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Gastrointestinal blood flow in the red Irish lord, *Hemilepidotus hemilepidotus*: long-term effects of feeding and adrenergic control

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Abstract Cardiac output, blood flow to the coeliac and mesenteric arteries, dorsal aortic blood pressure and heart rate were recorded simultaneously at rest and postprandial for 6 days in a teleost, the red Irish lord (*Hemilepidotus hemilepidotus*). We anticipated that gastrointestinal blood flow would increase postprandially, supported by an increase in cardiac output. However, we had no predictions for either the exact time-course of this response, or for the regional distribution of blood flow between to the two major arteries comprising the splanchnic circulation. In resting, unfed animals, blood flow to the coeliac artery and mesenteric artery was $4.1 \pm 0.6 \text{ ml min}^{-1} \text{ kg}^{-1}$ and $4.9 \pm 1.3 \text{ ml min}^{-1} \text{ kg}^{-1}$, respectively (mean \pm SEM, $n = 7$), which together represented 34% of cardiac output. Feeding increased blood flow to the coeliac and mesenteric arteries in a time-dependent manner. The increase in coeliac artery blood flow preceded that in the mesenteric artery, a finding that is consistent with the coeliac artery supplying blood to the liver and stomach, while the mesenteric artery supplies blood to the stomach and intestine. Coeliac blood flow had increased by $84 \pm 18\%$ after 1 day and had a peak increase of $112 \pm 40\%$ at day 4 postprandial. Mesenteric blood flow was not significantly elevated at day 1, but had increased by $94 \pm 19\%$ at day 4 postprandial. Cardiac

output also increased progressively, increasing by a maximum of $90 \pm 30\%$ at day 4. Because the increase in cardiac output was adequate to meet the postprandial increase in gut blood flow, the postprandial decreases in vascular resistance for the coeliac and mesenteric circulations mirrored the increases in blood flow. Intra-arterial injections of adrenaline and noradrenaline into resting fish more than doubled coeliac and mesenteric vascular resistances, and blood flow decreased proportionately. This adrenergic vasoconstriction was totally abolished by pretreatment with the α -adrenoceptor antagonist phentolamine, which in itself approximately halved coeliac and mesenteric vascular resistances. These observations indicate a significant α -adrenergic tone in the gastrointestinal circulation of the red Irish lord, the loss of which could not entirely account for the postprandial increase in gastrointestinal blood flow. Other control mechanisms are suggested.

Key words Gastrointestinal blood flow · Feeding · Adrenaline · α -Adrenoceptors · Teleost

Abbreviations f_H heart rate · P_{DA} dorsal aortic blood pressure · Q ventral aortic blood flow · q_{CoA} blood flow in the coeliac artery · q_{MeA} blood flow in the mesenteric artery

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Introduction

Relatively little is known about the regional distribution of blood flow in fishes. The circulation to the gastrointestinal tract is one of the two major components of the systemic circulation and yet information on the control of this circulation is particularly sparse despite its potential application in studies related to energetics, aquaculture, pharmacokinetics and toxicokinetics. In fact, there are only three previous studies that have measured gastrointestinal blood flow directly (with flow probes), using exercise, hypoxia and feeding as experimental interventions (Axelsson et al. 1989; Axelsson and

Fritsche 1991; Thorarensen et al. 1993). These studies indicated that the viscera received around 30–40% of cardiac output in unfed, resting animals (40% in Atlantic cod; 30% in sea raven; 36% in Chinook salmon, *Oncorhynchus tshawytscha*). Studies of gastrointestinal blood flow in fish using labeled microspheres are more numerous, but are not consistent with the direct measurements. The percentage of blood flow reaching the gastrointestinal circulation varied widely between species, ranging from 0.2% in albacore tuna to 18% in rainbow trout at 5 °C (Kent et al. 1973; Cameron 1975; Randall and Daxboeck 1982; Barron et al. 1987; White et al. 1988; Kolok et al. 1993). It has been suggested that the microsphere method underestimates gut blood flow in fish (Thorarensen et al. 1993).

