at 4 and 14°C, respectively. The water temperature on the sea floor generally remained at <4°C from winter through summer, but exceeded 10°C in the surface layer of Funka Bay, where pointhead flounders were sampled. Therefore, their growth rate should be considerably limited if they remain in the bottom layer. The unique ecology of this species among the flatfishes of floating from sea floor and feeding at pelagic zones may represent a strategy to compensate for the physiological limitation of growth at low temperatures.

1. Introduction

The pointhead flounder *Cleisthenes pinetorum* is distributed widely in Eastern Asia, extending from the waters off Hokkaido, Japan, to the East China Sea [1, 2]. The abundance and catch size of this species off southern Hokkaido increased rapidly in the 2010s, increasing its commercial importance [3]. Larval and juvenile pointhead flounders (4–11 mm total length) feed mainly on copepods in the Sea of Japan [4, 5]. Although knowledge on the feeding ecology of adult pointhead flounder is limited (e.g., [6]), the large gape size of this species suggests its potential role as a piscivore in coastal ecosystems. Therefore, identifying the physiological parameters of pointhead flounder will help to quantify the impact of this species as a predator. For example, recruitment of the Japanese Pacific stock of walleye pollock *Gadus chalcogrammus*, which uses the southern Hokkaido area as a nursery, has been declining since 2012 [7], and there is great interest in the factors affecting its mortality during the early life stages [8]. Pointhead flounders are active swimmers [9] that feed on pelagic prey, including unsettled juvenile walleye pollock. Such predation affects the recruitment of Pacific walleye pollock stock [10]. Thus, estimating the predation pressure exerted by pointhead flounder on walleye pollock will be indispensable for understanding the survival of walleye pollock. However, there is currently no information on the physiology of pointhead flounder.

The gastric evacuation rate (GER) is an indicator of digestion representing the volume of stomach contents moving from the stomach to the intestine within a given time [11]. When fish are saturated, their stomachs are filled and they are unable to continue feeding unless they evacuate their gastric contents. Therefore, the food consumption rate to satiation should be regulated by the GER. Thus, the GER represents the upper limit of the food consumption rate when there is sufficient food in the environment. The food consumption rate is often determined from the weight of stomach contents obtained during field surveys and experimentally obtained GERs [12–14]. Thus, GER measurements are important for determining the food consumption rates of fish. Various studies have shown that the response of GER to varying temperature differs greatly even among confamiliar fish species. For example, the GER of Pacific spiny dogfish *Squalus suckleyi* (0.024 at 10°C, body weight: 70–107 cm, prey: herring *Clupea harengus* or salmon *Oncorhynchus nerka* (17–27 cm), gravimetric experiment) [15] is more than two-fold higher than that of the confamiliar lesser spotted dogfish *Scyliorhinus canicula* (0.009 at 15°C, mean wet weight ± standard deviation (SD) = 698 ± 23 g, prey: moist diet based on squid *Loligo vulgaris*, X-radiography technique) [16] even at a lower temperature. Thus, the GER is expected to vary between species and should be measured for each species [17]. In addition to temperature, there are various factors affected to GER (meal type [18], size and energy density [19], type of stomach structure [20] and evacuation type), GER is complexly influenced by ambient environment.

The maintenance ration (MR) is defined as the amount of food per unit time required to maintain body weight [21], such that fish must maintain a food consumption rate above the MR to grow. Thus, the MR is the lower limit of the food consumption rate; it is an important indicator for estimating the food consumption rate from energetic models and varies among fish species. For example, the MR estimated from feeding experiment of Pacific cod *Gadus macrocephalus* is 12 $\mathrm{cal \cdot g^{-1}}$ at 6°C (body weight: 200–5000 g, prey: herring) [22], whereas that of the yellowfin sole *Limanda aspera* is 3.71 $\mathrm{cal \cdot g^{-1}}$ (body weight: 88–469 g, prey: herring) [23] at the same temperature, for a more than 3-fold difference between these two cold-water species. Because MR reflects resting metabolic rate, MR may change with resting metabolic rate, affected by activities such as temperature [24], movement activity [25], digestion [26], and reproduction [27].

Physiological indicators such as the GER and MR of fish vary depending on temperature. The response of the GER and MR to a change in temperature (e.g., the effect of a 10°C rise in temperature on the GER (Q_{10})) has been investigated in various fish species, revealing wide variation in Q_{10} values among species. For example, the Nile tilapia *Oreochromis niloticus* has a GER Q_{10} of 1.7 [28], whereas pikeperch *Stizostedion lucioperca* has a GER Q_{10} of 4.5 [29]. The sensitivity of the MR to temperature also differs among fish species. For example, the Atlantic halibut *Hippoglossus hippoglossus* and walleye pollock have Q_{10} values of 3.6 and 1.763, respectively [30, 31]. If the MR of a given species is smaller than the GER at a given temperature, then the GER becomes a bottleneck for somatic growth because it is insufficient for growth or body weight maintenance. Thus, water temperature fluctuations have the potential to limit the growth rate through changes in the GER and MR. The objective of the present study was to clarify the relationships among the GER, MR, and temperature in pointhead flounder.

