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INTEGRATED PHYSIOLOGICAL RESPONSES TO FEEDING IN THE BLUE CRAB *CALLINECTES SAPIDUS*

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Summary

The passage of a barium meal (15 % by mass) was followed through the digestive system of the blue crab *Callinectes sapidus* by flash-freezing crabs at set intervals, followed by radiography of specimens. Food moved from the oesophagus into the stomach region within 15 min. After 1–2 h, food was visible in the midgut, at 6 h it had reached the hindgut, and material was still present in the stomach at this time. The stomach was emptied between 8 and 10 h after feeding, and the entire digestive system was cleared of material after 18 h. A pulsed-Doppler flowmeter was used to monitor cardiac variables and arterial haemolymph flows during a 4 h control and 24 h postprandial period. Heart rate increased immediately upon food detection and remained elevated for 16–18 h after food ingestion. There was no significant change in stroke volume of the heart, and total cardiac output increased significantly and remained elevated above pre-feeding levels for 24 h after feeding. There was no change in haemolymph flow through the anterior or posterior aorta, but flow increased in the sternal, anterolateral and hepatic arteries. These changes in haemolymph flow reflected the use of the chelae and mouthparts in feeding, contraction of the visceral muscle surrounding the gut system and mobilisation of enzymes from the hepatopancreas. There was also a postprandial increase in the rate of oxygen uptake (apparent specific dynamic action). The rate of oxygen consumption ($\dot{M}_{O_2}$) reached maximal levels 4 h after feeding and decreased slowly thereafter, reflecting the increased use of oxygen in digestion and absorption.

Key words: *Callinectes sapidus*, digestion, feeding, cardiovascular, haemolymph flow, oxygen uptake, blue crab.

Introduction

The blue crab *Callinectes sapidus* is a commercially important species found in estuaries and shallow bays along the eastern and Gulf coasts of North America. It is an active predator, and its diet consists largely of molluscs, fish and small crustaceans (Tagatz, 1968).

The decapod crustacean gut is essentially an internal tube opening anteriorly and ventrally at the mouthparts and ending posteriorly at the anus. It is divided into the foregut, midgut and hindgut, but there is much interspecific variation within the decapod crustaceans (Icely and Nott, 1992). The foregut region is ectodermal in origin and lined with cuticle; it consists of a short oesophagus opening at the mandibles, leading to the stomach. The stomach is separated into the anterior cardiac chamber, with a smaller pyloric chamber lying ventral to the posterior half of the cardiac region (Barker and Gibson, 1978; Johnson, 1980; Icely and Nott, 1992; Heeren and Mitchell, 1997). The cardiac chamber contains calcified ossicles which form the gastric mill; its primary function is that of mastication, but it also breaks down food using enzymes from the hepatopancreas (Johnson, 1980; Icely and Nott, 1992). The pyloric region, which is separated from the cardiac region by the cardio-pyloric valve (Barker and Gibson, 1978; Icely and Nott, 1992), primarily regulates movement of material into the midgut region. In addition, setae in the posterior region of the cardiac and pyloric chambers form screens that filter out coarse material (Icely and Nott, 1992).

The midgut is endodermally derived and has a simple glandular epithelium but no cuticle (Icely and Nott, 1992); it starts at the junction with the pyloric region of the stomach and ends in a single coiled tube, the posterior midgut caecum (Smith, 1978). Early reports found the midgut of brachyuran crabs to be very short, only 10 mm long in an adult *Cancer pagurus* (Pearson, 1908) and 12–13 mm in the Indian field crab *Paratelphusa hydrodromus* (Reddy, 1938). However, later reports, using histological techniques outlined by Smith (1978), showed that the midgut consists of a significant portion of the gut system. The midgut of *C. sapidus* ends just anteriorly to the junction of the carapace and abdomen (Johnson, 1980). The midgut of *Scylla serrata* is of similar length, constituting 40–50 % of the entire postgastric gut (Barker and Gibson,

1978). It is somewhat shorter in the giant crab *Pseudocarcinus gigas*, making up approximately 24 % of the entire gut length (Heeren and Mitchell, 1997). The paired anterior midgut caeca arise from the midgut, close to the junction with the pyloric chamber (Johnson, 1980). The hepatopancreas (digestive gland) originates immediately behind the origin of the midgut caeca and occupies most of the dorsal anterior half of the cephalothorax (Pearson, 1908; Barker and Gibson, 1978; Johnson, 1980). The midgut caeca branch extensively within the hepatopancreas, forming blind-ending tubules. It is here that enzymatic digestion is begun and absorption of food by the hepatopancreas occurs (Johnson, 1980).

The hindgut, like the foregut, is lined with cuticle and arises behind the posterior midgut caeca (Smith, 1978). It runs the length of the abdomen to the anus, which opens ventrally on the telson (Pearson, 1908; Johnson, 1980). It functions in expelling the muco-peritrophic membrane and its contents by rhythmic peristaltic contractions along its length (Dall and Moriarty, 1983).

