CARDIAC RESPONSES OF FISHES IN ASPHYXIC ENVIRONMENTS[1]

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Many lung-breathing animals are adapted to an aquatic life. Whales, seals, penguins, and crocodiles are representative. Whenever these animals dive and swim submerged, they show marked physiological adjustments (Scholander, 1940; Andersen, 1961). Even though a pronounced bradycardia occurs, a nearly normal blood pressure is maintained. In addition, lactic acid builds up in the muscles and is flushed into the circulation when the animal surfaces and breathes. Analogous to these diving animals are certain species of fish that subject themselves to air. Some fish migrate over land, others spawn out of water, and a few take to the air in order to escape predators. Such animals as the hagfish also encounter asphyxic situations when they bury in the bodies of other vertebrates.

The question arises—do fishes that naturally venture into air exhibit compensatory physiological changes analogous to those found for lung-breathing animals? In the present work a few fishes that subject themselves to an asphyxic condition have been investigated—the beach-spawning grunion, the California flying fish, an air-dwelling mudskipper, and one of the scavenging hagfishes. Since heart frequency is a conspicuous manifestation of an asphyxial response, this parameter has been studied.

Methods

A portable Sanborn Visette electrocardiograph, model 300, proved adaptable for field work. This direct-writing instrument was powered by a Heathkit converter, model PC 1, operating from a storage battery.

Electrodes were made from number 28 stranded plastic-covered wire (Fig. 1). Two slits, 1–3 cm. apart, made in the insulation allow for exposure and removal of the wire between them, leaving a wire electrode protruding from each opening. The fish remains in water as electrodes are threaded through the body wall near the heart (Fig. 1). This method has proved practical in use on teleosts, sharks, rays, and even on writhing mucus-secreting hagfish.

An asphyxial condition was induced by various means. Containers were used to provide alternate flooding and draining for the grunion and the hagfish. The flying fish was lifted from water on a horizontal net, while a wire-mesh enclosure served for the mudskipper. Most of the teleosts and sharks studied remain calm during transitions from water to air, when supported by such a shallow net.

Description and Results

GRUNION (*Leuresthes tenuis*)

In the coastal waters of southern California lives one of the few fish species that lays eggs on land (Walker, 1952). The spawning process occurs on evenings

[1] Contributions from Scripps Institution of Oceanography, New Series.

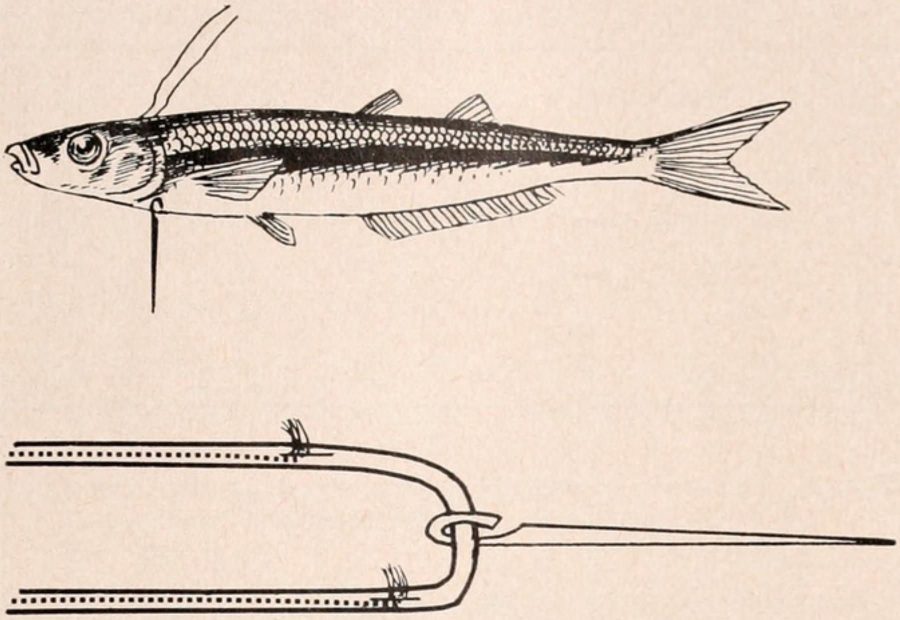

FIGURE 1. (Top) Grunion with inserted electrodes. (Bottom) Enlarged diagram of the electrodes.