2. Materials and Methods

2.1. Fish Collection. The pointhead flounders used in this study were collected by hook and line fishing in Funka Bay (approximate position 42.41°N, 140.82°E) in June 2019 for gastric evacuation experiments and in 2020 for growth experiments. The adult fish (45 and 75 individuals in 2019 and 2020) were immediately placed in a 200 L tank on board and then transferred to the laboratory. Juvenile walleye pollocks were caught as prey for pointhead flounder, using a pound net located at Furube, near the mouth of Funka Bay, in June 2019.

2.2. Rearing Conditions. The pointhead flounder and walleye pollock were reared in black 5-ton and 200 L water tanks, respectively, at the Hakodate Research Centre for Fisheries and Oceans (Hakodate, Japan). The tanks were supplied with seawater from Hakodate Bay at a flow rate of 0.5 $\mathrm{L \cdot min^{-1}}$. Water temperature was maintained at 13 ± 1°C, which was close to the surface water temperature of Funka Bay in June, using a water cooler (ZRW400, Zensui Co. Ltd., Osaka, Japan). The specimens were housed under a 12 h light/12 h dark cycle, illuminated with a fluorescent light (148 lx at the water surface) above the tank. The fish were fed ca. 1.5 $\mathrm{g \cdot day^{-1}}$ $\mathrm{ind^{-1}}$ of krill (either *Euphausia pacifica* or *Thysanoessa inermis*).

2.3. Evacuation Experiments

2.3.1. Experimental Conditions. The evacuation experiments were conducted under three thermal conditions (4°C, 9°C, and 14°C), which reflect the surface, middle, and bottom temperatures of Funka Bay in early summer [32]. The experiments were conducted at 14°C initially, then at 9°C, and finally at 4°C. The water temperatures were adjusted from the rearing water temperature to the target at a rate of 0.5$\mathrm{^{\circ}C \cdot day^{-1}}$. After reaching the target temperature, the fish were acclimated for 1 week before the experiments [33]. Sixteen individuals (mean wet weight ± SD = 179 ± 35 g, range of wet weight: 117–241 g), 10 individuals (200 ± 48 g, 117–281 g), and 7 individuals (201 ± 39 g, 163–260 g) were used in the experiments at 4°C, 9°C, and 14°C, respectively (Table 1). Fish exhibiting abnormalities such as missing eyes or damaged body surfaces were excluded from the experiments. To measure gastric evacuation time, one flounder in the 200 L tank was fed one juvenile walleye pollock (mean wet weight ± SD = 5.63 ± 0.79 g), whose length and body weight were measured before feeding (Table 1). Juvenile walleye pollocks were introduced into the tank and were fed by spontaneous predation by the flounder. The flounder was anaesthetised and sacrificed 3–120 h after feeding depending on the thermal condition (Figure 1). The stomach was removed and fixed in 10% formalin solution, and the wet weight of the stomach contents was measured after 2 days of fixation. The juvenile walleye pollock specimens were dehydrated in formalin [34]. To compensate for the loss of mass due to dehydration, we measured the wet weights of the juvenile walleye pollock ($n = 216$) before and after fixation

Table 1: Basic data (mean ± standard deviation (SD)) from gastric evacuation and feeding experiments on pointhead flounder (*Cleisthenes pinetorum*) fed walleye pollock (*Gadus chalcogrammus*) as prey.

	No. of fish	Body weight (g)	Total length (mm)	Prey weight (g)	% body weight of prey
Gastric evacuation experiment					
4°C	16	179 ± 35	267 ± 14	5.86 ± 1.05	3.35 ± 0.65
9°C	11	200 ± 48	278 ± 21	5.34 ± 0.25	2.84 ± 0.77
14°C	7	201 ± 30	277 ± 13	5.59 ± 0.54	2.84 ± 0.45
All data	34	190 ± 39	272 ± 17	5.63 ± 0.79	3.08 ± 0.70
Feeding experiment					
4°C	21	206 ± 63	289 ± 36	—	—
9°C	21	201 ± 62	288 ± 36	—	—
14°C	25	225 ± 76	286 ± 30	—	—
All data	67	211 ± 68	288 ± 33	—	—

