

**ARE FISH PRIMARILY STROKE VOLUME-MODULATORS? NOT  
ACCORDING TO CENTRARCHIDS**

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**Abstract**

In most animals, physical or chemical stressors usually elicit an increase in metabolic rate and consequently an increase in cardiac output and one or both of its components, heart rate and stroke volume. While mammals and birds primarily increase cardiac output through the elevation of heart rate (frequency modulation), fish are generally thought to increase cardiac output principally through changes in stroke volume (volume modulation). It has even been suggested that among vertebrates there is an evolutionary trend from volume-modulated to frequency-modulated cardiac output. Within fish, only a few species have been regarded as frequency-modulators including the highly active tuna and the Antarctic nototheniids. In an effort to expand our comprehension of cardiac function in fish, we collected data on several species from two common families, Salmonidae and Centrarchidae, under various conditions. Our preliminary findings indicate that frequency modulation is more prevalent than previously thought especially among centrarchids.

## Introduction

Recovery from burst exercise, specifically dealing with oxygen debt and lactate clearance, results in an increased metabolic rate and consequently an increase in cardiac output (CO) and one or both of its components, heart rate (HR) and stroke volume (SV) (Farrell and Jones, 1992). While mammals, birds, reptiles, and amphibians primarily increase CO by elevating HR (i.e., frequency modulation), fish are unique among vertebrates increasing CO primarily through the elevation of SV (i.e., volume modulation) (Farrell, 1991; Farrell and Jones, 1992; Thorarensen et al., 1996). The highly active and evolutionarily advanced tuna have typically been considered the main exception, increasing HR by 2-fold over resting values (Farrell, 1991). Consequently, it has been suggested that there is an evolutionary trend from volume-modulated to frequency-modulated CO in fish (Farrell, 1991). However, recent work in our laboratories has demonstrated that frequency modulation among fish may not be as rare as previously thought.

## Methods

We exposed fish to various perturbations that resulted in increased metabolic rate and therefore elevated CO. Our test subjects were fish from several species within the families Salmonidae and Centrarchidae. Brown trout (*Salmo trutta*), Atlantic salmon (*Salmo salar*), largemouth bass (*Micropterus salmoides*), and rock bass (*Ambloplites rupestris*) were chased by hand to elicit burst swimming for 30 to 150 sec and until the fish was completely fatigued (non-responsive, loss of equilibrium) (see Cooke et al., 2001). Immediately following this event, fish were exposed to air for 10 sec to 10 min. The centrarchids were held by the lower lip and supported on the ventral surface while salmonids were held out of water in a wetted sling. Rainbow trout (*Oncorhynchus mykiss*) were electroshocked at various settings for 2 to 32 sec. Smallmouth bass (*Micropterus dolomieu*) were swum in a Blazka-type respirometer and exposed to elevated velocities to elicit burst swimming for 20 to 180 sec and until the fish would no longer swim and/or had lost equilibrium (see Schreer et al., 2001).

Detailed descriptions of surgical procedures and general measurement theory are provided in Schreer et al. (2001). Briefly, in all cases fish were anesthetized and a flexible silicone cuff-type Doppler flow probe (subminiature 20 MHz piezoelectric transducer: Iowa Doppler Products, Iowa City, IA, USA) was placed around the ventral aorta. Cardiac output was monitored and recorded by

a hard-wired flowmeter (545C-4 Directional Pulsed Doppler Flowmeter: Bioengineering, The University of Iowa, Iowa City, IA, USA) and a digital strip-chart recorder (LabVIEW, Version 4.0.1, National Instruments Corporation, Austin, TX, USA). Cardiac output was calculated by averaging the flow index per unit time and HR was determined by counting peaks. The quotient of CO divided by HR yielded SV. Where possible, actual flow rates were calculated directly through a postmortem calibration. Following surgery fish were allowed to recover for at least 12 hr. Blood flow was monitored for at least 1 hr prior to experimentation and for at least 5 hr following the perturbation.

## Results and Discussion

There is no simple answer to the question of whether fish are primarily volume-modulators. Salmonids are perhaps the most well studied family of fish and our studies on various salmonids indicate that indeed most species are volume-modulators (Figure 1).

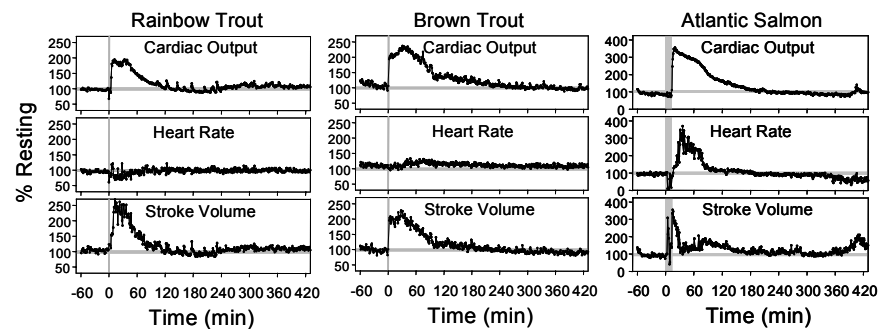


Figure 1. Example cardiac traces for salmonids exposed to various perturbations. All values are percent resting (100%) and the perturbation always begins at time 0. The grey lines indicate the approximate duration of the perturbation (vertical) and the 100% resting value (horizontal). The rainbow trout was held at 12°C and electroshocked with a pulsed DC electrofisher for 8 sec at 100 V, 80-8 Hz (frequency decreased over 2 sec), and 2 ms (pulse width). The brown trout was held at 12°C, chased by hand for 1 min, and exposed to air in a wetted sling for 10 sec. The Atlantic salmon was held at 5°C, chased by hand for 1 min, and exposed to air in a wetted sling for 10 min.

