II. PERSPECTIVES: THE PAST, PRESENT, AND FUTURE OF TUNA PHYSIOLOGY

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A. Introduction

The workshop from which this collection of papers arose was intended to provide a forum for review of the various current studies on the physiological ecology of tunas and their near relatives; the review should lead to efficient consolidation of research efforts over the next several years. In addition, we hope that publication of these proceedings will encourage other investigators to lend their own particular expertise in this area. We feel that studies on the physiology and behavior of tunas have tremendous potential for the scientist concerned with fundamental principles (consider the extreme degree of specializations by tunas for efficient use of energy) as well as for the applied scientist (consider the commercial value of the tuna harvest). Because we want this volume to be of interest and use to more than the very few of us working in the field, we present in this section a brief historical review of tuna physiology investigations not covered in the preceding chapters. We will also include a short description of research in progress at the time of printing and conclude with our view of future potentially fruitful areas of investigation.

B. The Captive Tuna

The majority of what is known about the physiology of tuna has been elucidated through experiments carried out on live-held specimens at the Kewalo Research Facility of the National Marine Fisheries Service. It is presently the only facility in the world designed to maintain tunas in captivity for research purposes. Although it is difficult and expensive to maintain tunas in captivity, it is less so than carrying out observations of free-ranging tunas in the open ocean. In addition to providing fundamental data on how tuna function, the experiments on live-held tuna have delineated specific experiments that are best carried out on free-ranging tunas and have provided data for predictions regarding the distribution of tunas.

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The Kewalo Research Facility had its genesis in a contract awarded by the Pacific Oceanic Fishery Investigations (POFI) to Dr. Albert L. Tester of the University of Hawaii to do a literature search on the reaction of tuna to environmental stimuli (light, sound, chemicals, electric fields, etc.), to develop capture and holding procedures, and study the reaction of tunas to the above listed stimuli. Holding pens and tanks were constructed in 1951 at the Hawaii Institute of Marine Biology at Coconut Island, Kaneohe, Hawaii, and work commenced. The literature search was easy; there was no previous work. Fish were captured by trolling methods and returned for study. No skipjack tuna were returned alive, although they were often captured. Dr. Tester was successful at maintaining a few small kawakawa and several larger (up to 60 cm) yellowfin tuna (Tester, 1952). Experiments were designed to investigate sensory responses that might be exploitable with artificial bait. A well-developed chemical sense was established; tests of other sensory systems were not promising (Hsiao, 1952; van Weel, 1952). In the following year a second contract was awarded and the work continued on responses to chemical stimuli and to combined chemical and visual stimuli. Results revealed that amino acid fractions were the most excitatory and that colored lures had less attractive power than white ones (Hsiao and Tester, 1955; Tester, van Weel, and Naughton, 1955).

In 1956 POFI was incorporated into the new Bureau of Commercial Fisheries (BCF), and in 1957 a tuna behavior program was added to the organizational structure of the Honolulu Laboratory. Initial efforts were devoted almost exclusively to observing behavior of feeding skipjack tuna at sea. The Kewalo Research Facility was subsequently built in 1958 on 39,000 sq. ft. of land leased from the State of Hawaii; it was to serve jointly as the dock facility of the fishery vessels deployed by the BCF Lab and as the first aquarium facility devoted to the maintenance of live tunas for experimental purposes.

In 1961, John Magnuson, a fresh Ph.D. from the University of Minnesota, took command of the behavior program. Shortly after John arrived, he sailed on a 90-day cruise to the Line, Marquesas, and Society Islands on the *Charles H. Gilbert* (recently outfitted with underwater viewing ports). The mission: the comparative study of feeding behavior of skipjack and yellowfin tunas. As a result of his ocean-going experience, John returned convinced that too much research time was wasted while at sea and initiated a vigorous shoreside program of sensory and feeding studies.