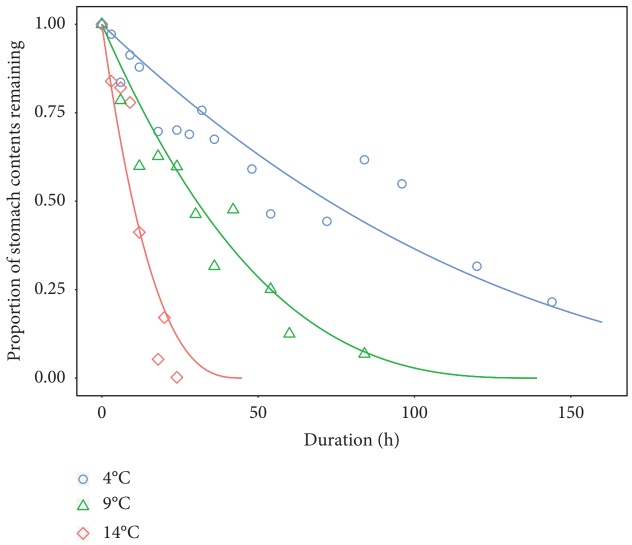

Figure 1: Gastric evacuation of the pointhead flounder *Cleisthenes pinetorum* fed juvenile walleye pollock *Gadus chalcogrammus* under different ambient temperatures: 4°C (○), 9°C (△), and 14°C (◇). The curves for each temperature were determined using a general model based on a body weight of 189.1 g: $S_t = [1 - 0.00000716M^{0.581}e^{0.189T}t]^{2.78}$, where S_t is the stomach content proportion, M is the body weight (g), and t is the time elapsed after feeding (h).

and obtained the following relationship: $W_{\text{wet}} = 1.0233W_{\text{fix}} + 0.0095$, where W_{wet} and W_{fix} represent the wet weight (g) before and 2 days after formalin fixation, respectively (Appendix 1). The fixed stomach content weight was corrected using this equation.

2.3.2. Gastric Evacuation Model. Gastric evacuation was examined using a general model [35]. Assuming that the GER is affected only by the volume of stomach contents, the relationship between the proportion of stomach contents, the original total contents (S), and time (t) is

$$\frac{dS_t}{dt} = -\text{GER} \cdot S_t^B, \tag{1}$$

where S_t is the stomach content mass (g) at time t, GER is the gastric evacuation rate (h^{-1}), and B is the shape parameter determining the model characteristics, as follows:

(a) $B < 0$: smaller S values indicate faster evacuation

(b) $B = 0$: a linear model in which the GER remains stable

(c) $B = 0.5$: a square root model based on a cylinder function, describing the evacuation of a cylindrical volume of food [36]

(d) $B = 0.67$: a surface area-dependent model in which the GER is dependent on the surface area of the gastric contents because stomach contents are digested from the surface inward [37]

(e) $B = 1$: an exponential model in which the GER and stomach content volume are proportional

(f) $1 < B$: a model similar to (e), except with a stronger effect of stomach content volume

Integrating equation (1) yields

$$S_t = \left[S_0^{1-B} - \text{GER}(1-B)t\right]^{(1-B)^{-1}} \text{(if } B \neq 1\text{)}, \tag{2}$$

$$S_t = S_0 e^{-\text{GERt}} \text{(if } B = 1\text{)}. \tag{3}$$

When the effects of temperature and body weight are exponential, GER in equations (2) and (3) was expressed as

$$\text{GER} = \rho M^{\gamma} e^{\delta T}, \tag{4}$$

where M is body weight (g), T is temperature (°C), ρ is a prey-specific parameter, γ is a body size parameter, and δ is the temperature coefficient.

Applying equation (4) to equations (2) and (3) yields

$$S_t = \left[S_0^{1-B} - \rho M^{\gamma} e^{\delta T}(1-B)t\right]^{(1-B)^{-1}}, \tag{5}$$

$$S_t = S_0 e^{-\rho M^{\gamma} e^{\delta T} t}. \tag{6}$$

Parameters B, ρ, γ, and ς were estimated by applying the proportion of stomach contents and the time elapsed after feeding to equation (5) using the results of the feeding experiments with different predator body weights and ambient temperatures. The range of pointhead flounder body size was insufficient to estimate λ (17–281 g) [38]. Therefore, we substituted a value of 0.39 for λ based on the common dab *Limanda limanda*, another member of order Heterosomata [39].

2.3.3. Review of Q_{10} Values in Marine Fish.

We evaluated the magnitude of the temperature effects on the GER among adult temperate marine fish using the Q_{10} value based on an exponential function. Q_{10} was defined using the GER values (GER_1 and GER_2) at different temperatures (T_1 and T_2), or δ in equations (5) and (6) as follows:

$$Q_{10} = \left(\frac{GER_1}{GER_2}\right)^{(10/(T_2-T_1))} \approx e^{10\delta}. \quad (7)$$

Q_{10} of each species was calculated using either the GER values determined at different temperatures or the δ values from the studies included in this review. When multiple references were available for a single species, the Q_{10} values were arithmetically averaged for the interspecific comparison. To determine the effect of species relatedness on Q_{10} of the GER, we used the Mann–Whitney *U*-test to examine differences in Q_{10} values among the seven orders.