The duration of passage of food through the crustacean gut system is highly variable: foregut clearance rates can be as short as 3–6 h in the New Zealand paddle crab *Ovalipes catharus* (Haddon and Wear, 1987), but food can remain in the stomach of *Liocarcinus puber* for up to 24 h (Choy, 1986). More commonly, the decapod crustacean stomach is emptied after approximately 12 h (Dall, 1967; Hill, 1976; Hopkin and Nott, 1980; Joll, 1982; Sarda and Valladares, 1990). Even within species, movement of material through the digestive system differs and is highly dependent on temperature (Haddon and Wear, 1987). Release of enzymes from the hepatopancreas and digestion occur fairly rapidly, usually within 30–60 min of food ingestion (Dall, 1967; Barker and Gibson, 1977, 1978; Hopkin and Nott, 1980), and extracellular and intracellular digestion continue for up to 24 h (Barker and Gibson, 1977, 1978; Hopkin and Nott, 1980). The first faeces appear as coiled tubes surrounded by a peritrophic membrane 5–8 h after food ingestion (Dall, 1967; Hopkin and Nott, 1980), although this can take as long as 15 h in *Liocarcinus* spp. (Choy, 1986). The gut system is completely cleared of food at times ranging between 12 h (Dall, 1967; Joll, 1982; Sarda and Valladares, 1990) and 48 h (Hopkins and Nott, 1980), although indigestible material such as shell and bone can remain in the foregut for a number of days before being regurgitated (Hill, 1976; Choy, 1986).

Many taxa, including fish, amphibians, reptiles and mammals, show a significant increase (threefold) in metabolic rate during the process of digestion/assimilation (Beamish, 1974; Dumsday, 1990; Brown and Cameron, 1991; Wang et al., 1995). This phenomenon has been termed specific dynamic action (SDA) and appears to be the metabolic cost of digestion and its associated processes. To support the increase in metabolic rate and to facilitate the uptake and distribution of absorbed nutrients, changes in cardiac output and vascular distribution also occur during the digestive process. In general, heart rate and cardiac output increase after ingestion of a meal and remain elevated for a period of hours in most species (Dumsday, 1990; Wang et al., 1995). There is also a redistribution of blood towards the digestive system, which functionally supplies the increased oxygen demand of the active digestive tissues as well as supporting the process of nutrient uptake and dispersal (Axelson and Fritsche, 1991).

Food ingestion also stimulates metabolism in a number of crustacean species (Wallace, 1973; Newell et al., 1974; Hiller-Adams and Childress, 1983; Carefoot, 1987, 1990; Houlihan et al., 1990; Burggren et al., 1993; Hervant et al., 1997). The rate of oxygen uptake increases as soon as food is ingested (Burggren et al., 1993), but reaches a maximal level in *C. maenas* 2.5–4 h (Houlihan et al., 1990) and in terrestrial crabs 4–10 h (Burggren et al., 1993) after feeding. The rate of oxygen uptake declines slowly thereafter, but remains elevated for a number of days after feeding (Wallace, 1973; Houlihan et al., 1990; Burggren et al., 1993), which reflects the increased use of energy in protein synthesis (Houlihan et al., 1990). Lobsters (*Homarus americanus*) exposed to yeast extract or peptone exhibit dramatic changes in heart rate and arterial blood flow patterns, and anterior aortic and sternal blood flow increase by at least 50 % (C. L. Reiber and B. R. McMahon, unpublished data). However, changes in heart rate, stroke volume and cardiac output have not been documented during feeding in crustaceans, nor have distributional changes in blood flow patterns.

The aim of the present study was to follow the passage of a meal over time through the digestive system of *C. sapidus* and to relate this to specific changes occurring in the cardiovascular and respiratory physiology of this crab.

Materials and methods

Adult male and female blue crabs (*Callinectes sapidus* Rathbun) of 12–14 cm carapace width (170–220 g) were obtained from Gulf Specimens, Panacea, Florida, USA. They were kept in a recirculating artificial seawater system (Instant Ocean) at an osmolality of 1000–1050 mosmol kg^{-1} (100 % sea water) and a temperature of 20 °C. Crabs were fed clams or fish twice weekly, but were starved prior to each experiment to ensure that each animal was in a similar physiological state.

Food clearance rates

Crabs that had been starved for 3 days were held in small tanks in which feeding of individual animals could be monitored. Fish and clams were liquified in a blender, and barium sulphate was added (15 % by mass); agar was added to the mixture to produce a gel feed. Crabs were fed approximately 5 cm^3 of the food and allowed to eat until satiated. At set time intervals thereafter, four crabs were flash-frozen in liquid nitrogen. Crabs were X-rayed in the Radiology Department at the University of Nevada – Las Vegas. For radiography of the specimens, a Schimadzu single-phase radiographic unit with a 500 mA, 125 kVp generator was used. The technical factors for employed exposures were 100 mA (small focal spot), 0.12 s and 58 kVp.

Cardiovascular variables

A pulsed-Doppler flowmeter was used to measure heart rate and haemolymph flow rates in each of the five major arterial systems leaving the heart (Fig. 1). Doppler probes were either implanted in grooves abraded in the carapace directly above each artery or guided to lie adjacent to the artery *via* catheter-mounted probes. The probes were manoeuvred to obtain a maximal signal and were held in place with dental wax and superglue. Details of this experimental procedure and calibration of the pulsed-Doppler flowmeter are given elsewhere (Airriess et al., 1994; Reiber et al., 1997). Summation of arterial flows (flow in paired arteries was doubled) gave a value for cardiac output, and division of this value by heart rate yielded the stroke volume of the heart.

During experiments, crabs (N=10) were held in a covered circular glass tank (diameter 28 cm, 30 cm deep) with recirculating aerated sea water (Instant Ocean 1000–1050 mosmol kg^{-1}) at a temperature of 18–20 °C. The tank was filled with sand to a depth of approximately 5 cm. Crabs had their chelae loosely banded during experiments; this did not hamper their use during feeding, but did prevent them from removing the probe implants. Crabs were monitored for 5 min intervals every 15 min for a 4 h control period. A small amount of fish (approximately 5 cm^3) was then added, and the crabs were then monitored for a further 24 h. Experiments were carried out in constant dim light, and the results were recorded on Sable Systems data-acquisition package. After the experiments, the crabs were dissected for measurement of arterial diameter and verification of the positioning of probe implants.

