Tuna Behavior and Physiology

The ranges of tuna species span entire ocean basins from east to west. While these large-scale distributions often overlap, there are important differences between species in their small-scale distribution. Fishers who understand these small differences have exploited them to direct their fishing effort toward different species. Scientists are catching up with the fishermen and have learned a great deal about the biological differences among tunas. The vertical and horizontal boundaries of the habitats of the different tuna species are based on important behavioral and physiological differences. In the near future, we will use this biological information to make general predictions of the large-scale distribution and abundance of tunas.

Tuna Telemetry in Tahiti

Fisheries biologists worldwide have used acoustic telemetry (the transmission of measurement results to a distant station) to study tuna. Pressure, temperature, tail beat frequency, electromyograms from expaxial and opercular muscles, electrocardiogram and body temperature have been recorded through telemetry. Of these, pressure appears to be the most used and has resulted in findings on the horizontal and vertical movements of tuna in the presence of environmental anomalies, such as fish aggregation devices (FADs) and seamounts, and on the vertical structure of abiotic variables, such as temperature, oxygen and salinity. Other experiments have interpreted changes in the body temperature of tuna in relation to their vertical movements.

The relationship between the biotic environment and the vertical and horizontal movements of tuna, however, has generally been ignored.

To address this subject, a recent study by Erwan Josse, Pascal Bach and Laurent Dagorn of the Office de Recherches Scientifiques et Technologique d’Outre Mer (ORSTOM) in Papeete, Tahiti, employed simultaneous use of acoustic trackings and acoustic surveys to interpret the movements of tuna in relation to the biotic factors of the environment. Results of the study have shown the important role of prey distribution and tuna foraging behavior on tuna dynamics.

Fishing operations for the study were conducted aboard an ORSTOM research vessel and aboard longline fishing units. During the tracking, echo soundings were conducted between the surface and 500 m depth. At the same time, depth and geographical coordinates (GPS data) of the tuna were recorded with a second recording unit.

Behavior of a Yellowfin Tuna Caught by Drop-Stone

A yellowfin tuna of 60 m fork length is caught by drop-stone technique at 120 m depth at midday close to a FAD near Maupiti.

(continued on page 2)
Island (16°27' S and 152°17' W), an island of the Leeward Islands of the Society archipelago. After being equipped with an acoustic tag and released, the fish displays four distinct periods of horizontal movement: (i) a FAD association just after release, (ii) a free-swimming phase directed offshore until sunset, (iii) a progressive return to the FAD until 11 p.m. and (iv) a free-swimming phase near the reef coast between 11 p.m. and midnight. The fish also displayed two periods of vertical movement: (i) below the mixed layer during the day and (ii) in the mixed layer during the night.

The biotic environment during the experiment consists of a sound scattering layer (SSL), indicative of prey concentration, in the vicinity of the FAD (Figure 1).

The yellowfin crosses the SSL twice, first during the daytime and later at night (see figure on page 1). At each crossing, the tuna changes its horizontal movement (leaving the FAD during the daytime, even though tuna are generally strongly associated with FADs during this period) as well as its vertical movement (swimming in the mixed layer during the night except when it visits the SSL, probably to forage).

**Behavior of a Bigeye Caught by Trolling**

Repeated echo soundings around an open-ocean oceanographic buoy (5° S and 140° W) confirm the regular presence of a tuna school composed of juvenile bigeye, 35 to 84 cm fork length, during the day. In the afternoon, an individual of this species (77 cm fork length) is caught by trolling longline and equipped with an acoustic tag.

After its release, the fish remains with the school during the daytime. While the depth and spread of the school remain constant, the fish exhibits vertical movement within the school. Maximum depth of the school and vertical movement of the fish seem to be limited by the presence of a well-defined oxycline (oxygen change) at 200 m depth. Because of this limit, the SSL could be inaccessible by tuna during the daytime.

At the end of the afternoon, the school structure disappears and the fish leaves the buoy. At dusk, the fish swims into the SSL, which has migrated to the surface layer. The mean swimming depth of the tuna (60 m) corresponds to the maximum acoustic intensity (i.e., maximum prey concentration) in the SSL.