Our understanding of active regulation of gastrointestinal blood flow in fishes is even more scant. We have information on the changes that occur 24 h postprandial. Coeliac artery blood flow increased by 100% in the sea raven (Axelsson et al. 1989), intestinal blood flow increased by 70% in Chinook salmon (Thorarensen et al. 1993), and blood flow to the coeliac and mesenteric arteries of Atlantic cod increasing by 72% and 42%, respectively (Axelsson and Fritsche 1991). Thus, though our expectation is that postprandial gut blood flow will increase, the longer-term changes in gastrointestinal blood flow as food is digested and passed through the digestive tract have not been investigated in fishes. In these earlier studies the food in the stomach was only partially digested when the studies were terminated 24 h postprandially (Axelsson et al. 1989; Axelsson and Fritsche 1991). In mammals, blood is redistributed with time from the coeliac artery to mesenteric arteries as digested food moves from the stomach to the intestines. In view of this, the main aim of this study was to quantify over several days the postprandial changes in coeliac and mesenteric blood flow in the red Irish lord, *Hemilepidotus hemilepidotus*. In addition, the effects of α -adrenergic agents were also studied to estimate the relative contribution of this control mechanism to the postprandial changes in gastrointestinal blood supply.

Materials and methods

Red Irish lords, *H. hemilepidotus*, of either sex and with a body mass of 300–1200 g, were caught by hook and line in English Bay off West Vancouver, BC, Canada. They were kept large tanks with aerated, running seawater at the Department of Fisheries and Oceans West Vancouver Laboratory. The water temperature during the experimental period (March–April) was 7–9 °C and the salinity 3.0–3.2%. Animals were fed daily until a week prior to surgery.

Surgical procedures

The fish were anaesthetized in MS222 (tricaine methanesulphonate; 100 mg l⁻¹, Sigma) until breathing movements ceased, and placed ventral side up on an operating sling. The gills were continuously irrigated with aerated seawater containing the anaesthetic (50 mg l⁻¹). A polyethylene (PE) cannula (PE50) filled with

heparinized (100 IU ml⁻¹) 0.9% NaCl was occlusively implanted into the efferent branchial artery of the 3rd gill arch for measuring dorsal aortic blood pressure (P_{DA}) and heart rate (f_H) (Axelsson and Nilsson 1986). In order to measure cardiac output (Q = ventral aortic blood flow), the ventral aorta was exposed through a midline incision anterior to the base of the pectoral fins. The ventral aorta was dissected free by separating the connective tissues of the surrounding tissues with minimal to no blood loss. A cuff-type pulsed Doppler flow probe (P. Pohl International) with an internal diameter of 2.2–3.0 mm was placed around the vessel.

Corrosion casts of the arterial system revealed that the coeliac artery supplied the stomach and liver region while the mesenteric artery supplied part of the stomach and the intestine. Blood flow in the coeliac (q_{CoA}) and mesenteric (q_{MeA}) arteries was measured in the following way. The animals were placed on their left side and an incision between the pelvic and pectoral fin was made to expose both vessels. After careful blunt dissection, cuff-type pulsed Doppler probes (ID 1.2–1.6 mm, P. Pohl International) were placed around each vessel. Care was taken not to damage the nerves running along the vessels. The leads from the probes were tunneled to the dorsal side of the animals and secured to the skin with two sutures each. After surgery the animals were transferred to the experimental chamber and allowed to recover from surgery for 24–36 h before experiments commenced. The flow probes were connected to a pulsed Doppler flow meter system (Iowa University). The dorsal aortic cannula was connected to a Micron pressure transducer (Narco, Houston, Tex.). Blood pressure was calibrated against a static water column. The flow and pressure signals were amplified and recorded using a Grass recorder model 7D.

Calibration of Doppler flow probes

To estimate absolute values of cardiac output and gastrointestinal blood flow, a careful *in situ* calibration of the flow probes was performed after the experiment was completed. The fish was anaesthetized, killed by cervical dislocation and placed on its left side on the operating table. The heart was then exposed and a PE90 cannula was secured in the ventricle for perfusion of the ventral aorta. The coeliac and mesenteric vessels were exposed and a PE50 cannula was implanted on either side of the flow probe. A Haake-Buckler (MCP2500) peristaltic pump delivered heparinized physiological saline (0.9% NaCl), to which blood had been added to a hematocrit of around 4–5%, to each vessel at four different flow rates. Flow rates were determined gravimetrically. An accurate calibration as determined by linear regression analysis (i.e., $R^2 > 0.9$) was achieved in only four of the eight animals.

Experimental protocols

Feeding experiment

After the recovery period, initial recordings were made of resting blood pressure, heart rate, cardiac output, and coeliac and mesenteric blood flow. The animals were divided into two groups of eight animals. One acted as unfed controls and were handled in the same way as the fed group. The animals were fed pieces of fish muscle by gavage, equivalent to approximately 10–15% of body mass. All the cardiovascular variables were then recorded once every 24 h over a period of 6 days.