following highest spring tides when the grunion ride onto the beach on large waves. As a wave recedes, they swim vigorously, so as to strand themselves high on the beach. By twisting the body the female digs tail-first into the sand, and then lays eggs that are fertilized by nearby males. (These eggs remain undisturbed by water until inundation by high tides about two weeks later causes them to hatch.) Freeing herself from the sand, the spent fish takes a few flops toward the water, or lies until a high wave takes her to sea. A total time of approximately one minute elapses while the grunion's gill chambers are out of contact with water. At times, however, a fish will be stranded out of water's reach for several minutes. This exposure it tolerates well.

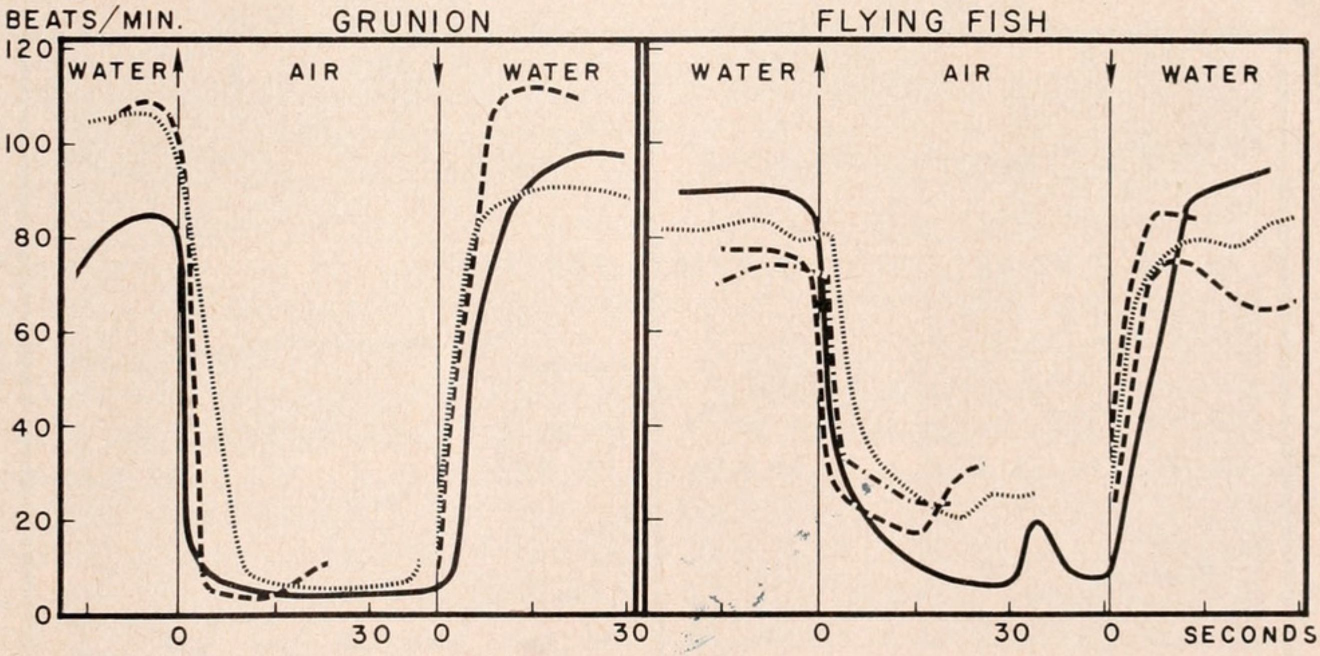

FIGURE 2. Heart rates of grunion and flying fish before, during, and following air exposure. Air exposures terminate at different times but recoveries are synchronized.