2.4. Growth Experiments

2.4.1. Experimental Conditions.

The Japanese horse mackerel *Trachurus japonicus*, which feeds in schools under natural conditions, ingests less food when fed *ad libitum* if the experimental population is limited [40]. Because pointhead flounder may also feed in schools, the ration could be underestimated if they are reared in limited numbers. Therefore, we conducted the experiment with several individuals into the same tank. After each individual was anaesthetised with 2-phenoxyethanol ($200\,\mu\text{L}\cdot\text{L}^{-1}$) [41], a coloured 7 × 7 mm plastic tag was attached to the gill cover using nylon thread as a fish ID. The water temperature was increased or decreased by $0.5^\circ\text{C day}^{-1}$ for acclimation, and the fish were acclimated to the temperature for 1 week after reaching the target temperature [42, 43]. Due to limited availability, it was impossible to use walleye pollock as feed in the growth experiment; therefore, krill was used as a substitute. Krill were placed singly into a 5-t tank containing 21–25 pointhead flounder once per day, and the flounder ID and number of krill ingested were recorded (Table 1). The total weight of the krill was measured before each feeding and divided by the number of individuals to estimate the weight of individual krill. At 4°C, 9°C, and 14°C, 21 (84–343 g in BW, 225–378 mm in TL), 21 (77–326 g, 223–373 mm), and 25 (122–421 g, 240–368 mm) pointhead flounders were used for the 58-, 49-, and 62-day experiments, respectively (Table 1). The total length and wet weight of all fish were measured at the beginning and end of the experiments.

2.4.2. Data Analysis.

Daily growth rate (DGR) and ration were estimated as follows:

$$\text{DGR} = (W_2 - W_1)(t_2 - t_1)^{-1}, \quad (8)$$

$$\text{Ration} = C_t (t_2 - t_1)^{-1}, \quad (9)$$

where W_1 is the initial weight (g), W_2 is the terminal weight (g), t_1 is the initial day, t_2 is the terminal day, and C_t is the total amount of food consumed (g).

The effect of ration on DGR was estimated using a linear model. The slope of the model was the net conversion efficiency (NCE)) [44], the x-intercept was MR, and the y-intercept was the catabolic rate (CR), respectively [45]. NCE was calculated by dividing the increase in fish body weight by the amount of food available for actual growth, which was equal to the amount of food ingested minus the amount used for basal metabolism plus normal activity [46]. The effects of temperature on the slope and y-intercept of the linear model were examined by hierarchical multiple regression analysis.

The GER and MR were compared at each temperature. To compare the GER and MR on a calorie basis, the caloric value of krill was calculated to be $976\,\text{cal}\cdot\text{g}^{-1}$ (lipid: 5.1%, protein: 12.9%, ash: 3.5%, and water: 78.2%) [47] and that of juvenile pollock was $956\,\text{cal}\cdot\text{g}^{-1}$ (lipid: 0.74%, protein: 10.1%, ash: 2.7%, and water: 86.5%) [48]. Gross conversion efficiency (GCE) was estimated using the equation below [49, 50]; GCE was estimated by dividing the weight gain of each fish by the amount of food consumed.

$$\left[\frac{\text{Body weight increase (g)}}{\text{Food consumed (g)}}\right] \times 100. \quad (10)$$

2.5. Ethical Statement.

All procedures in this study adhered to the National University Corporation Hokkaido University Regulations on Animal Experimentation.

3. Results

3.1. Evacuation Experiments

3.1.1. Experimental Conditions.

The body weights of the pointhead flounder used in the experiment ranged from 116 to 280 g (Table 1). In all experiments, the pointhead flounder swallowed the juvenile walleye pollock spontaneously. The pointhead flounder fed immediately when the prey was dropped into the tank. After feeding, most fish remained inactive at the bottom of the tank. A greater proportion of stomach contents was evacuated at higher temperatures. About 21.5% of the stomach contents remained 144 h after feeding at 4°C, whereas only 0.2% remained 24 h after feeding at 14°C (Figure 1).

3.1.2. Gastric Evacuation Model.

The parameters of the gastric evacuation model based on equation (5) are summarised in Table 2. The gastric evacuation model was estimated as follows:

Table 2: Summary of parameter estimates for the general pointhead flounder model.