**Behavior of a Bigeye Caught by Longline**

A bigeye tuna of 100 cm fork length is caught in the open ocean by a longline fishing unit at 1 a.m. off Tetiaroa Island (17°00' S and 149°35' W), an atoll of the Windward Islands of the Society archipelago. After its tag and release, the fish principally remains in the upper part of the SSL, between the surface and 40 m depth. Rapid and small-scale changes in depth are observed until the fish reaches 110 m depth, which corresponds to the lower limit of the SSL (Figure 2).

At dawn (about 5 a.m.), the fish leaves the mixed layer and swims slowly down to 350 m depth. The simultaneous mapping of the fish’s vertical movement and echo-sounding records clearly show the fish following the SSL migration at first light (Figure 2).

For unexplained reasons, the fish stops its descent at 350 m depth (water temperature 15° C) while the SSL continues its migration until 550 m depth.

**Conclusion**

It has generally been accepted that tuna movements are controlled by abiotic factors that determine habitat limits. The current study shows that biotic factors, such as prey distribution and movement, are also important considerations.

In the future, the technique of simultaneous acoustic trackings and acoustic surveys to interpret the movements of tuna in relation to the biotic factors of the environment could be employed to develop a behavioral model to predict large-scale movements of tuna and improve our knowledge of tuna catchability in the longline fisheries.

**PFRP**
How Tuna Physiology Affects Tuna Movements and Distribution

Introduction

Tuna biologists generally agree that temperature, ambient oxygen (i.e., the oxygen in the surrounding environment) and prey abundance are the principal factors determining the movements of tunas. These parameters not only dictate tuna habitat but also influence the different tuna species’ vulnerability to various types of fishing gear. The specifics of how these factors act and interact are, however, not well understood.

In fisheries management, movements and stock dynamics of species are most often inferred from catch-per-unit-effort (CPUE) data. To use this index, fisheries biologists are often forced to assume that the “catchability” of a target species is constant. Also, factors which modify the catchability of tuna—such as changes in fishing technology, variations in fishing tactics and, most importantly, the effect of environmental conditions—are not always considered. As a result, population assessments based on CPUE data have difficulty differentiating over-harvesting from environmental influences.

Numerous studies have attempted to delineate the environmental conditions that tunas prefer, can withstand or will avoid by employing catch statistics and data on oceanographic conditions averaged over time and space. Unfortunately, this method can sometimes obscure, rather than clarify, the relationships between species density and environmental conditions. This obscurity occurs because oceanographic and fisheries data are often gathered separately and because the inherent variability in both averages is usually too broad to clearly explain exact meaningful relationships. More importantly, correlations of environmental conditions and catch rates do not prove causation but rather perpetuate a circular logic: If tunas are rarely or never caught under a particular set of environmental conditions, we assume the conditions are unsuitable because tunas are rarely or never caught when and where these environmental conditions occur. Entrapping circular arguments, missing data parameters, limitations of CPUE indexes and the enormous difficulty of producing integrative models are just some of the obstacles fisheries biologists and fisheries managers face when attempting to resolve, with some confidence, tuna population assessment issues and resource allocation questions.

Before a comprehensive model describing the movements and stock dynamics of the tunas can be developed, it is first necessary to understand (1) the changes in oceanographic conditions and (2) how the physiological abilities and tolerances of tunas cause them to respond to these changes. It is the latter subject, namely, the physiological abilities and environmental tolerances of the tunas, that is the focus of the research conducted by Richard W. Brill, Joint Institute of Marine and Atmospheric Research senior fellow, and Katherine L. Cousins, research associate, at the National Marine Fisheries Service-Honolulu Laboratory’s Kewalo Research Facility under the Tuna Movements and Distribution Project, sponsored by the Pelagic Fisheries Research Program. The studies described here are just two examples of several ongoing activities.

The Unique Blood of Bigeye Tuna

Tracking of bigeye tuna (Thunnus obesus) carrying ultrasonic depth sensitive transmitters in the open ocean has shown that the species has behaviors, depth distributions and a thermal ecology different from skipjack (Katsuwonus pelamis) and yellowfin tunas (Thunnus albacares). The latter two species occupy the warm uniform temperature surface layer (typically around 25° C, or 77° F, at the center of their range) and do not go below depths where the water is more than 8° C (14° F) colder than the surface water temperature. In contrast, bigeye tuna tend to swim deeper and normally occupy water 15° C (59° F) or colder.