Drug injections

To study the adrenergic control of the gut circulation, adrenergic agonists (10 nmol kg⁻¹ adrenaline and 10 nmol kg⁻¹ noradrenaline) were injected into a separate group of eight animals. Preliminary dose-response tests showed that this dose produced consistent responses. Subsequently the fish were treated with the α -adrenergic antagonist phentolamine (2 mg kg⁻¹) and after 2–3 h a second dose of adrenaline was injected to confirm that α -adrenergic responses had been fully blocked.

Data acquisition, calculations and statistics

A computer-based data acquisition system (Labtech Notebook, ver. 5.0) was used in combination with the Grass polygraph recordings. All variables were sampled at 2 Hz and a further data reduction was performed through on-line averaging. The averaged data were stored on a disk every 5 s. Data are presented in graphs as means \pm SEM, where each point in the feeding experiments represents a mean value of a 30-min sampling period taken every 24 h, while for adrenaline and noradrenaline each point represents a mean value for a 30-s sample period.

The vascular resistance was calculated as pressure difference divided by the blood flow. We assumed that pressure in the central venous system was zero and that the dorsal aortic blood pressure was the driving pressure for the coeliac and mesenteric vascular circuits (Axelsson et al. 1989). We also assumed that no significant changes in blood viscosity took place during the experiments. f_H , expressed in beats per minute (bpm), was derived from the pulsatile pressure signal by the software program.

Wilcoxon's signed-ranks test for paired samples (two-tailed) were used to evaluate the statistical significance of the observed effects of the adrenergic agonists/antagonists, and a Mann-Whitney U -test was used to compare daily values for groups A and B. The level of statistical significance was set to $P < 0.05$. Asterisks in the figures indicate significant changes. In case of repeated tests, a modified Bonferroni procedure was used to reduce the risk of discarding a true null hypothesis (Holm 1979). All statistical treatments of the data were made using absolute values. Blood flow, blood pressure and vascular resistance are presented in figures as percentage changes from the control value. The control value was derived from the period 24–36 h postsurgery and prior to the force feeding/sham treatments. In the drug injection experiments, the control period represents the 30 s prior to the injection of either adrenaline or noradrenaline.

Drugs used

The following drugs were used: L-adrenaline bitartrate, DL-noradrenaline, and phentolamine methanesulphonate. All drugs were purchased from Sigma Chemical and diluted in 0.9% NaCl.

Results

Effects of feeding

Resting cardiovascular values are presented in Table 1. Feeding significantly increased blood flow in the coeliac artery for the entire 6-day postprandial period, with the exception of day 5 (Fig. 1). After 1 day, coeliac artery blood flow was $84 \pm 18\%$ higher than that in the unfed controls, reaching a maximum difference $112 \pm 40\%$ on day 4. Significant decreases in the vascular resistance

Table 1 Resting values for dorsal aortic blood pressure (P_{DA}), heart rate (f_H), cardiac output (Q) and coeliac and mesenteric artery blood flow (q_{CoA} , q_{MeA} , respectively). The coeliac and mesenteric blood flow is also shown as percentage of cardiac output. Data shown are mean \pm SEM

Variable	<i>n</i>	Value	Units	% of Q
P_{DA}	8	3.5 ± 0.1	(kPa)	
f_H	8	48.0 ± 1.7	(bpm)	
Q	4	24.4 ± 1.0	(ml min ⁻¹ kg ⁻¹)	
q_{CoA}	7	4.1 ± 0.6	(ml min ⁻¹ kg ⁻¹)	16.7 ± 4.2
q_{MeA}	7	4.9 ± 1.3	(ml min ⁻¹ kg ⁻¹)	17.7 ± 2.3

mirrored these changes in coeliac blood flow (Fig. 1). Feeding also increased blood flow in the mesenteric artery, but was delayed compared with that in the coeliac artery, increasing significantly from day 2 onwards. Mesenteric vascular resistance decreased significantly from day 4 onwards (Fig. 1). The maximum increase in mesenteric artery blood flow, though delayed, was similar ($94 \pm 18\%$) to that for the coeliac artery.

In unfed fish, the total gastrointestinal blood flow (coeliac plus mesenteric) was $9 \text{ ml min}^{-1} \text{ kg}^{-1}$ and represented 34% of cardiac output. The postprandial increase in gastrointestinal blood flow was supported by a statistically significant increase in Q from day 3 onwards (Fig. 1). In fact, the postprandial increase in cardiac output (from $24.4 \text{ ml min}^{-1} \text{ kg}^{-1}$) was more than adequate to account for the maximum increase in gastrointestinal blood flow.