One-way repeated-measures analysis of variance (ANOVA) followed by least significant difference (LSD) pairwise comparison tests were used to test for significance in the data sets.

Rates of oxygen consumption ($\dot{M}_{O_2}$)

A flow-through respirometer was used to measure oxygen consumption rates before, during and after feeding in eight crabs that had previously been starved for 3 days. Crabs were held in a sealed cylindrical respirometry chamber (diameter 22 cm, depth 30 cm; volume 10 l) with a stirbar in the bottom to ensure equal mixing of the water in the chamber. A header tank of aerated filtered sea water at 20 °C (considered as saturated with oxygen) was pumped through the chamber at a measured rate by a peristaltic pump (Cole Parmer Instruments). The oxygen content of the outflow from the chamber was monitored using a blood gas meter (Cameron Instruments Co.), and oxygen uptake was determined by subtracting this value from the oxygen level in the header tank (taking into account the water flow rate through the chamber). Any microbial respiration from faeces or uneaten food was assumed to be negligible: after removal of the crab from the chamber, oxygen levels were monitored for 2 h, at which time they had returned to pre-experimental levels. Crabs were left to settle in the chamber for 12 h, and recordings were carried out at 30 min intervals for 4 h. A small amount of food was then introduced through a permanently fitted tube inside the respirometer, and recording was carried out for a further 24 h. The respirometer was covered by a black plastic sheet to minimize disturbance to the animals.

Results

Crabs fed for 10–15 min, the food being passed quickly through the oesophagus into the stomach, seen as the heart-shaped area in the anterior region of the crab (Fig. 2A). After 1–2 h, small amounts of food material had started to move into the midgut region. Over the next 4 h, food moved through the

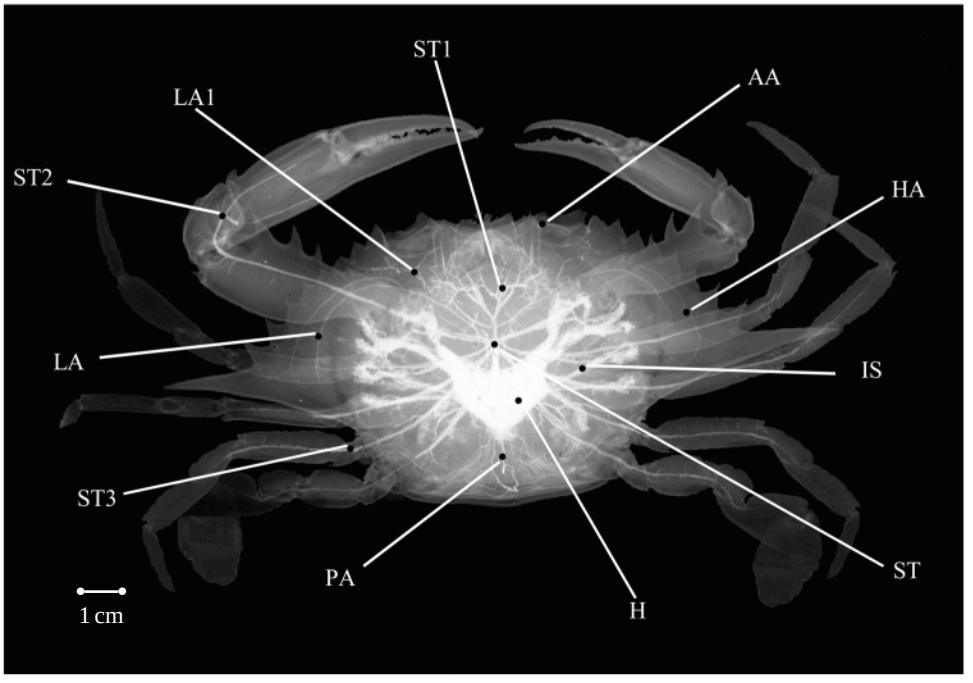
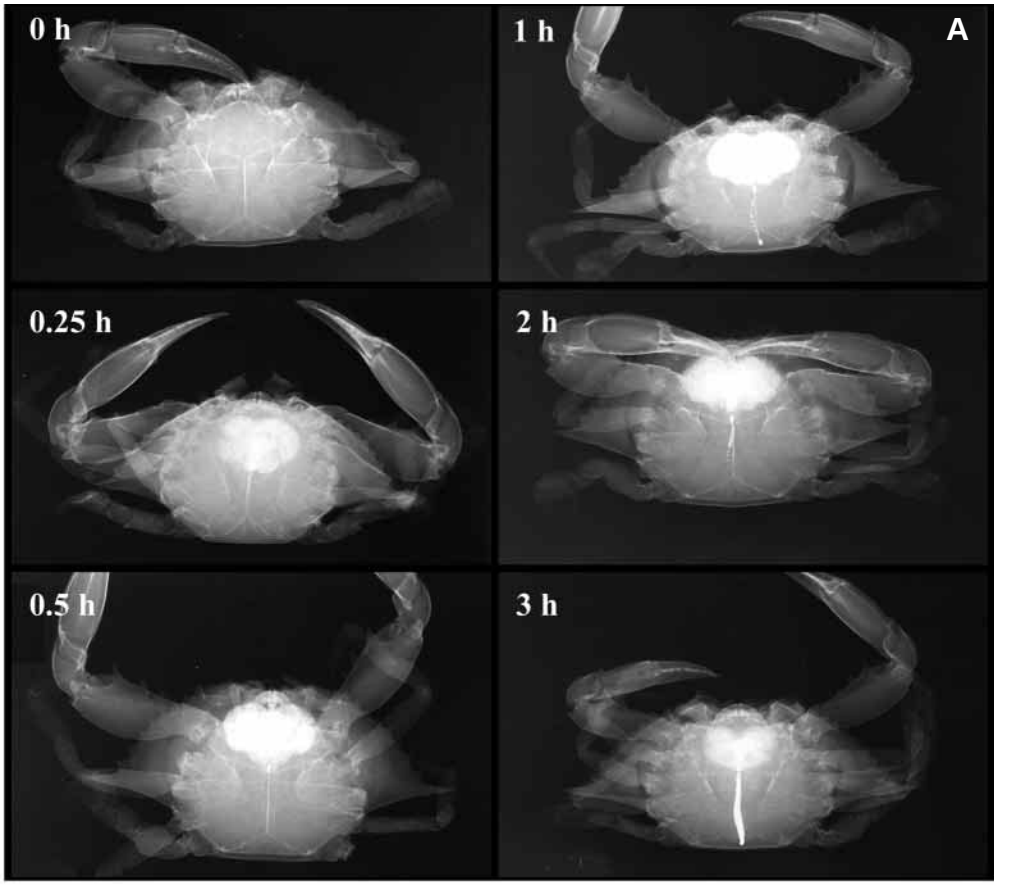