Based on the depths at which longline fishing gear captures most bigeye tuna, it also appears that bigeye tuna often occupy waters with low oxygen content. The objective of the current study was to understand the physiological basis for the observed differences in bigeye tuna behaviors and their responses to environmental change.

Bigeye tuna possess, as do other tuna species, vascular counter-current heat exchangers that allow muscle temperatures to be sustained significantly above ambient temperature. Vascular counter-current heat exchangers (Figure 1) act as a thermal barrier and decouple metabolic heat production in the muscle from the inevitable heat loss to the water that occurs when the blood passes through the gills. Vascular counter-current heat exchangers also reduce rates of heat transfer to, or from, the environment following abrupt changes in water temperature. As a consequence, changes in muscle temperature lag significantly behind changes in water temperature.

Blood carries oxygen to all the organs of the body, not by holding oxygen in solution, but rather by binding oxygen to hemoglobin, a special oxygen carrying protein within the red blood cells. Each hemoglobin molecule can carry four molecules of oxygen. As the first molecule of oxygen binds, it slightly changes
the three dimensional structure of the hemoglobin molecule thereby making it easier for the second molecule of oxygen to bind (i.e., increases the oxygen affinity of hemoglobin) and so on.

The ability of hemoglobin to bind oxygen also depends on temperature and intracellular acidity. At higher temperatures or at lower intracellular acidity, hemoglobin is less able to bind oxygen. In other words, it has a lower oxygen affinity.

Interestingly, different fish species generally have blood oxygen binding curves that reflect their ability to withstand low ambient oxygen. Species tolerant of low ambient oxygen have blood that is able to bind oxygen at the gills (and become fully saturated) at a low water pO2 (partial pressure of oxygen). There is a price to be paid for this capability, however. Blood that is able to load oxygen at a low pO2 will usually not easily “off-load” oxygen at the tissues where it must ultimately be delivered. Consequently, species that can tolerate low ambient oxygen environments are usually sedentary or have low metabolic rates.

However, bigeye tuna blood has a unique functional ability that enables it to load oxygen onto the hemoglobin in the gills at low ambient oxygen levels (i.e., at low pO2), while still ensuring adequate and rapid oxygen off-loading in the tissues. When bigeye tuna blood is warmed, its ability to bind oxygen is dramatically reduced (i.e., has a lowered binding affinity for oxygen), which is exactly the situation necessary to rapidly off-load oxygen in the tissues (Figure 2). This reduction means the off-loading of oxygen in the warmed bigeye tuna muscle is not compromised by the tuna’s high oxygen affinity at the gills. Indeed, as shown in Table 1, the estimated P50 (pO2 required to bring the blood to 50% oxygen saturation) of skipjack, yellowfin and bigeye tuna blood occurring in the muscle is the same in all three species.

<table>
<thead>
<tr>
<th>Species</th>
<th>Temperature Change</th>
<th>Gills</th>
<th>Muscle</th>
</tr>
</thead>
<tbody>
<tr>
<td>bigeye tuna</td>
<td>15°C → 25°C</td>
<td>7.8 ± 0.9</td>
<td>43.4 ± 1.9</td>
</tr>
<tr>
<td>yellowfin tuna</td>
<td>20°C → 30°C</td>
<td>16.5 ± 1.5</td>
<td>42.0 ± 3.6</td>
</tr>
<tr>
<td>skipjack tuna</td>
<td>20°C → 30°C</td>
<td>22.8 ± 0.9</td>
<td>51.0 ± 4.7</td>
</tr>
</tbody>
</table>

The results from this study are the first to explain how bigeye tuna are able to tolerate the deeper oxygen-poor waters and utilize food resources not available to other tuna species. Moreover, these findings complement the historical catch statistics that have long implied, but never conclusively explained, bigeye tuna’s tolerance to low ambient oxygen levels.