Since Tester's early work at Coconut Island, Eugene Nakamura and his co-workers have been responsible for many improvements in both handling and holding techniques (Nakamura, 1960, 1962, 1964b, 1966, 1972; Magnuson, 1965). Two developments have contributed much to insure survival of returned tuna: (a) development of fiberglass transfer tanks with adequate amounts of supplied water and structured nonturbulent current flow (Nakamura, 1966) and (b) airstones constructed of grinding wheels that produce an oxygen stream of very fine bubbles allowing supersaturated levels of dissolved oxygen (Baldwin, 1970). These devices and an effort to insure that the captive tuna did not contact hard or abrasive surfaces made it possible to capture and deposit at the Kewalo Research Facility over a hundred 45-cm skipjack tuna with no mortalities.

Paralleling development of handling procedures were studies of sensory physiology. Investigations of behavioral responses to visual stimuli have spanned many years (Hsiao, 1952; Hsiao and Tester, 1955; Nakamura, 1968; Nakamura, 1969; Tamura, Hanyu, and Niwa, 1972; Hanyu, Tamura, and Niwa, 1973). Chemical sensing capabilities have also been studied extensively (van Weel, 1952; Tester, Yuen, and Takata, 1954; Tester, van Weel, and Naughton, 1955; Atema, Holland, and Ikehara, ms). Auditory responses of captive tunas were investigated by Iversen (1967, 1969).

Studies of behavioral facets of tuna feeding, swimming, and communication (reviewed by Nakamura, 1972) have been important to the conceptualization of the complex behavior and capabilities tunas exhibit. (In this volume, Kitchell *et al.*; Dizon, Brill, and Yuen; and Magnuson have reviewed previous studies of feeding, respiration, and hydrodynamics of tunas.) Matsumoto and Skillman (ms) are attempting to document relevant fisheries' information from scientific and fishery studies of Pacific skipjack tuna.

C. *The Warm-bodied Tuna*

The observation that tunas are warm has preoccupied most of the recent investigators in tuna physiology, and indeed most of the studies dealing with tunas (hydrodynamics, feeding, and energetics) have been undertaken to ascertain the reasons for warm-bodiedness (for detailed review, see Chapter 4, The Thermal Biology of Tunas). Yet, the fact that they are unequivocably warm has only been established within the last 20 years and the adaptive value of warmness, while being the subject of intense speculation, has yet to be established.

Although no evidence of thermoregulation arose from the studies of skipjack tuna at Kewalo Basin during the early 1970's, it was established that skipjack tuna can be very hot, relatively speaking, and that swimming activity seemed constant in the face of decreasing ambient temperatures. A Q_{10} of 1.0 was observed for swim speed of skipjack tuna, and this could be construed as support for a constant internal temperature.

The researchers working at Kewalo Basin were primarily interested in determining factors that would provide insight into the adaptive advantage of being warm (Neill *et al.*, 1976) and focused on the ability of tuna to detect temperature and temperature change (Dizon *et al.*, 1974, 1976; Steffel *et al.*, 1976) as well as the curious temperature compensation of swimming speed in skipjack tuna (Dizon *et al.*, 1977). Yet, no evidence of short-term physiological thermoregulation was obtained; in fact, the interpretation of thermoregulation by the ultrasonic transmitter-carrying giant bluefin tuna was questioned (Neill and Stevens, 1974). Because of the large mass and retarded thermal exchange of tunas, once warm they tend to stay warm, at least over periods of hours. Tunas have significant thermal inertia; using equations developed for quantifying this inertia, Neill and Stevens were able to account for the constant body temperature of Carey's giant bluefin tuna on the basis of thermal inertia. A dewar flask with an internal heat source could have done just as well. Unfortunately, the bluefin tuna carrying the ultrasonic transmitting gear did not stay in the cold water long enough to establish active physiological thermoregulation. Even now the question is unanswered, but it appears that completion of a few relatively simple experiments given present facilities will confirm that at least rudimentary thermoregulation exists, even in the small tunas.