	General model: $S_t = [1 - \rho M^{\gamma} e^{\delta T}(1-B)t]^{(1-B)^{-1}}$						
	B	GER	ρ	δ	λ	RSS	Adj. r^2
All data	0.646	—	0.000199	0.189	【0.390】	0.274	0.87
4°C	【0.646】	0.0085	—	—	—	0.096	0.76
9°C	【0.646】	0.0203	—	—	—	0.097	0.79
14°C	【0.646】	0.0624	—	—	—	0.071	0.88

B, shape parameter; GER, gastric evacuation rate ($h-1$); ρ, prey-specific parameter; δ, temperature coefficient; λ, body size parameter. The residual sum of squares and adjusted r^2 were also estimated. Values in parentheses were fixed in the estimates.

$$S_t = \left[1 - 0.000199 M^{0.390} e^{0.189T}(1-0.646)t\right]^{(1-0.646)^{-1}}. \tag{11}$$

The value of the shape parameter B was estimated to be 0.646, which approximated the value representing the surface area-dependent model (0.67). The GER increased exponentially from 0.0085 to 0.0203, and to 0.0624 h^{-1} as the temperature was increased from 4 to 9°C, and then to 14°C, respectively (Figure 2). Using these GER values, the duration required for 95% gastric evacuation was estimated to be 208, 81, and 32 h at 4°C, 9°C, and 14°C, respectively (Appendix 2). The relationship between the GER and temperature in pointhead flounder was expressed as

$$\mathrm{GER} = 0.00417 e^{0.189T}. \tag{12}$$

Using $\delta = 0.189$, Q_{10} of pointhead flounder was estimated to be 6.55.

3.1.3. Interspecific Comparison of Q_{10} for the GER.

Table 3 summarises the data from 12 temperate fish species belonging to seven orders and 22 studies. Among these, the Q_{10} values ranged from 1.5 to 12.2. Demersal flatfish exhibited a wide range of Q_{10} values (1.7–6.6), whereas *Gadus* remained within a relatively narrow range (2.0–3.7). Q_{10} of pointhead flounder was the highest among the demersal fishes but was lower than those of Atlantic herring and Atlantic mackerel (Table 3). The effect of species relatedness on Q_{10} of the GER was examined; no significant difference in Q_{10} of the GER was detected among the seven orders (p = 0.09, Mann–Whitney U-test).

3.2. Feeding Experiments

3.2.1. Experimental Conditions.

Most individuals remained at the bottom of the tank and ascended to the surface for feeding. Because multiple fish fed spontaneously in one tank, feeding rates throughout the experimental period differed by individual. At 4°C, 9°C, and 14°C, the feeding rates ranged as 0–1.86, 0.02–2.91, and 0–3.02 $\mathrm{g \cdot day^{-1}}$ and the increases in body weight ranged as −0.12 to 0.29, −0.15 to 0.61, and −0.32 to 0.44 $\mathrm{g \cdot day^{-1}}$, respectively. No significant increase in body length occurred during the experiment at any temperature (Student's t-test, $p > 0.05$).

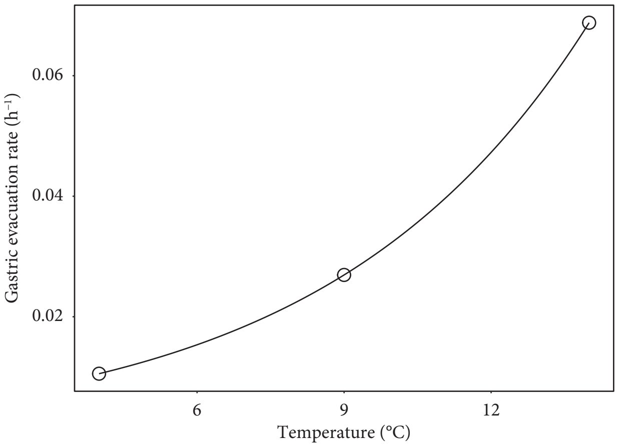

Figure 2: Relationship between the gastric evacuation rate (GER) and temperature (T) estimated using a general model. When body weight was 189.1 g, the relationship was estimated to be GER = $0.00417e^{0.189T}$.

3.2.2. Physiological Indicators Affecting Growth.

The relationship between DGR and ration was estimated using the linear model (Figure 3). Hierarchical multiple regression analysis was conducted with DGR as the objective variable and ration and temperature as explanatory variables. The slope of the relationship between DGR and ration did not differ significantly by temperature ($p > 0.05$); however, the intercepts varied significantly ($p < 0.05$) (Figure 3). The MR increased with increasing temperature, and the Q_{10} value was 2.04 (MR (%BW $\mathrm{day^{-1}}$) = 0.0469 temperature (°C) + 0.2259, $R^2 = 0.99$) (Table 4). NCE exhibited no significant difference by temperature ($p > 0.05$, Table 4). Hierarchical multiple regression analysis indicated that the slope of the linear model did not differ among temperatures, but a significant difference was observed in the y-intercept among temperatures ($p < 0.05$). The y-intercept increased from 0.072 to 0.172%BW $\mathrm{day^{-1}}$ with increasing temperature (4°C to 14°C; CR (%BW $\mathrm{day^{-1}}$) = 0.01 temperature (°C) + 0.0337, $R^2 = 0.99$) (Table 4). The GCE decreased with increasing temperature (GCE = −1.245 temperature (°C) + 16.605, $R^2 = 0.78$) (Table 4). The difference between GER and MR decreased with decreasing temperature; although it accounted for 30.7 $\mathrm{cal \cdot g^{-1} \cdot day^{-1}}$ at 14°C, it decreased to 2.8 $\mathrm{cal \cdot g^{-1} \cdot day^{-1}}$, which was lower than MR at 4°C (5.9 $\mathrm{cal \cdot g^{-1} \cdot day^{-1}}$; Figure 4).