Fig. 1. The cardiovascular system of *Callinectes sapidus* showing the major arteries and venous return system after injection of a barium sulphate solution into the heart. AA, anterior aorta; LA, LA1, left anterolateral artery; HA, right hepatic artery; PA, posterior aorta; ST, ST1–ST3, sternal artery; IS, infrabranchial sinus; H, heart.



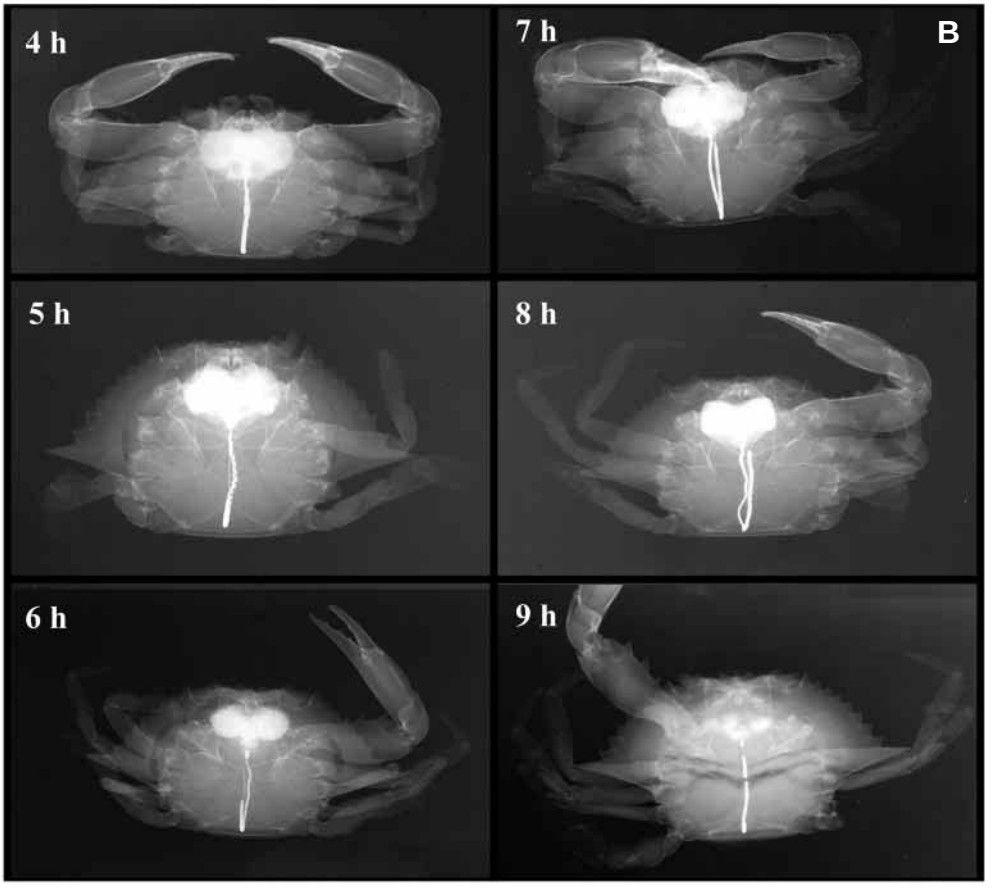
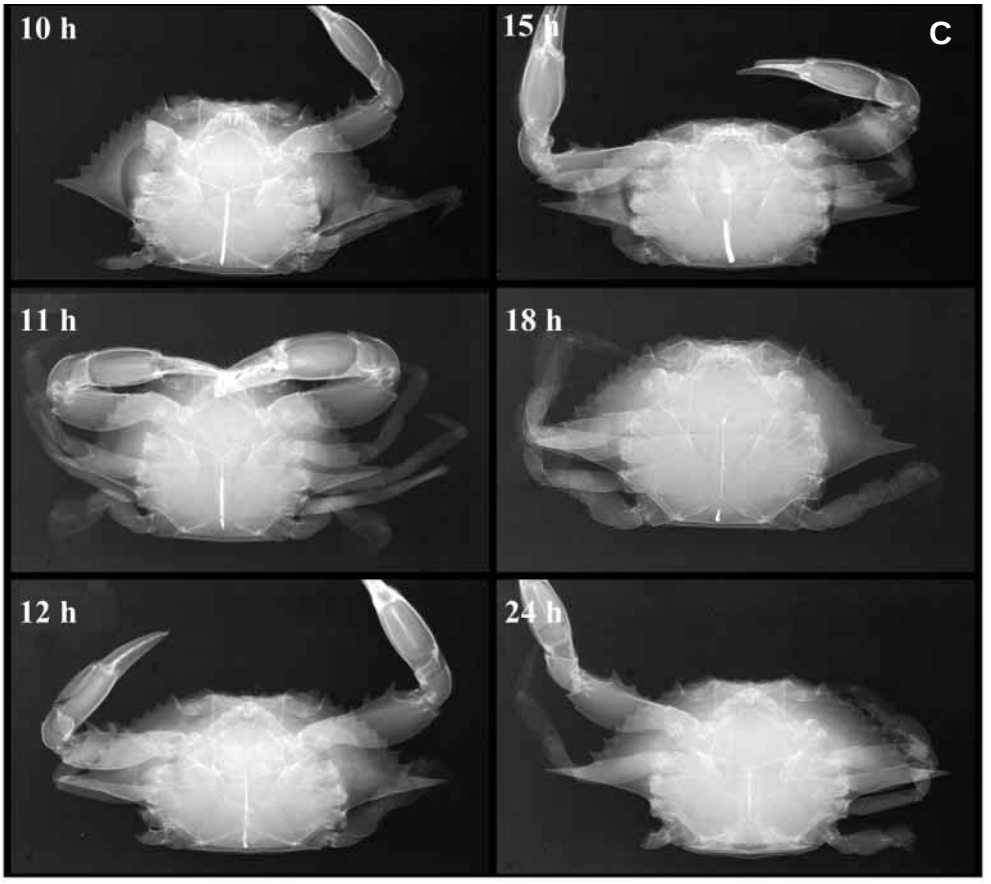