D. *Recent Projects*

Behavioral and physiological experiments of great sophistication are now possible at the Kewalo Research Facility. Techniques have been developed that allow at least some limited experimental manipulation of captive animals. Laboratory telemetry devices have been developed that allow continuous monitoring of deep body temperatures (see Dizon, Brill, and Yuen, this volume), and recently of muscle activity. An active respirometer has been built and oxygen utilization at speeds above basal rates is being determined, since extrapolations of existing respiration data beyond 2 lengths sec^{-1} yield suspiciously high values. A swimming tunnel (aquatic treadmill) that allows control of swim speeds to about 4 lengths sec^{-1} is available which also allows tubes and wires to be positioned on a continuously swimming fish. Metabolic, heat flow, and electrophysiological studies are under way using the swimming tunnel. Work continues to collect stasis metabolic rate (respiration rates at zero overt activity). A promising study has been initiated to investigate the involvement of the adrenocorticosteroid hormones in causing stress-related mortalities in our captive fish. Use of corticosteroid blocking drugs may prove to be an effective remedy.

The studies of the biochemists continue (Guppy; Guppy, Hulbert, and Hochachka, this volume) with the intention of obtaining data from tunas performing specific activities above minimum hydrostatic swim speeds. Recently initiated studies of behavioral responses to water turbidity have not yet yielded sufficient results to warrant discussion.

Elsewhere in the world, Inoue and co-workers are continuing to study larval tuna development with an eye toward culturing tunas for the Japanese markets (Inoue, 1973). In La Jolla, the Southwest Fisheries Center maintains an active tuna oceanography program that has concentrated its efforts on the North Pacific albacore. Within this program there are continuing efforts to develop a "life-support" system to return live albacore to shoreside facilities.

To date, the Kewalo Research Facility in Hawaii remains the only site where captive tunas are routinely kept for experimental purposes. Skipjack tuna, kawakawa, and yellowfin tuna are available year round for study. Size ranges available are 30 to 70 cm for three tropical species. Efforts are continuing to make a larger size range available.

E. Future Research

The success of any ambitious program for physiological research on tunas requires a commitment to develop a routine and dependable system for capture, transportation, and maintenance of a variety of species of tunas; diverse temperature requirements of the tunas preclude a facility that would be capable of experimental work on both the temperate and tropical forms. Other favorably located facilities should be sought. The success of the Kewalo Research Facility of the Southwest Fisheries Center's Honolulu Laboratory is due in part to efforts of its personnel toward developing maintenance techniques. Fortuitous location of the laboratory (virtually next door to the tuna boat docks) and an active, interested, and cooperative fishery allows acquisition of specimens of tropical tunas with an absolute minimum amount of handling.

A full-scale "animal husbandry" approach would be ideal but possibly unrealistic, if only because of funding exigencies. We can, however, begin to lay the foundation for the transition from today's "maintenance-oriented" programs. Problems of transportation to the facility and experimental manipulation (even weighing is a risky undertaking for these delicate fish) would be vastly simplified by employment of a fast acting-fast recovering anesthetic. Two types are necessary: *(a)* oral delivery via food; and *(b)* injectable (intravenous injection is, however, virtually impossible). The study of stress and stress-related diseases is in order. Skipjack tuna develop "puffy-snout," a cluster of symptoms characterized by a lumpy, bumpy snout. Crowding or other types of stress causes development of the symptoms in less than 1 week. The study of hormones and hormone-blocking agents will, we hope, yield insights into causes and solution to this problem. So many other important and potentially manipulatable physiological properties of tunas are simply unknown; a program collecting baseline clinical data is needed. Considering the worldwide value of the tuna resource, we ought to know at least as much about the tunas' biological properties as we do about the salmonids.