Adrenergic control of the gastrointestinal circulation

Adrenaline (A) and noradrenaline (NA) injections caused dose-dependent changes in the recorded variables and maximum responses were reached 1–2 min after injection (data not shown). The effects of injections of 10 nmol kg^{-1} adrenaline and noradrenaline are presented in Figs. 2 and 3. Both agonists significantly increased vascular resistance in the coeliac (A, $291 \pm 52\%$; NA, $154 \pm 44\%$) and mesenteric (A, $238 \pm 106\%$; NA, $58 \pm 12\%$) circulations, with the response to adrenaline being significantly larger than that for noradrenaline. Significant reductions in coeliac (A, $-62 \pm 5\%$; NA, $-45 \pm 6\%$) and mesenteric (A, $-46 \pm 9\%$; NA, $-31 \pm 5\%$) blood flow accompanied these changes in vascular resistance. Cardiac output did not change significantly, but dorsal aortic pressure increased (A, $3.5 \pm 0.1 \text{ kPa}$ to $4.0 \pm 0.1 \text{ kPa}$; NA, $3.4 \pm 0.1 \text{ kPa}$ to $3.9 \pm 0.1 \text{ kPa}$). The coeliac circulation appeared to be more sensitive to the vasoconstrictory actions of adrenaline.

The alpha-adrenergic antagonist phentolamine significantly decreased coeliac and mesenteric vascular resistance ($-56 \pm 9\%$ and $-42 \pm 8\%$, respectively) and dorsal aortic blood pressure ($3.4 \pm 0.2 \text{ kPa}$ to $2.4 \pm 0.3 \text{ kPa}$), and significantly increased cardiac output ($26 \pm 9\%$) and coeliac artery blood flow ($69 \pm 30\%$). The $53 \pm 31\%$ change in mesenteric artery blood flow was not statistically significant (Fig. 4). Phentolamine also blocked all the cardiovascular changes associated with an adrenaline injection, except for the significant increase in dorsal aortic blood pressure ($2.9 \pm 0.3 \text{ kPa}$ to $3.5 \pm 0.3 \text{ kPa}$) (Fig. 2).

Discussion

This is the first paper to report the progressive effects of feeding on intestinal blood flow in any fish over a period

Fig. 1 A summary of the cardiovascular responses to feeding in the red Irish lord (*Hemilepidotus hemilepidotus*). Filled circles represents sham-fed animals and open circles represents fed animals; Mean values \pm SEM; $n = 6-8$. P_{DA} , dorsal aortic blood pressure; Q , cardiac output; q_{CoA} , q_{MeA} , coeliac and mesenteric artery blood flow, respectively; R_{CoA} , R_{MeA} , coeliac and mesenteric vascular resistance, respectively. Asterisks indicate statistically significant differences between sham-fed and fed animals