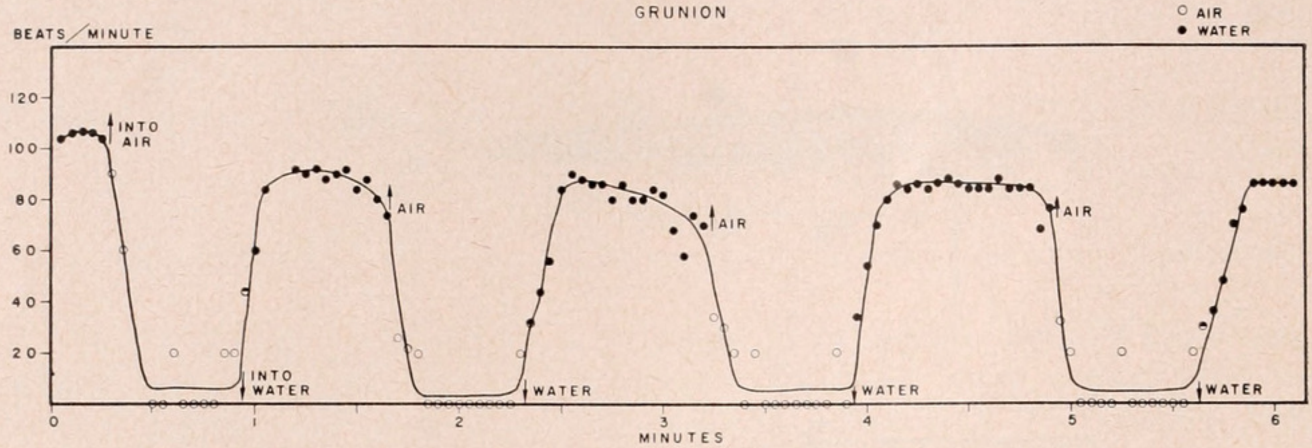

FIGURE 3. Repetitive exposures of a grunion to air. Observations are at three-second intervals.

Grunion, when taken out of water, immediately develop an extreme bradycardia (Fig. 2). The heart rates often slow from more than 100 to fewer than 10 beats per minute. The original, or slightly higher, pace is quickly resumed when the fish are returned to water (Figs. 2, 3). However, prolonged exposures of 5–10 minutes produce slow cardiac recovery. These laboratory results were confirmed by records taken on the beach during spawning.

CALIFORNIA FLYING FISH (*Cypselurus californicus*)

Flying fishes are pelagic plankton feeders that take to the air when pursued by predators. Their flight of as much as 200 yards is initiated by an accelerated take-off ("taxi") and continues as a passive glide. Compound flights, consisting of intermittent glides and tail accelerations, may keep the fish exposed to air for relatively long periods. Hubbs (1933, 1937) observed that the simple flights average about two seconds, although he noted single flights lasting as long as