Table 3: Summary of the effect of a 10°C temperature increase on the gastric evacuation rate (GER) Q_{10} among adult temperate marine species, including order, feeding habitat, body size range, and minimum (Min) and maximum (Max) temperature (temp).

Scientific name	Common name	Order	Feeding habitat	Body size	Q_{10}	Min temp	Max temp	Source	No.
Squalus acanthias	Spiny dogfish	Squaliformes	Demersal	2228–3950 g	2.7	12	15	[17]	1
Clupea harengus	Atlantic herring	Clupeiformes	Pelagic	309.8 ± 44.8 g	12.2	6.2	8.1	[51]	2
Clupea harengus	Atlantic herring	Clupeiformes	Pelagic	16–28 cm	3.9	5	18	[52, 53]	3
Salvelinus alpinus	Arctic char	Salmoniformes	Pelagic	40–100 g	3.3	6	14	[54]	4
Gadus morhua	Atlantic cod	Gadiformes	Demersal	180–2330 g	3.7	1	10	[55]	5
Gadus morhua	Atlantic cod	Gadiformes	Demersal	1000–1500 g	3.0	10.5	15.4	[56]	6
Gadus morhua	Atlantic cod	Gadiformes	Demersal	262–2066 g	2.9	1	14	[57]	7
Gadus morhua	Atlantic cod	Gadiformes	Demersal	150–375 g	1.5	2	15	[58]	8
Merlangius merlangus	Whiting	Gadiformes	Demersal	57–606 g	2.3	6	15	[59]	9
Merlangius merlangus	Whiting	Gadiformes	Demersal	18–33 cm	2.0	10	18	[60]	10
Lophius americanus	Goosefish	Lophiiformes	Demersal	2627–6306 g	2.8	10	15	[17]	11
Scomber scombrus	Atlantic mackerel	Scombriformes	Pelagic	25–45 cm	7.4	14.5	17	[61]	12
Scomber scombrus	Atlantic mackerel	Scombriformes	Pelagic	120–420 g	4.1	9	19	[62]	13
Cleisthenes pinetorum	Pointhead flounder	Pleuronectiformes	Pelagic	117–281 g	6.6	4	14	This study	14
Limanda	Dab	Pleuronectiformes	Demersal	35–225 g	2.3	8.5	15.5	[39]	15
Limanda	Dab	Pleuronectiformes	Demersal	10–200 g	1.7	8.5	16.4	[63]	16
Paralichthys dentatus	Summer flounder	Pleuronectiformes	Demersal	390–1259 g	2.3	15	20	[17]	17
Pleuronectes platessa	Plaice	Pleuronectiformes	Demersal	38–380 g	2.4	9.5	15.5	[64]	18
Pleuronectes platessa	Plaice	Pleuronectiformes	Demersal	15–200 g	2.0	5	15.5	[65]	19
Pleuronectes platessa	Plaice	Pleuronectiformes	Demersal	280–320 g	1.8	2	20	[66]	20
Scophthalmus maximus	Turbot	Pleuronectiformes	Demersal	60–700 g	3.2	8	19	[67]	21
Scophthalmus maximus	Turbot	Pleuronectiformes	Demersal	254 ± 63 g	2.2	10	19.7	[20]	22