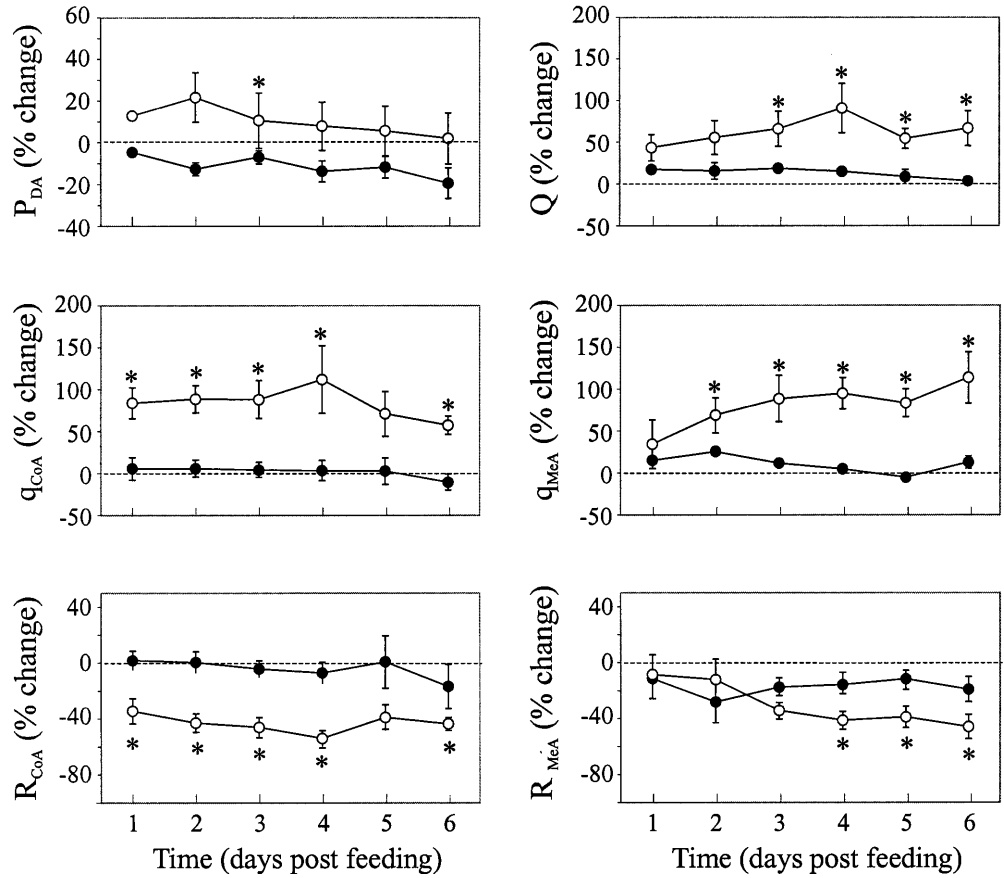


Fig. 2 A summary of the cardiovascular responses to adrenaline (10 nmol kg^{-1}) injected into the dorsal aorta in *H. hemilepidotus*. Mean values \pm SEM; $n = 5-7$. Open circles shows the effects of adrenaline in untreated animals, filled circles shows the response to adrenaline after phentolamine pretreatment (2 mg kg^{-1}). Asterisks indicate statistically significant differences compared to the control period (time = 0). Abbreviations as in Fig. 1

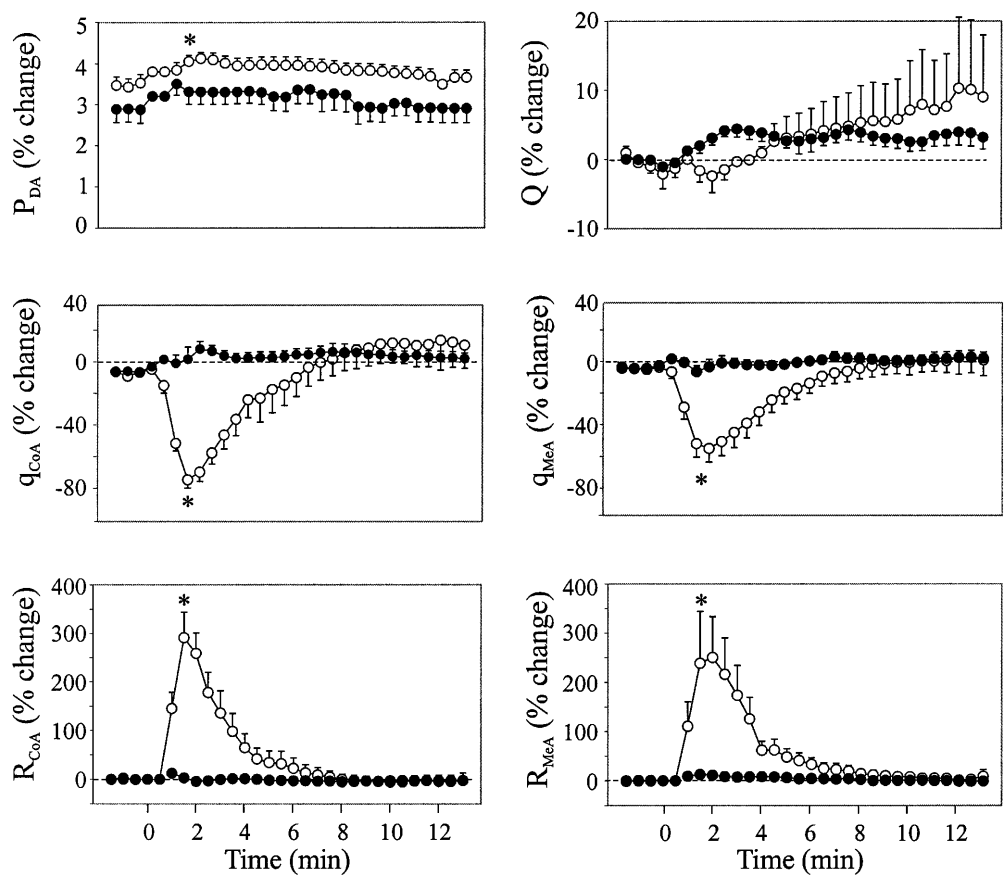


Fig. 3 A summary of the cardiovascular responses to noradrenaline (10 nmol kg^{-1}) injected into the dorsal aorta in *H. hemilepidotus*. Mean values \pm SEM; $n = 5-7$. Asterisks indicate statistically significant differences compared to the control period. Abbreviations as in Fig. 1