Tunas have been kept alive for up to a year in the Kewalo Research Facility. If we can routinely accomplish this, especially on the puffy-snout-prone skipjack tuna, physiological studies requiring measurements on the same animal at different sizes become practical. Thus a great deal of sampling variability is eliminated. At present, the continuous flow of individual specimens almost insures that experiments are conducted on a mix of at least two different stocks (Sharp, this volume). As the ability to keep tunas improves, the potential for a breeding and rearing program becomes obvious. Domestication is not a goal, but at present individuals smaller than 30 cm or larger than 70 cm are unavailable for experimental study. The logistic problems of capturing and transporting large fish for study are almost insurmountable. Tank-bred stock might be a solution. Accessibility of larval and post-larval tunas would allow application of experimental strategies perfected by Reuben Lasker and his colleagues (Southwest Fisheries Center, La Jolla) to study fish year-class abundance questions. Whatever goals are eventually achieved, improvement in transportation, maintenance, and manipulation can only lead to more rigorous experimentation and more valuable information for interpretation of habitat-related behavior of high seas tunas.

Captive-fish studies must be supplemented by studies conducted in the field. We are currently planning experiments based on deployment of sonic tags on free-ranging tunas. A multisensor sonic tag can be developed using state-of-the-art electronics that will sequentially transmit information from a variety of sensors. Information from a practical four-function tag will generate real time information on ambient water temperature (surrounding the fish), depth of swimming, fish core temperature, and, most importantly, swimming activity. The latter information will be measured as tail beat rate. We propose that development of such tags be cooperative so that redundant costs will be minimized. As long as tags remain small enough to be deployed on 70 cm fish, one tag design should be adequate for all species.

Among the experiments which can be directly applied to practical problems of fishery management are studies of school cohesiveness. Tagging of several fish (requiring either heroic endurance of the tracking personnel or well-engineered equipment) would very rapidly yield information of school cohesiveness as a function of stock, fish size, and species. Present-day fishery strategies are predominantly two-dimensional and surface-oriented where fish are vulnerable only when they appear at the surface (longline fisheries are an exception); depth telemetering capabilities provide the necessary third dimension to location. Tagging a tuna with a high-output sonic tag and following it may prove to be an effective method of locating fish which spend only a small proportion of time at the surface. Tags and tracking gear are inexpensive and simple to operate relative to the cost in time and fuel resources that go into scouting for fish schools. Certainly, tuna are much more adept at finding conspecifics than fishermen are at finding their prey; a "Judas" fish location strategy may well be very cost effective.

Simultaneous collection of ambient temperature, core temperature, and activity parameters are necessary to elucidate the mechanics and strategies of tuna thermoregulation. These three parameters segregated and studied by fish size, stock, and species provide the basic, and probably most likely, data set that will clarify the adaptive advantages of thermoregulation, resolve stock and species differences, and perhaps, most importantly, allow development of an accurate energy budget for the various species and stocks. The latter is imperative for any future development of biomass models. For a tuna, the greatest energy cost is swimming; yet we have only the most rudimentary estimates of daily activity patterns. As Sharp (this volume) suggests, activity (and the respiration that quantifies its cost) is the ultimate character upon which natural selection operates to segregate stocks and species. Knowledge of activity patterns will always be the sine qua non of any live tuna studies, and tracking of free-swimming fish is the most cost effective manner in which to collect realistic information.

Considering the vast amount of material to be gathered and the unanswered questions, it seems likely that it will be a while before the total description of the various tunas' habitats will be made. It should be apparent, however, that existing information can be integrated into present-day fisheries strategies to provide for more efficient and effective exploitation of the tuna resources. The process of getting the knowns implemented into the fishing communities has its own set of problems, and increasing the knowledge about tunas has others. It takes intense dedication to get either job done. We hope that this volume will be a start and help to provide conceptual guidelines for researchers, administrators, the fishing communities, and other interested individuals, so that some day it will be possible to say that we truly "understand" the tunas and be able to apply that understanding to the benefit of both men and tunas.