**Limitations of the Yellowfin Tuna Heart**

Using ultrasonic depth sensitive transmitters, studies of adult (up to about 75 kg or 150 lb.) yellowfin tuna off the Kona Coast of the Big Island (Island of Hawai‘i) revealed that these fish spend the majority of their time in water shallower than 120 m (about 360-foot) depth. Surprisingly, the depth distribution of the adult fish was found to be nearly identical to that of the juvenile fish (approximately 2–5 kg or 4–10 lb.) followed in the same area some years earlier. This observation of identical depth distributions of adult and juvenile yellowfin tuna conflicted with much of what was thought to be understood about tuna thermal physiology, i.e., a slower rate of muscle cooling should provide large yellowfin tuna with an even greater ability to spend more time in deeper and cooler water and to exploit whatever food resources are found in this environment. How then to explain these observations?

Historically, the basic premise underlying the idea that larger fish cool more slowly and are able to spend more time in deeper, colder water is that body temperature is the most important factor limiting tuna movements. Experiment results, however, imply that it is the temperature of the heart that really limits vertical movements of yellowfin tuna. A careful examination of Figure 1 shows that the heart and gills are on the “water” side of the vascular countercurrent heat exchangers. This means that the temperature of the heart, unlike body temperature, will change immediately with water temperature regardless of the size of the fish. This relatively simple recognition, namely, that the temperature of the heart is a limiting factor in tuna behavior, is a novel idea, but can it really explain the observed vertical movements of adult and juvenile yellowfin tuna in the open ocean?
Ongoing physiological experiments using yellowfin and skipjack tuna at the Kewalo Research Facility demonstrate how the temperature of the heart can directly limit the vertical movements of tunas. For instance, Figure 3 (upper panel) shows the response of a yellowfin tuna exposed to an abrupt 25° to 15° C (77° to 59° F) change in water temperature. Note that heart rate (i.e., the number of heart beats per minute) does not follow the change in muscle temperature, which lags significantly behind, but rather follows the change in water temperature. This is strong evidence that ambient water temperature directly impacts the cardiac output of yellowfin tuna, thereby limiting swimming performance and ultimately influencing their vertical movements.

Moreover, a key observation is that at 15° C, yellowfin tuna have no ability to increase their heart rate. The vagus nerve (i.e., the 10th spinal nerve) regulates the heart rate in yellowfin tuna as it does in other vertebrates. Heart rate, in turn, sets the amount of blood the heart pumps per unit time. The vagus nerve acts as a regulatory “break” on heart rate and its action can be pharmacologically blocked with atropine. During exercise, tunas, more so than other fishes, increase their heart rate and thus the amount of blood pumped per unit time. This occurs due to a reduction of activity within the vagus nerve. When a yellowfin tuna is given atropine at 25° C (77° C), its heart rate doubles (Figure 3, lower panel), but at 15° C (59° F) atropine has no effect (Figure 3, lower panel). In other words, at 15° C yellowfin tuna have no ability to increase heart rate or the amount of blood pumped by the heart to the tissues. Therefore, at the colder temperature, yellowfin tuna have little or no ability to meet any increase in oxygen demanded.
Tuna physiology (continued from page 5)

Figure 3. Effects of an abrupt water temperature (dark gray) change (25°C to 15°C; 77°F to 59°F) on heart rate (light gray) in yellowfin tuna. Note that muscle temperature (black) lags significantly behind. Note also that heart rate and cardiac output follow the temperature change in both the non-atropine (upper panel) and the atropine treated tunas (lower panel). These data show that yellowfin tuna at 15°C (59°F) do not have the ability to increase their heart rate (or cardiac output) in response to any increase in energy demand of the muscles. It appears, therefore, that the effect of temperature on the heart is a better explanation of how changes in water temperatures limit the vertical movements of tunas than the effects of water temperature on muscle temperature.

by the swimming muscles while chasing prey or escaping a predator. Hence, it appears that the effect of temperature on the yellowfin tuna heart explains the limiting effects of water temperature on the vertical movements of yellowfin tuna.

Yellowfin Tuna Biology and Fisheries in the Pacific

Introduction

The annual harvest of yellowfin tuna (Thunnus albacares) from the warm-water oceans of the world is immense, with the fisheries of the western and central Pacific producing near or above 350,000 metric tonnes annually since 1990. Yet conservative stock assessments currently indicate that western Pacific yellowfin resources are only moderately exploited with some increase in catch possible without significant biological implications. If these assessments are correct, the resiliency of yellowfin tuna populations likely depends on beneficial life history parameters such as a rapid growth, early maturity and high fertility.