Fig. 2. (A–C) X-ray photographs showing the time of passage of a barium meal through the gut system of *Callinectes sapidus* (12–14 cm carapace width). Time after food ingestion is shown in the top left-hand corner. Food is seen in the heart-shaped stomach area at 0.25 h, appears as fine threads in the midgut after 1–2 h and is first visible in the hindgut region at 6 h. The stomach starts to empty at 9 h, and the digestive system is emptied after 18 h.



midgut, although there was still food in the stomach (Fig. 2B). At 6 h, material started to empty into the hindgut, and it continued moving along the abdomen towards the anus over the following 2 h (Fig. 2B). Food was still evident in the stomach and midgut region at this time (Fig. 2B). Depending on the individual animal, the stomach was completely emptied between 8 and 10 h, with food still visible in the midgut. Food was not seen in the midgut region after 10 h, but was still passing through the hindgut at this time and continued along length of the hindgut region between 10 and 15 h. The digestive system was emptied completely at approximately 18 h (Fig. 2C).

The heart rate of *C. sapidus* increased significantly as soon as food was detected and during feeding (F=5.95, P<0.0001) and reached a maximal mean value of 125 beats min^{-1} 45 min after ingestion of food (Fig. 3A). Heart rate declined steadily thereafter, but remained significantly elevated above pre-feeding levels for 16–18 h after ingestion of food (Fig. 3A). The changes in stroke volume of the heart were more variable (Fig. 3B). There was a slight, sustained increase in stroke volume after feeding, with a short-term decrease occurring between 8 and 12 h. However, these changes were small and proved not to be statistically significant (F=1.08, P>0.05). The total cardiac output increased in a similar fashion to heart rate, rising from control levels of 22–28 ml min^{-1} and reaching maximal values of 40 ml min^{-1}, 1 h after feeding (Fig. 3C). With the exception of a transient decrease between 8 and 12 h after feeding, cardiac output remained significantly elevated (F=3.18, P<0.0001) above pre-feeding levels until the end of the experimental period.

Changes in haemolymph flow rate through each artery also occurred during and after feeding, the magnitude and duration of which differed for each arterial system (Fig. 4). Haemolymph flow rates through the anterior aorta remained fairly constant (Fig. 4A), with mean values of approximately 1.8±0.6 ml min^{-1} (mean ± S.E.M., N=10), and there was no significant change in flow rates during or after feeding (F=1.29, P>0.05). There was a significant increase in haemolymph flow through the anterolateral arteries (Fig. 4B) (F=2.65, P<0.000). Flow rates increased steadily from approximately 0.7 ml min^{-1} and reached a maximal value of 1.2 ml min^{-1} 6 h after feeding. There was a steady decline thereafter, with flow rates reaching levels that were not significantly different from control rates 10 h after food ingestion. Haemolymph flow through the hepatic arteries (Fig. 4C) increased rapidly (F=2.64, P<0.0001), and maximal flow rates of 3 ml min^{-1} were achieved within 45 min after feeding. After this initial increase, flow rate decreased, but still remained elevated over pre-feeding levels for a further 8 h. Although there was a slight increase in flow through the posterior aorta after feeding, this change proved not to be statistically significant (Fig. 4D) (F=1.27, P>0.05). The greatest increase in haemolymph flow occurred through the sternal artery (Fig. 4E). Mean pre-treatment flow rates varied between 17 and 20 ml min^{-1}. There

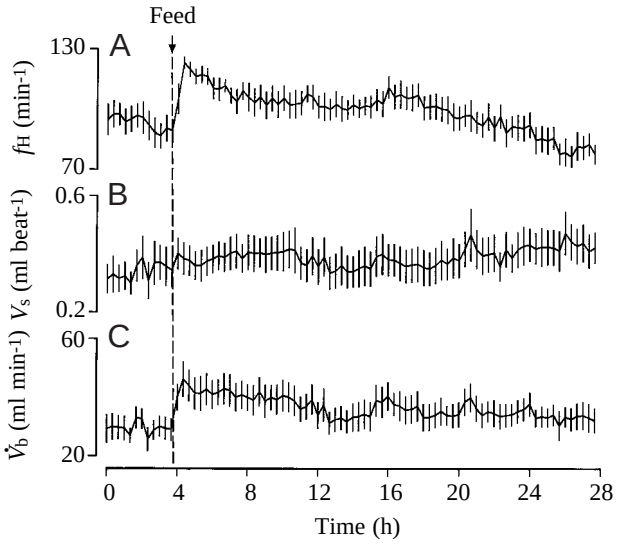


Fig. 3. (A) Heart rate (f_H; beats min^{-1}), (B) stroke volume of the heart (V_S; ml beat^{-1}) and (C) cardiac output ($\dot{V}_b$; ml min^{-1}) of 10 *Callinectes sapidus* monitored during a 4 h control period and for 24 h after feeding. Values are means ± S.E.M. The beginning of the 10–15 min feeding period is marked.