However, among the centrarchids, frequency modulation is apparently quite common (Figure 2). This puts centrarchids in the same company as tuna and Antarctic nototheniids (Farrell, 1991; Farrell and Jones, 1992; Farrell, 1996). In the tuna frequency modulation has been explained by their high activity levels with standard metabolic rates approaching that of mammals (Farrell, 1991). As well, tuna, like mammals, have large ventricles that can beat faster and may have relatively fixed stroke volumes which are normally near maximum values (Farrell, 1991). Similarly, Antarctic nototheniids also have large ventricles and high stroke volumes at resting levels (Farrell, 1996). Centrarchids are generally an active group of fish (above  $\sim 10^{\circ}\text{C}$ ), but their activity levels are still not comparable to that of tuna. It has been hypothesized that frequency modulation (in addition to a suite of other physiological and anatomical adaptations, e.g. coronary circulation) in centrarchids may have evolved in concert with parental care provided by the males (Cooke, *unpublished data*). This type of cardiac control may allow centrarchids to provide protracted and heightened care to developing offspring and to respond quickly to predator threats.

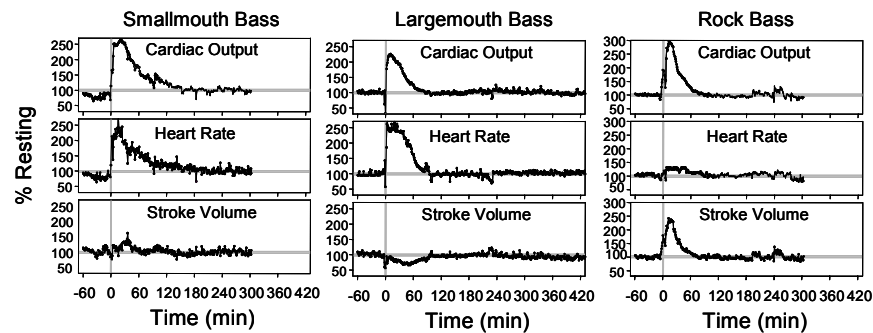


Figure 2. Example cardiac traces for centrarchids exposed to various perturbations. All values are percent resting (100%) and the perturbation always begins at time 0. The grey lines indicate the approximate duration of the perturbation (vertical) and the 100% resting value (horizontal). The smallmouth bass was held at  $12^{\circ}\text{C}$  and exposed to a series velocity burst for 3 min in a Blazka-type respirometer. The largemouth bass and the rock bass were held at  $16^{\circ}\text{C}$ , chased by hand for 150 and 30 sec, and exposed to air for 150 and 30 sec, respectively.

It is important to note, however, that even within a family of fish or within a specific experiment, results are not always consistent. Atlantic salmon have been shown to increase HR only slightly following angling (Anderson et al., 1998) which is consistent with our results for rainbow trout and brown trout. However, when Atlantic salmon were chased by hand and exposed to air they showed a strong increase in HR (Figure 1). The rock bass were also anomalous among the centrarchids showing very little change in HR (Figure 2). As previously mentioned this may be due to the amount of paternal parental care as rock bass generally provide very little relative to largemouth bass and smallmouth bass (Cooke, *unpublished data*).

In considering trends in the relative contributions of HR and SV to CO it is important to consider the type of stressor. In a limited number of cases, it has been suggested that following anaerobic, burst exercise, increases in CO were due to elevated HR (Lucas et al., 1991; Farrell and Jones, 1992). However, HR in electroshocked rainbow trout and in brown trout chased and exposed to air increased very little as compared to the >100% increase in HR for smallmouth bass and largemouth bass post-simulated angling (Figure 2). All of these events would likely result in anaerobic activity (Mitton and McDonald, 1994; Kieffer, 2000).

An additional factor to be considered in the interpretation of the relative contributions of HR and SV to increased CO is recovery time following the surgical procedure. In Atlantic cod, *Gadus morhua*, HR remains elevated for up to 8 to 10 days following surgery (Webber et al., 1998). Therefore, if the relative contributions of HR and SV to increases in CO during exercise are examined within this recovery period, elevated post-surgery resting HR values may prevent typical increases in HR from being observed. However, even though all the fish in the present study were only allowed to recover for greater than 12, but less than 24 hr following surgery, considerable increases in HR were observed for several species especially within the centrarchids. Therefore, it is highly unlikely that these fish had abnormally high resting HRs. Further, we have held smallmouth bass and largemouth bass for extended periods of time (1 to 2 weeks) and not observed any further decrease in cardiac parameters after the 12 hr recovery period (Schreer and Cooke, *In press*; Cooke, *unpublished data*).

In conclusion, as with most biological questions, there is no clear answer as to whether fish are primarily volume-modulators. It is important to note that in our studies we have only examined CO, HR, and SV, and not other physiological or

anatomical variables that also play important roles in determining the relative contributions of HR and SV to changes in CO. However, the findings in this study indicate frequency modulation may be more prevalent than previously thought, at least among the centrarchids, and more work is needed to fully describe and understand evolutionary trends in cardiac function.

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