To better understand the link between yellowfin tuna biology and fisheries, a PFRP-funded investigation on the reproductive biology and spawning activity of yellowfin tuna in the central and western Pacific region in relation to fisheries vulnerability and interaction is being led by David Itano with collaboration from the South Pacific Commission, the Micronesian Maritime Authority, the National Research Institute of Far Seas Fisheries, the National Marine Fisheries Service and the Forum Fisheries Agency.

The study area encompasses the region of the main surface tuna fishery of the western Pacific, stretching from the highly productive waters of the southern Philippines and Indonesia in the west to the Line Islands of Kiribati in the east as well as a large area surrounding the Hawaiian Islands. The reproductive parameters of size at maturity, spawning frequency, time of spawning and peak spawning areas and seasons were determined by examining more than 10,000 yellowfin tuna ovary samples collected over a two-year period from purse-seine, longline, handline and troll vessels of several distant water and domestic fishing fleets. Fishery and biological data—such as the set type, school association type, fishing gear configuration and school behavior—were recorded for each sample to examine fishery interaction and gear vulnerability issues. Stomach contents of sampled fish were also examined to investigate the relationship between feeding activity and reproduction.

Reproductive Biology of Yellowfin Tuna

The estimated length at maturity for western Pacific yellowfin was made from a subset of the database of 7,501 tuna ovary samples collected from purse-seine, longline and handline vessels within 10° of the equator. Fish were classified as mature if fully yolked oocytes (well-developed eggs) or the atresia (resorption) of fully yolked oocytes was observed in the ovary sample by microscopic observation. Fifty percent of the fish sampled at 105 cm (approximately 50 lb. and two years in age) were classified as sexually mature. Ninety per cent of fish sampled at 121 cm in fork length (approximately 76 lb.) had reached maturity.

Yellowfin tuna, like other members of the tuna family, are serial spawners that release several batches of eggs throughout the
year. Estimates of the number of eggs released per batch from the equatorial region ranged from 0.55 to 4.01 million eggs per batch for a mean relative rate of 54.7 oocytes/gram body weight. Estimates from fish near Hawai’i were more variable ranging from 0.43 to 10.61 million eggs per batch with a similar relative estimate of 54.1 oocytes/gram body weight.

Fifty-one percent of the ovary samples that were classified as mature had spawned within 24 hours of capture indicating a spawning frequency average of once every 1.96 days. However, ovary samples with only fully yolked oocytes indicate near daily spawning frequencies (average once every 1.18 days). The conclusion is the fish engage in uninterrupted periods of daily spawning interspersed with periods of reproductive inactivity, during which the yolked oocytes regress to various unyolked or partially yolked stages. It is not known how long a particular fish can maintain a daily spawning rhythm. However, observations of captive yellowfin suggest it can be maintained for several weeks or more.

The only area that indicated a strong and repeated seasonal pattern of peak spawning during the sampling period was in the southern Philippines from samples collected in the Moro Gulf and Celebes Sea. Decreases in spawning activity among mature fish were noted to coincide with slight drops in sea surface temperature for this region between February and May. Previous authors have also indicated this seasonal spawning pattern and proposed a link to the changes in monsoon weather patterns and local productivity.

Different peak areas and seasons of yellowfin spawning have been proposed for the central and western Pacific equatorial region. Peak spawning to the west (135°–165° E) has been proposed to occur during the fourth and first quarters, and a central Pacific region of peak spawning (180°–140° W), during the second and third quarters. Findings from the current study indicate active spawning among mature fish sampled all along the equator throughout the year but with a decrease in spawning activity from December 1994 to June 1995 from 140°–160° E, which is in contrast to earlier studies. It is likely that a regular and repeatable seasonal pattern to tuna reproduction in this equatorial region does not exist but varies with productivity and environmental conditions peculiar to each year.

The spawning season for yellowfin tuna around the Hawaiian Islands occurs between April and October and peaks in June, July and August when mature yellowfin become more abundant close to the main islands. During the short summer spawning peak, more than 85% of the mature yellowfin sampled were in a near daily spawning mode. During the winter season, mature yellowfin caught in this area exhibit only unyolked or partially yolked oocytes and complete shut down of reproductive activity.