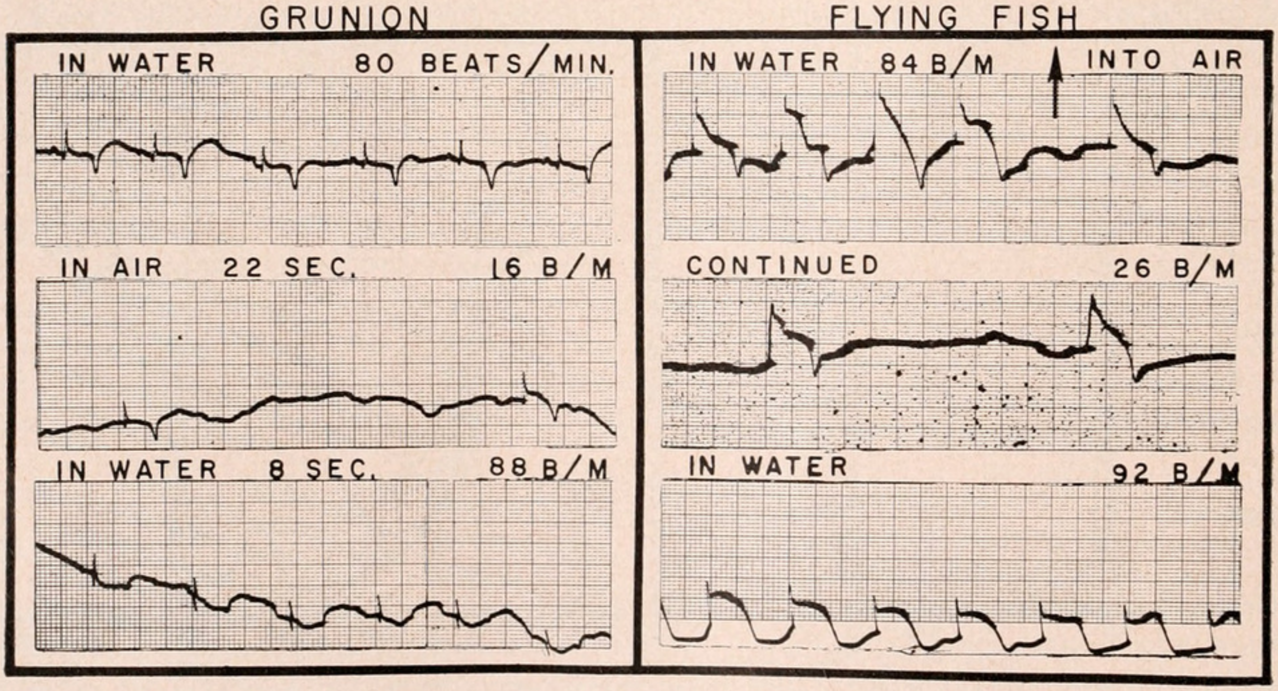

FIGURE 4. Electrocardiograms of grunion and flying fish in and out of water.

13 seconds, and compound flights of 28 seconds. (A flight of 42 seconds has been reported.)

When flying fish are taken out of water a pronounced bradycardia occurs (Figs. 2, 4). This slowdown to one-third of normal continues until submergence initiates a sharp acceleration of rate. Fish swimming in the ocean with attached electrodes displayed similar effects when pulled from the water and returned.

MUDSKIPPER (*Periophthalmodon australis*)

This mudskipper inhabits the brackish and marine mangrove-fringed mudflats of tropic seas in the Australian region. The mudskippers act more like amphibians