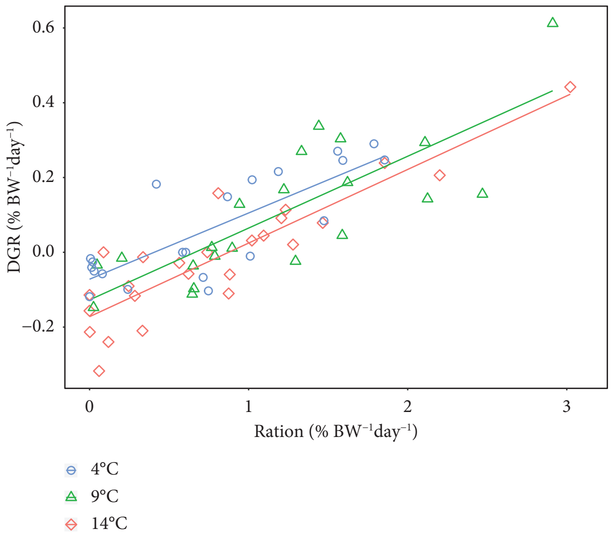

Figure 3: Relationship between the ration (%BW day^{-1}) and daily growth rate (DGR) (%BW day^{-1}) for each individual at 4°C (◯), 9°C (△), and 14°C (◇). Lines were estimated by a linear model for each temperature (blue, 4°C; green, 9°C; red, 14°C). The slopes, x-intercept, and y-intercept of each line indicate the net conversion efficiency, maintenance ration (%BW day^{-1}), and catabolic rate (%BW day^{-1}). Higher temperatures resulted in higher maintenance rations and catabolic rates, whereas net conversion efficiency did not differ significantly among temperatures (see also Table 4).

Table 4: Physiological indicators from feeding experiments under different ambient temperatures (4°C, 9°C, and 14°C).

Temp. (°C)	NCE (slope)	CR (%BW day^{-1}) (y-intercept)	MR (%BW day^{-1}) (x-intercept)	GCE
4	0.177	0.072	0.406	9.69
9	0.192	0.127	0.663	9.27
14	0.197	0.172	0.875	−2.76

The slope, y-intercept, and x-intercept of the relationship between ration and specific growth rate represent the net conversion efficiency (NCE), catabolic rate (CR), and maintenance ration (MR), respectively. Gross conversion efficiency (GCE) was calculated by dividing the increase in body weight (g) by the total amount of food consumed (g).

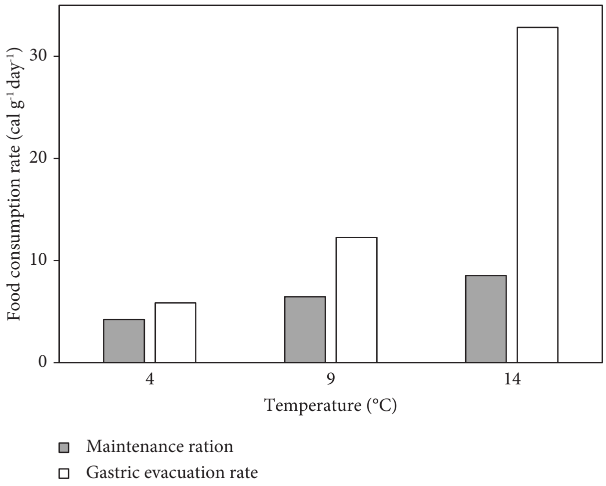

Figure 4: Differences between the maintenance ration (cal g^{-1}·day^{-1}; grey bars) and gastric evacuation rate (cal g^{-1}·day^{-1}; white bars) on a caloric basis at 4°C, 9°C, and 14°C. The difference between the GER and MR was 30.7 cal·g^{-1} day^{-1} at 14°C, compared to 2.8 cal·g^{-1}·day^{-1} at 4°C.

4. Discussion

Our study showed that Q_{10} of the GER for pointhead flounder was highest among adult demersal fish species, suggesting that pointhead flounders have stenothermal gastric evacuation, and that this species can digest more food in warmer conditions (>10°C). This study was unable to identify factors explaining the high Q_{10} of the GER in this species. Nevertheless, many factors can affect the thermal sensitivity of GERs. First, life stages affect GER thermal sensitivity. Q_{10} of Atlantic mackerel increases from 1.38 in the postlarval stage (7–14 mm fork length) [68] to 4.1 in the juvenile and adult stages (120–420 g body weight) [62]. Because adult fish actively move to areas with suitable temperatures and larvae are passively transported [69, 70], the temperature dependency of the GER may be low for adults. Second, taxonomically similar species generally have similar Q_{10} values. For example, Q_{10} of the GER is 4.5 for pikeperch [29] and 4.1–4.3 for the perch *Perca fluviatilis* [71, 72] as percids are distributed in tropical freshwater. However, we did not find close GER values among taxonomically related species in our brief study. The Q_{10} values of the demersal fish in the four families ranged from 1.7 to 3.7, with minimum and maximum values occurring in pleuronectids. Our findings suggest that Q_{10} of adult temperate marine fish is likely to have more species-specific differences, with no or a slight relationship with taxonomy. Third, the difference in enzyme activity have an effect on GER thermal sensitivity. The gastric evacuation mode of this species is closer to the square root model with a shape parameter B value of 0.67, and the gastric evacuation may reflect degradation by digestive enzymes rather than physical extrusion from the stomach into the intestine. Therefore, high Q_{10} of GER may be attributed to the stenothermal nature of the enzymatic activity of this species.