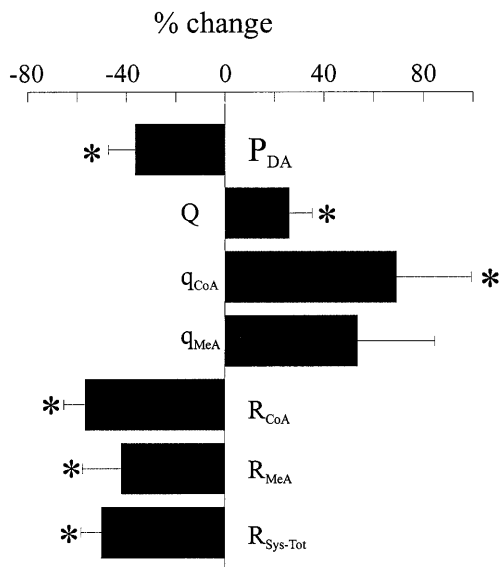
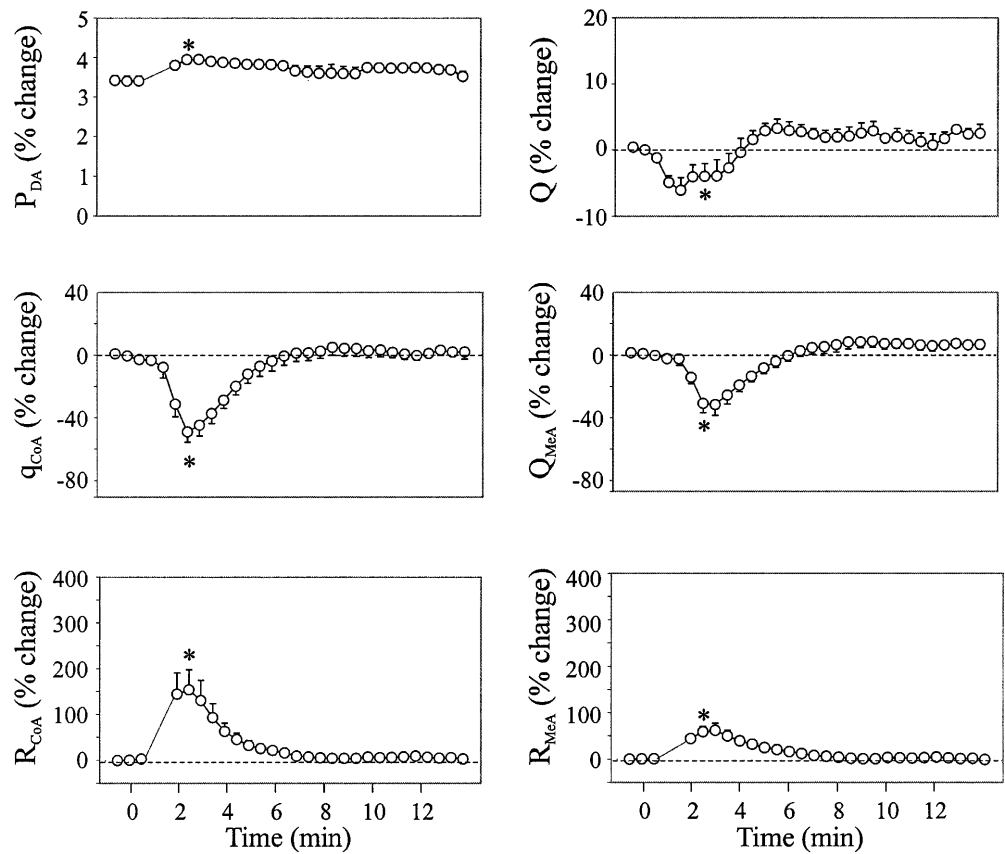


Fig. 4 Histogram showing the effects of phentolamine (2 mg kg^{-1}) as percentage change from the pre-injected values on the recorded and calculated cardiovascular variables in *H. hemilepidotus*. Mean \pm SEM; $n = 10$. Asterisks indicate statistically significant changes compared to the pre-injected values. Abbreviations as in Fig. 1

of several days. It is also the first study to make cardiovascular measurements in *H. hemilepidotus*. The resting cardiovascular variables reported here ($P_{DA} =$