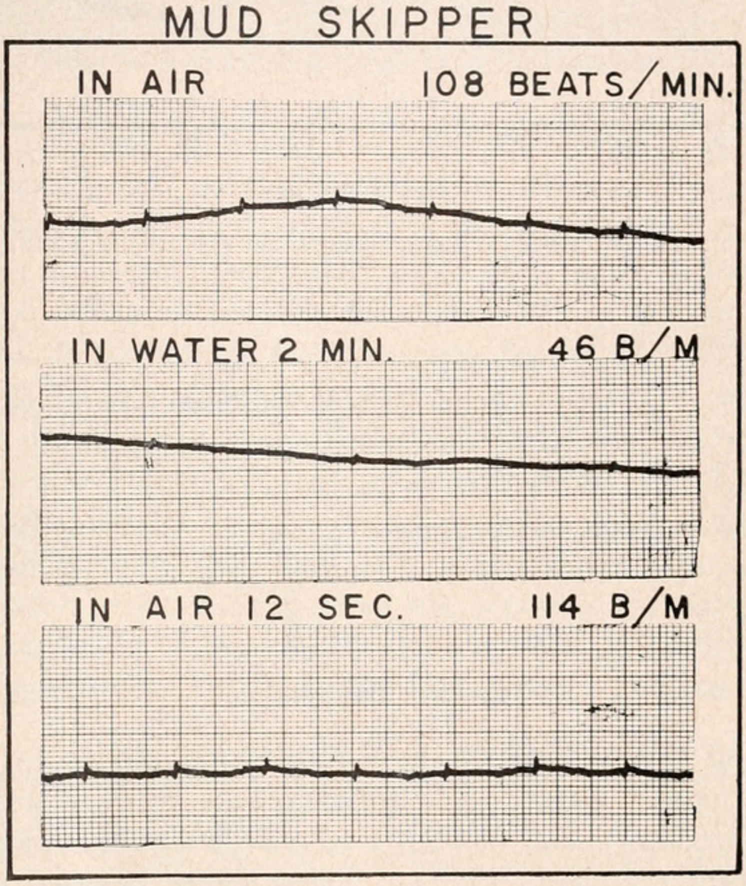

FIGURE 5. Electrocardiogram of a mudskipper in air and in water.

than fishes, in that they perch on the mud and mangrove roots and seldom stay in water. When approached by humans, they scurry into a mud burrow or skitter away atop the water.

When a mudskipper is put into water it almost always develops a bradycardia, but when it is exposed to air its cardiac rate increases (Fig. 5). It was noted that heart rates decrease after 3–4 minutes in either water or air. Squeezing air from gill pouches, physical agitation, noise, and noxious gas have no noticeable effect upon cardiac rate. It is well known that mangrove mud is highly anaerobic (Scholander *et al.*, 1955). A check on the mud in one burrow showed it to be almost free of oxygen. The anaerobic nature of the burrow is physiologically reflected in a greatly reduced heart rate when the mudskipper is underground (Fig. 6).

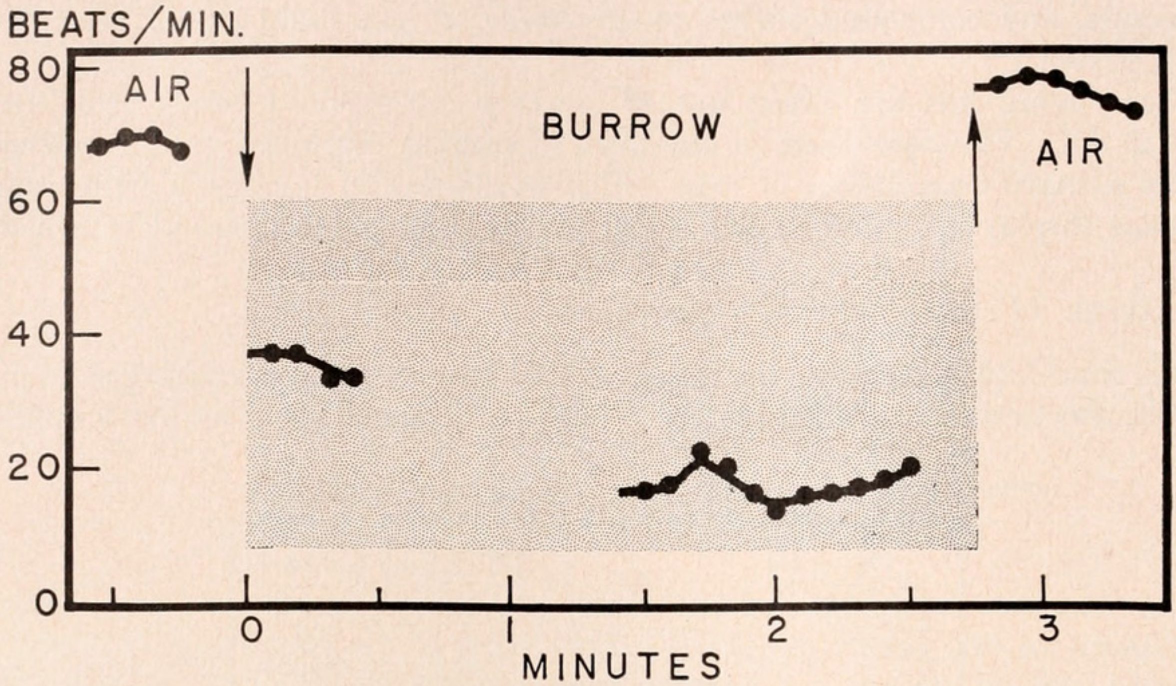

FIGURE 6. Heart rates of a mudskipper in air and in mud burrow.