Fish Behavior and Fishing Methods

The tuna fishermen of the western Pacific utilize fishing techniques that take advantage of the behavior of the fish. Purse-seine vessels operating in the tropical western Pacific generally employ two different fishing methods to capture large tuna schools. The majority of the catch consists of juvenile tuna caught in association with drifting objects, such as natural logs, jettisoned cargo or man-made rafts set out to attract tuna schools. These “log sets” can be accomplished before dawn when the tuna can not see and avoid the nets, and most sets are successful.

So called “free schools,” or unassociated schools, which are also set on, produce the majority of mature-sized yellowfin taken by western Pacific purse-seine fleets. These schools are not truly “unassociated” but are actively feeding schools aggregated to huge concentrations of small baitfish. These schools are called “boilers” or “foamers” by the fishermen due to the foaming white appearance of the schools as they whip the surface to a froth in pursuit of the baitfish. Tuna become so preoccupied in these feeding frenzies that they fall easy prey to purse-seine gear.

Longline fleets of the western Pacific employ one of two basic styles of longline fishing. For the most part, Japanese longline vessels set 15 to 30 hooks between long floatlines and set with a line shooter to throw additional line in the set to sink the gear very deep in the water column. Their gear is normally fished during daylight hours targeting large bigeye that inhabit deep waters close to the thermocline during the day. In sharp contrast, the Taiwanese and mainland Chinese longline fleets set very shallow gear with only 5 hooks per basket hung from short floatlines. They fish close to the surface at night and concentrate effort during full moon periods. They hope to catch bigeye but also catch many large yellowfin, marlin and sharks.

Handline fishermen of the Philippines and Indonesia drop baited handlines near anchored fish aggregation devices (FADs) for large yellowfin and bigeye tuna. Lines are often baited with juvenile yellowfin as the adults are highly cannibalistic.

Gear Interaction and Tuna Vulnerability

Interesting differences in reproductive activity were noted between sexually mature yellowfin taken from different types of tuna schools or by different gear types. In general, purse-seine caught fish were more reproductively active compared to longline caught fish. Mature yellowfin from foaming schools were typically in a daily spawning, whereas fish caught in association with drifting objects had a higher proportion of fish with eggs in a regressed state.

Fish sampled from the shallow-set longline gear more closely resembled purse-seine caught yellowfin in that many were more reproductively active with high spawning frequencies. In contrast, only 37% of fish sampled from deep-set longline gear on the equator were observed to be actively spawning; the majority were in a sexually mature but regressed stage.

The importance of forage fish became apparent during the course of study, and the stomach contents of sampled yellowfin were noted and preserved for analysis after the first year of sampling. In most cases, successful purse-seine operations on free schools of large yellowfin appeared to depend on large concentrations of the ocean anchovy Engraulis japonica. This small, silvery fish exists in massive quantities in the western Pacific. Its distribution is apparently patchy, but when large concentrations occur, the vulnerability of large yellowfin to purse-seine gear can

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Yellowfin tuna biology (continued from page 7)

increase dramatically. Increased catch rates of mature-sized yellowfin by purse-seine gear in turn increases direct interaction between purse-seine and longline fleets.

The Hawai‘i-based fisheries for large yellowfin depend to a large degree on reproductively active fish caught during the brief summer season. The surface troll fishery for ‘ahi, or yellowfin tuna over 100 pounds, and the ika shibi handline fishery are both based on spawning aggregations of large fish close to the main Hawaiian islands. Yellowfin landings by Hawai‘i-based longline vessels also peak during the summer season. However, direct gear interaction problems between the small gears and longline vessels have been essentially eliminated by restricting longline gear within 50 to 75 miles of the main Hawaiian islands during the summer months.

Summary

Rapid growth brings the yellowfin tuna into sexual maturity soon after the second year when mass spawning commences. The females are capable of generating millions of eggs per day for extended periods of time. Such production requires a great deal of energy, limiting large spawning events to particular seasons or productive areas with adequate forage resources. At other times, the tuna apparently shut down their reproductive processes, absorb yolked oocytes and enter a resting stage until their next spawning session. Feeding and spawning aggregations and FADs dramatically increase the vulnerability of adult yellowfin to purse seine, longline, troll and handline gear resulting in increased catch and interaction rates.

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