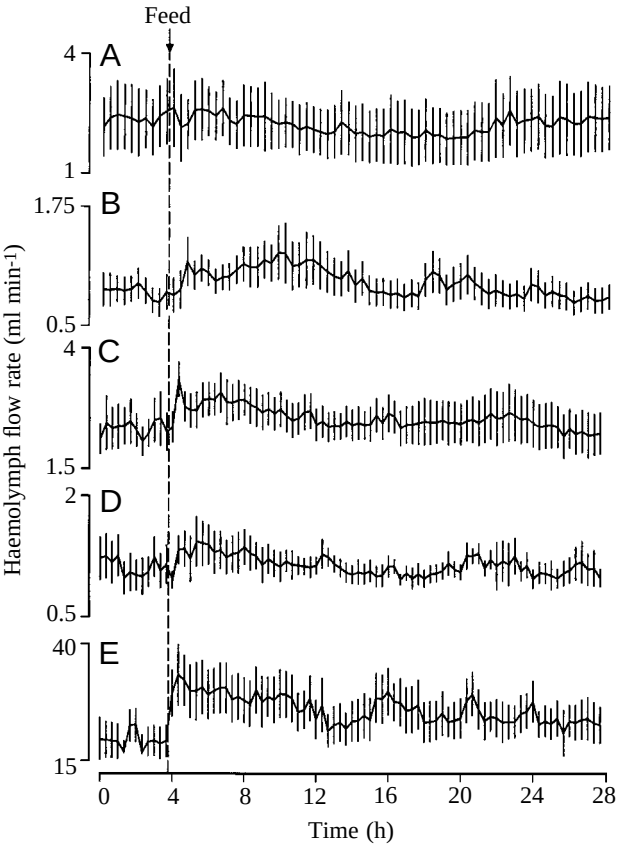


Fig. 4. Haemolymph flow rates (ml min^{-1}) through (A) the anterior aorta, (B) the left anterolateral artery, (C) the right hepatic artery, (D) the posterior aorta and (E) the sternal artery of 10 *Callinectes sapidus* during a 4 h control period and for the 24 h post-feeding period. Values are means ± S.E.M. The beginning of the 10–15 min feeding period is marked.

was an immediate and significant increase in haemolymph flow through this vessel when food was introduced into the tank (F=2.68, P<0.0001). Maximal mean values of 33±10 ml min^{-1} (mean ± S.E.M., N=10) were reached 30 min after feeding, and flow through this artery remained elevated at approximately 30 ml min^{-1} for 8 h. Flow decreased between 8 and 12 h after feeding to levels that were not significantly different from control flows. However, this decrease was only transient, and flow rate increased again after 12 h and remained significantly elevated above pre-feeding values for up to 24 h after the introduction of food.

There was also a large increase in the rate of oxygen consumption ($\dot{M}_{O_2}$) during and after feeding (Fig. 5). At rest, $\dot{M}_{O_2}$ varied between mean levels of 50 and 58 μmol kg^{-1} min^{-1}. $\dot{M}_{O_2}$ doubled when the crab was fed (F=12.56, P<0.0001). The increase was slower than that for the cardiovascular variables: maximal mean levels of 115 μmol kg^{-1} min^{-1} were reached approximately 4 h after feeding, and these levels were sustained for a total period of 24 h. $\dot{M}_{O_2}$ declined slowly after 20 h, but remained elevated above pre-feeding levels for 40–50 h after feeding (results not shown).

Discussion

In contrast to previous studies (Elner and Hughes, 1978; Haddon and Wear, 1987), the time for passage of food through the gut of *Callinectes sapidus* was fairly uniform between individual crabs. Experiments were carried out at a set temperature, and only crabs with carapace widths of 12–14 cm were used, thus reducing some of the possible sources of intraspecific variation (Haddon and Wear, 1987).

Food appeared in the stomach after 15 min (Fig. 2A). The paddle crab *Ovalipes catharus* can take as little as 15 s to fill its stomach (Haddon and Wear, 1987). After 1–2 h, material was visible in the midgut (Fig. 2A); similar values were reported for *Metapenaeus bennettae* (Dall, 1967), *Scylla serrata* (Hill, 1976) and *Cancer pagurus* (D. Grove, unpublished results). The finger-like midgut caeca do not appear in the X-ray photographs (Fig. 2): neither food particles (Dall, 1967) nor inert material (Smith, 1978) is found in this region because it is filtered out by setae (Dall, 1967). The material continues its passage along the midgut of *C. sapidus*, reaching the hindgut after approximately 6 h (Fig. 2B). The first faeces appear wrapped in a peritrophic membrane at approximately 6 h, which is somewhat faster than other reports of 5–8 h for *M. bennettae* (Dall, 1967), 8 h for *Carcinus maenas* (Hopkin and Nott, 1980) and 15 h for *Liocarcinus* spp. (Choy, 1986). This is probably due to differences in both experimental temperature and food type as well as to interspecific differences (Haddon and Wear, 1987).