Increases in the feeding rate of pointhead flounder caused an increase in body weight but not in body length during the experiments. Mature individuals of several cold-water species, including walleye pollock [73], the haddock *Melanogrammus aeglefinus*, and the whiting *Merlangius merlangus* [74] gain body weight, but not body length, when fed more than the MR. The body lengths of the pointhead flounder (240–368 mm) used in this study corresponded to ages of 6–14 years according to the growth curve estimated for this species in Ishikari Bay [75], indicating that most individuals were mature adults. It would be reasonable for mature individuals that have escaped the critical period in which they need to increase body length to allocate energy to weight gain to cope with starvation and other problems.

As we detected no significant differences in the slopes of linear regressions among temperatures, NCE is considered insensitive to temperature in pointhead flounder. Similar results have been reported for other cold-water fish species, including Japanese flounder *Paralichthys olivaceus* [76], whiting [77], and Eurasian minnow *Phoxinus phoxinus* [78]. NCE is independent of temperature within the normal range of most species [79, 80]. In contrast to the NCE, the intercepts of the linear model differed among temperatures, indicating that CR changes depending on the temperature. An increase in the CR with increasing temperature has been reported in some cold-water species such as walleye pollock [73] and yellowfin sole [23], and these results are consistent with this study. GCE decreased with increasing temperature as previously reported for cold-water species [81, 82]. As GCE is the sum of NCE and CR, the decrease in GCE with increasing temperature was attributed to an increase in CR, but not NCE. If the food consumption rate remains constant over a given temperature range, lower temperatures result in more efficient pointhead flounder growth. However, as the amount of food consumed is limited by other temperature-dependent factors including GER, higher GCE would not be advantageous for growth at lower temperatures.

Q_{10} of the GER was 3.2-fold that of MR, and Q_{10} of the GER was the highest among the demersal fishes reviewed in this study. Q_{10} of the GER for pointhead flounder (6.55) in the present study was estimated to be 2.5-fold higher than the average value (2.6) for demersal fish. Although few studies have been conducted on pleuronectids, MR was 1.7-fold lower than that of Atlantic halibut [31]. These results indicate that the sharp decrease in the GER–MR at low temperatures reflects the stenothermal nature of the GER.

The difference between the GER and MR at 14°C was 30.7 $\mathrm{cal\cdot g^{-1}\cdot day^{-1}}$, which decreased to 2.8 $\mathrm{cal\cdot g^{-1}\cdot day^{-1}}$ at 4°C. Since the decrement of GER is greater than that of MR with decreasing water temperature, there is little difference between the GER (maximum energy available for feeding) and the MR (minimum energy required to maintain body weight) at 4°C, meaning that the surplus energy that can be allocated to activity (growth, reproduction, etc.) other than body weight maintenance is quite limited. A low GER becomes a bottleneck at 4°C, such that even when surplus food is available, most of the acquired energy is used to maintain body weight while somatic growth is very limited. Although the movement of experimental pointhead flounder in this study was limited within the tank, additional energy is required for migration and reproduction in a wild habitat. Therefore, the MR in this study was considered to be the minimum requirement. Thus, the actual energy allocated to growth would be smaller than the GER and MR values obtained in the present study, and the actual growth of wild fish at low temperatures would be more limited. The bottom temperature in Funka Bay, where pointhead flounders are distributed, is approximately 4°C from winter to summer [32]. If this species remains near the sea bottom, it may be unable to grow due to the physiological constraints described above. In contrast, the water temperature in the upper layers exceeds 4°C [32], enabling the fish to grow if the food supply is sufficient. Such a physiological constraint elucidates the unique pelagic feeding ecology of pointhead flounder. This species has been reported to remain within the water column for extended durations [9], allowing it to ingest and digest more prey in the warmer pelagic zone.

In conclusion, Q_{10} of GER for pointhead flounder was the highest among the adult demersal fishes reviewed. This high thermal sensitivity of GER might have resulted in the stenothermal nature of digestive characteristics of this species. It was estimated that the high Q_{10} of GER limits the energy allocated to growth at lower temperature and it can grow little at winter-spring sea bottom in their habitat. This temperature-dependant physiological limitation of this species successfully explained its unique feeding ecology, leaving the colder sea floor and feeding at warmer pelagic layers.

Data Availability

The data used to support the findings of this study are available on request from the corresponding author. The data are not publicly available due to privacy or ethical restrictions.

Conflicts of Interest

The authors declare that they have no conflicts of interest.

Acknowledgments

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Supplementary Materials

Appendix 1: relationship between the wet weights of juvenile walleye pollock *Gadus chalcogrammus* specimens ($n = 216$) before and after 10% formalin fixation. The line was fitted as $y = 1.0233x + 0.0095$. Appendix 2: estimated gastric evacuation times (h) of different proportions of stomach contents (25%, 50%, 75%, and 95%) in pointhead flounder *Cleisthenes pinetorum* under different ambient temperatures (4°C, 9°C, and 14°C). (*Supplementary Materials*)

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