$3.46 \pm 0.14 \text{ kPa}$, $Q = 24.4 \pm 1.0 \text{ ml min}^{-1} \text{ kg}^{-1}$, $q_{CoA} = 4.1 \pm 0.6 \text{ ml min}^{-1} \text{ kg}^{-1}$, $q_{MeA} = 4.9 \pm 1.3 \text{ ml min}^{-1} \text{ kg}^{-1}$, $f_H = 48.0 \pm 1.7 \text{ bpm}$) were similar to values recorded previously for sea raven and Atlantic cod (Axelsson et al. 1989; Axelsson and Fritsche 1991), but total gastrointestinal blood flow was lower than that recorded previously in Chinook salmon ($13-18 \text{ ml min}^{-1} \text{ kg}^{-1}$; Thorarensen et al. 1993).

The diameters of the coeliac and mesenteric arteries of *H. hemilepidotus* were comparable, as were their routine blood flows ($4.1 \text{ ml min}^{-1} \text{ kg}^{-1}$ and $4.9 \text{ ml min}^{-1} \text{ kg}^{-1}$, respectively). With 34% of cardiac output supplying the gastrointestinal circulation, this proportion is comparable to values obtained previously in Atlantic cod (40%; Axelsson and Fritsche 1991) and Chinook salmon (36%; Thorarensen et al. 1993). In the sea raven (*Hemitripterus americanus*) blood flow only to the coeliac artery was measured (Axelsson et al. 1989), but if we assume equal flow to the coeliac and mesenteric arteries, then total gastrointestinal blood flow would have equaled 30% of cardiac output. Thus, based on the observations for four teleost fish species, around 30-40% of cardiac output is normally directed towards the gut of resting, unfed fish. This value is very much in line with observations for mammals where gastrointestinal blood flow is around 27-30% of cardiac output (Greenway 1982).

Feeding

Feeding increased gastrointestinal blood flow as a result of decreased vascular resistance as well as increased cardiac output. Both the coeliac and mesenteric artery blood flow approximately doubled although the time course of these changes was different in the two vascular beds. The delayed increase in mesenteric blood flow would be consistent with a time-dependent passage of food through the gut. In the only other study to measure both coeliac and mesenteric blood flow (Axelsson and Fritsche 1991), the increase in coeliac blood flow (72%) was greater than that for the mesenteric artery (41%) 24 h postprandial. Quantitatively the postprandial increase in coeliac artery blood flow after 24 h (84%) was similar to values previously reported for other fish at 24 h postprandial (Atlantic cod, 72%, Axelsson and Fritsche 1991; sea raven, 100%, Axelsson et al. 1989). The coeliac artery in the Atlantic cod and *H. hemilepidotus* (and probably the sea raven), supplies the stomach and liver region (Allen 1905). In mammals, the postprandial increase in gastrointestinal blood flow is localized to those parts of the gut containing food, and the increase in the coeliac artery also precedes that in the mesenteric artery (Biber 1974; Gallavan et al. 1980).

Gastric emptying time is strongly affected by temperature, food composition, food particle size, the amount of food ingested and possibly other factors. In mammals, gut blood flow starts to increase minutes after the arrival of food and lasts for 4–6 h (Fara 1984). Numerous studies have been performed with fish on gastric evacuation times and the duration of heat increment (or specific dynamic action) (see reviews by Brett and Groves 1979; Fänge and Grove 1979; Jobling 1981). Gastric evacuation time and the duration of heat increment both increase exponentially with decreasing water temperature. Furthermore, they are linearly related with each other in plaice, *Pleuronectes platessa*, but with heat increment lasting longer than gastric evacuation time. This, as well as other observations, has led to the idea that heat increment reflects post-absorptive effects rather than just the metabolic costs of gastrointestinal motor activity. Gastric evacuation time and the duration of heat increment have not been measured previously in RIL, and while they are likely related to the duration of the postprandial increase in gut blood flow, the exact nature of this relationship is unknown. Nonetheless, it would not be unreasonable to expect gastric emptying times of several days given the cold water temperature and large meal size (Fänge and Grove 1979; Jobling 1981). Therefore, our finding that gut blood flow was elevated for 6 days postprandially suggests that there could be quite a tight correlation between both gastric evacuation time and duration of heat increment. In the Atlantic cod gastric emptying times of 12–45 h have been reported (Tyler 1970; Jones 1974), but in these studies small amounts of food were given (0.2–2.7% kg^{-1} body mass). In feeding experiments with

sea raven and Atlantic cod, partially digested food was still present in the stomach 24 h after feeding (Axelsson et al. 1989; Axelsson and Fritsche 1991). Sea ravens have been observed to eat prey up to 50% of their own body mass and complete digestion of such large meals takes several weeks (A. P. Farrell, unpublished observation). In the present study, the stomach contents were examined at the end of the study. Only small pieces of food and bones were found in the stomach, indicating that the stomach emptying was almost completed 6 days after feeding. This observation is consistent with coeliac but not mesenteric blood flow decreasing 4 days postprandial.