The stomach of *C. sapidus* was emptied between 8 and 10 h after feeding (Fig. 2C). This is longer than the 3–6 h reported for *O. catharus* at comparable temperatures (Haddon and

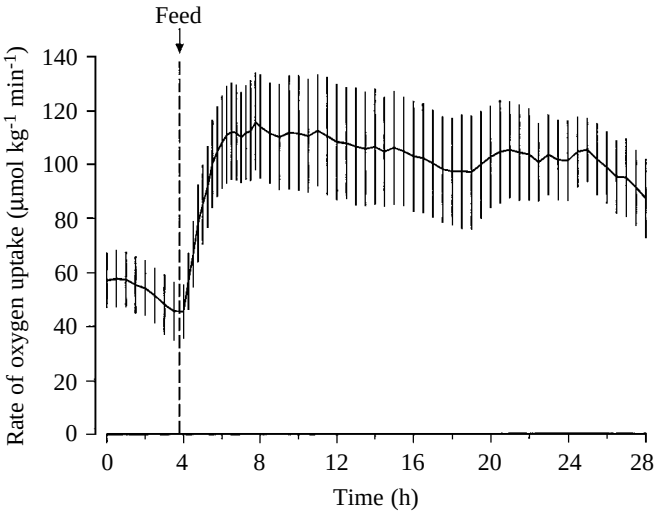


Fig. 5. Rates of oxygen uptake ($\mu mol\,kg^{-1}\,min^{-1}$) of eight *Callinectes sapidus* during a 4 h control period and for the 24 h post-feeding period. Values are means ± S.E.M. The beginning of the 10–15 min feeding period is marked.

Wear, 1967), similar to stomach clearance rates of *M. bennettae* (Dall, 1967) and *S. serrata* (Barker and Gibson, 1978) and somewhat shorter than the 12 h reported for *C. maenas* (Hopkin and Nott, 1980) and 20 h for *L. puber* and *L. holsatus* (Choy, 1986). The entire gut system of *C. sapidus* was emptied between 18 and 24 h (Fig. 2C). Again, there is much discrepancy between species: *S. serrata* (Barker and Gibson, 1978), *Nephrops novergicus* (Sarda and Valladares, 1990) and *Panulirus cygnus* (Joll, 1982) all take approximately 12 h to empty the entire gut, whereas the gut of *M. bennettae* is emptied at 12–20 h (Dall, 1967) and that of *C. maenas* between 24 and 48 h (Hopkin and Nott, 1980).

The presence of 15 % barium sulphate in the feed appeared to have no effect on the time of movement of material through the gut system. Both the barium meal and a fish and agar meal were voided in the initial faecal strand at similar mean times of 6 h (S.E.M.=1.73, N=15) and 6.17 h (S.E.M.=1.90, N=15), respectively (Student's t-test, P=0.81).

The cardiovascular system of decapod crustaceans consists of a single-chambered heart suspended within a second chamber, the pericardial sinus, by 11 suspensory ligaments. Five arterial systems (seven arteries) leave the heart to supply distinct body regions (Pearson, 1908). These branch into fine capillary-like vessels that empty into tissue lacunae. Haemolymph then drains into the infrabranchial sinus before passing through the gills and back to the lateral pericardial sinus. Each main artery has a muscular innervated valve at its origin, and contraction or relaxation of these valves aids in selective organ perfusion (Alexandrowicz, 1932). A number of peptide neurohormones are known to control cardiac function and modulate haemolymph flow in intact crabs (Airriess and McMahon, 1992; McGaw et al., 1994a, 1995; McGaw and McMahon, 1995, 1999).

The heart rate of *C. sapidus* increased as soon as the food was detected and reached maximal levels approximately 45 min after food ingestion (Fig. 3A), reflecting the greater metabolic demand involved in mechanical handling of the food and digestion. Heart rate returned to pre-feeding levels after 16–18 h (Fig. 3A), which was close to the time when the gut was emptied (Fig. 2C). The stroke volume of the heart was essentially unaffected (Fig. 3B). Therefore, changes in total cardiac output were largely driven by changes in heart rate (Fig. 3C). Changes in heart rate have previously been reported to determine cardiac output in portunid crabs (Spaargaren 1974, 1976, 1982; McMahon et al., 1996; McGaw and Reiber, 1998), whereas stroke volume has a greater effect in cancrid crabs (McGaw et al., 1994b; McGaw and McMahon, 1996). Cardiac output remained significantly elevated over pre-treatment levels for the duration of the experimental period (Fig. 3A). An increased cardiac output ultimately leads to an increased gill blood flow, aiding an increase in the rate of oxygen uptake (Carefoot, 1987, 1990; Houlihan et al., 1990; Burggren et al., 1993; Fig. 5). We are aware of no other reports of cardiovascular changes during feeding in invertebrates. In addition, there are only limited data dealing with cardiovascular dynamics during feeding in the lower vertebrates. Heart rate increases in the toad *Bufo marinus* (Dumsday, 1990; Wang et al., 1995), and gut blood flow increases in the Atlantic cod *Gadus morhua* (Axelson and Fritsche, 1991) after a meal. These increases in heart rate are thought to support the increased metabolic demand resulting from specific dynamic action as well as food handling and nutrient transport.

There were also differential changes in haemolymph flow through each arterial system (Fig. 4). The anterior aorta supplies the eyestalks, supraoesophageal ganglion, antennae and antennules (Pearson, 1908; McLaughlin, 1983). The antennules of crabs are known to have a chemosensory role in prey detection (Rittschoff, 1992), and an increased flicking rate allows the animal to locate food items (Rebach et al., 1990). However, in the present study, there was no change in blood flow in the anterior aorta (Fig. 4A). Food was detected almost immediately, so that any changes in blood flow were probably of too short a duration to be detected.