HAGFISH (*Eptatretus stoutii*)

A hagfish is included in this investigation because it is plausible to assume that it creates for itself an anaerobic condition when it burrows into the bodies of living or dead fish.

Recording of the hagfish's heart rate reveals no bradycardia when it is out of water. Indeed, the rate continued at a steady pace of 44–45 beats per minute in both air and water.

DISCUSSION

The grunion and the flying fish show interesting ability to carry on essential life activities while out of water. The effectiveness of these adjustments is clear. Flying fish escape predators, and mortality of unrestricted grunion during spawning is almost non-existent (Walker, 1952). These fishes respond to aerial situations of low- or high-energy demand with a drop in heart rate. This decrease indicates an overall circulatory reduction, because increased stroke volume cannot offset bradycardia of these magnitudes. Of interest is the similar bradycardiac response exhibited when these fishes enter air and when lung-breathers swim submerged.

Experimental studies suggest that a diving animal's musculature becomes uncirculated and shifts to anaerobic function, thus conserving the oxygen stores (Scholander *et al.*, 1942). It is believed that oxygen-demanding tissues, such as the heart and brain, are selectively supplied with oxygen while peripheral circulation is restricted (Irving, 1939). Pronounced rise of lactic acid in the blood of fishes during the recovery period following air exposure (Black, 1955; Leivestad *et al.*, 1957) supports these views. Our investigation of a few grunion on the beach showed an acute three-fold increase in lactic acid during recovery in water.

Unlike most other teleosts the mudskippers seem physiologically well adjusted to the world of air. They show an evolutionary development to aerial respiration (Carter, 1957; Whitley, 1960), and their bradycardiac response to water is unique among investigated fishes. Indeed, an aquatic existence may now constitute an asphyxic environment for the mudskippers.

The hagfish, an internal predator, presents an exception to the cardiac responses of all investigated vertebrates. Its cardiac rate is unaffected by transitions from water to air. This passiveness, however, reflects a peculiarity in this cyclostome's anatomy—it lacks cardioregulative nerves. The hagfish evidently cannot exhibit cardiac adjustments to the anaerobic conditions it encounters, for in fishes and other animals the heart is controlled by the vagi (Skramlik, 1935; Jensen, 1961).

The sudden changes in cardiac rates of the fishes studied indicate a decisive mechanism of control. An aerial bradycardia is not peculiar to the air-venturing grunion and flying fish, however, for cod (*Gadus morhua*), river trout (*Salmo trutta*), and carp (*Cyprinus carpio*), which are not normally exposed to air, show similar cardiac adjustments (Leivestad *et al.,* 1957; Serfaty and Raynaud, 1958). It has been suggested that the asphyxia causes the onset of bradycardia. However, response of the grunion and the flying fish is so immediate that other factors must be involved. Also, it seems likely that the heart control does not result from simple skin-initiated reflexes, because it is known that psychological factors can induce bradycardia in mammals and in some fishes. Whatever this asphyxial defense mechanism, triggered when animals encounter the unfamiliar world of air or water, likely it aids in survival of the individual and of the species.

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Summary

1. Cardiac frequencies of fishes that normally expose themselves to asphyxic situations were studied.

2. The grunion and the flying fish displayed pronounced bradycardia upon exposure to air with rapidly regained rate when immersed.

3. The air-inhabiting mudskipper responded to water with a heart slowdown and a speedup in air.

4. The hagfish, which lacks cardioregulative nerves, showed no cardiac frequency compensation when placed in air.

5. Comparison is made with the asphyxial adjustments exhibited by land animals when they swim submerged.

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