The postprandial increase in cardiac output in *H. hemilepidotus* adequately accounted for almost the entire increase in gastrointestinal blood flow. Cardiac output increased from 24 to 32, a change of 8, whereas total gastrointestinal blood flow was increased by about $9 \text{ ml min}^{-1} \text{ kg}^{-1}$. Thus, it is unlikely that a significant redistribution of cardiac output is needed to meet the postprandial increase in gastrointestinal blood flow in otherwise resting animals. A similar finding was reported earlier for the Atlantic cod where the increase in cardiac output matched the increase in gastrointestinal blood flow (Axelsson and Fritsche 1991). In contrast to this situation, the postprandial increase in splanchnic blood flow in many mammals involves a redistribution of blood from other tissues rather than an increase in cardiac output (Vatner et al. 1974).

Control mechanisms for gastrointestinal blood flow

Previous studies have focused on the adrenergic control of gastrointestinal blood flow in fish. α -Adrenoceptor blockade reduced vascular resistance in both the coeliac and mesenteric arteries of unfed sea raven, showing the existence of a tonic alpha-adrenergic vasoconstriction of the gut vasculature (Axelsson et al. 1989). However, this was not the case in Atlantic cod where α -adrenergic tonus was found only in the mesenteric circulation (Axelsson and Fritsche 1991). In the present study, phentolamine reduced routine vascular resistance in both the mesenteric and coeliac circulations, and adrenaline and noradrenaline injections markedly increased coeliac and mesenteric vascular resistance, a response that was blocked by phentolamine. Thus, *H. hemilepidotus* shows a greater similarity to the sea raven than with the Atlantic cod in this regard.

The potent α -adrenoceptor vasoconstriction mechanism, reported here for *H. hemilepidotus*, has been recognized previously for Atlantic cod, spiny dogfish and sea raven (Axelsson and Fritsche 1991; Holmgren et al. 1992; Axelsson et al. 1989) and for reptiles, birds and mammals (Ross 1971; Rothe 1984; Butler et al. 1988; Axelsson et al. 1991). Thus, adrenergic (either humoral or nervous) regulation of the gastrointestinal

circulation has been conserved among all of the vertebrate groups studied so far. However, this type of regulation appears to be relatively short acting (minutes to hours) because prolonged sympathetic nerve stimulation of the nerves to the gut, or prolonged infusion of noradrenaline, causes an initial reduction in blood flow, but then blood flow returns toward control levels despite continued stimulation or infusion. This "autoregulatory escape" phenomenon (Ross 1971) is a well described in mammals and has also been observed in the Atlantic cod, although a mechanistic explanation is still lacking (Greenway 1984; Axelsson and Fritsche 1991).

Postprandial control of gastrointestinal blood flow needs to act over several days in fishes. Based on the present study, adrenergic regulation of gastrointestinal blood flow could not quantitatively account for all of the postprandial increase in blood flow. Phentolamine, which released the tonic α -adrenergic constriction of the gastrointestinal circulation, resulted in only about half of the maximal postprandial increase in gastrointestinal blood flow. Therefore, it is likely that other factors such as peptides, cholinergic controls and local factors are involved in the long-term regulation of gut blood flow. In the Atlantic cod (Jensen et al. 1991) and spiny dogfish (Holmgren et al. 1992), substance P lowered the coeliac vascular resistance, producing a marked increase in blood flow, while vasoactive intestinal polypeptide (VIP) increased coeliac vascular resistance in the spiny dogfish, but had no effect on gastrointestinal blood flow.

General conclusion

Data presented in this paper for the gastrointestinal blood supply in *H. hemilepidotus*, lends further support for previous direct measurements of gastrointestinal blood flow in other teleost species under resting, unfed conditions, as well as 24 h postprandial. We discovered that the postprandial increase in gastrointestinal blood flow is extended for at least 6 days and that the increase in blood flow to the coeliac artery precedes that in mesenteric artery. Furthermore, the powerful α -adrenergic control mechanism found in both gastrointestinal vessels and that provides a tonic α -adrenergic vasoconstriction in unfed fish, would could contribute significantly towards, but cannot fully account for, the maximal postprandial increase in gastrointestinal blood flow.

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