The paired anterolateral arteries arise anteriorly from the heart, and branches of these arteries supply some of the muscles of the mandibles, the muscles surrounding the cardiac stomach and portions of the midgut (Pearson, 1908). Haemolymph flow in the anterolateral arteries increased after approximately 1 h and remained elevated for 10 h (Fig. 4B). There was no immediate increase in flow through the anterolateral arteries related to mastication of food by the mandibles. This can be explained by the fact that the sternal artery, rather than branches of the anterolateral arteries, is the major artery supplying the mandible muscles. An increased blood flow to the muscle surrounding the cardiac stomach would aid contraction, forcing food into the midgut region. There was a close correlation between emptying of the stomach at 8–10 h (Fig. 2C) and a decreased flow through the anterolateral arteries thereafter (Fig. 4B).

The hepatic arteries are the main arteries supplying the hepatopancreas (Pearson, 1908; McLaughlin, 1983), dividing profusely into small capillary-like vessels within this organ. Flow through these paired vessels increased significantly 45 min after feeding and remained elevated for 8 h (Fig. 4C). Digestion by the hepatopancreas begins within 0.5–1 h after feeding (Dall, 1967; Barker and Gibson, 1978; Hopkin and Nott, 1980), which corresponds closely with the increase in blood flow at this time (Fig. 4C). Although intracellular digestion can continue for up to 48 h (Hopkin and Nott, 1980), most extracellular digestion in *M. bennettae* and *S. serrata* occurs within 8 h (Dall, 1967; Barker and Gibson, 1978) and in *C. maenas* is largely complete within 12 h (Hopkin and Nott, 1980). Therefore, the total time (8 h) of increased perfusion of the hepatic arteries appears to correlate with the period of digestion. In addition to the hepatic arteries, branches of the anterolateral arteries supply the dorsal regions of the hepatopancreas (Pearson, 1908), and the time frame of increased perfusion of these vessels was similar (Fig. 4B).

The small posterior aorta perfuses the posterior midgut caecum as well as regions of the hindgut and muscles of the abdomen (Pearson, 1908). Flow in this small vessel is sporadic and often low (McGaw et al., 1994b; McGaw and Reiber, 1998), which may have led to our failure to detect any significant changes in flow (Fig. 4D).

The sternal artery primarily supplies the chelae and legs and muscles of the mandibles. The immediate and large increase in flow through this vessel (Fig. 4E) is due to use of the chelae to manipulate food and tearing of food by the mandibles. However, crabs only fed for approximately 15 min and, with the exception of a transient decrease between 8 and 12 h, flow through the sternal artery remained elevated for the experimental period (Fig. 4E). Branches of the sternal artery also supply the hepatopancreas and the muscles surrounding the gut (Pearson, 1908). It would therefore appear that additional perfusion of these structures accounts for the persistent elevated flow in this vessel.

A postprandial increase in the rate of oxygen consumption is termed specific dynamic action (SDA) or, more correctly, apparent SDA (Beamish, 1974), and this includes the metabolic costs of food handling and transport of material through the gut. In the present study, *C. sapidus* only fed for a short time (15 min), and mechanical costs resulting from ingestion of indigestible material in crustaceans accounts for 5–8 % of apparent SDA (Carefoot, 1987, 1990). Feeding and transport of food through the gut are therefore thought to have a negligible effect on SDA (Carefoot, 1990). The respirometer in the present study was covered with a black plastic sheet; increases in oxygen uptake due to 'investigator disturbance' (Carefoot, 1990) were considered to be negligible.

The rates of oxygen consumption (Fig. 5) agree closely with those reported previously for *C. sapidus* (Mangum and Weiland, 1975). The rate of oxygen consumption doubled following feeding (Fig. 5), and maximal levels were reached 4 h after ingestion of food. As for the timing of food movement through the gut, there are interspecific differences in rates of oxygen consumption following a meal. In *C. maenas*, $\dot{M}_{O_2}$ increases by 44 % (Wallace, 1973) or up to 2.3-fold (Houlihan et al., 1990), and a peak increase in $\dot{M}_{O_2}$ of 150 % was recorded in the isopod *Ligia pallasii* (Carefoot, 1990), whilst the rate of oxygen uptake increased 2.5-fold in the terrestrial crabs *Cardiosoma guanhumi* and *Ocypode quadrata* (Burggren et al., 1993). Differences between studies can be accounted for by spontaneous activity in some animals (Burggren et al., 1993), by differences in fasting period and feeding rates (Ansell, 1973; Wallace, 1973; Aldrich, 1975) or by differences in diet (Carefoot, 1987). The time course for maximal $\dot{M}_{O_2}$ in *C. sapidus* (Fig. 5) is similar to that of other crab species (Houlihan et al., 1990; Burggren et al., 1993), reflecting the start of extracellular digestion within the hepatopancreas. The rate of oxygen consumption declined slowly in *C. sapidus* after the 4 h postprandial peak and remained elevated over pre-feeding levels for up to 40–50 h (not shown). A similar period of elevation has been observed in other crustaceans (Wallace, 1973; Burggren et al., 1993), reflecting the use of oxygen in intracellular digestion (Hopkin and Nott, 1980) and protein synthesis (Houlihan et al., 1990).

The present study is the first detailed account of cardiovascular changes in an invertebrate system during feeding. Ingestion of a meal resulted in a doubling of metabolic rate in the blue crab, which was sustained for approximately 50 h after feeding (Fig. 5). Cardiovascular changes were of a shorter duration and may be related to increased activity during feeding. Haemolymph flow distribution to different gut regions during the passage of food through the digestive system reflects the specific regional demands and may aid digestive processes.

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