

The Reproductive Biology of Yellowfin Tuna (*Thunnus albacares*) in Hawaiian Waters and the Western Tropical Pacific Ocean: Project Summary

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ABSTRACT

The reproductive biology of yellowfin tuna (*Thunnus albacares*) was examined in relation to seasonality, their vulnerability to capture, and fisheries interaction in the central and western Pacific Ocean. Reproductive parameters were determined by the examination of 10898 yellowfin ovary samples collected from surface and sub-surface fisheries operating in the central and western tropical Pacific and from Hawaii based fisheries, between May 1994 and April 1996. Histological criteria were used to assess maturity stage, spawning periodicity, spawning frequency and spatio-temporal patterns in spawning distributions. Spawning occurs primarily at night, at sea surface temperatures above 24–25°C and was estimated to peak between 2200 and 0300 hours. Mean batch fecundity estimates from counts of migratory nucleus or hydrated oocytes from yellowfin tuna in the equatorial western Pacific and Hawaii region were 2.160 and 3.455 million oocytes or 54.7 and 63.5 oocytes per gram of body weight respectively. Continuous spawning of yellowfin within 10 degrees latitude of the equator was histologically confirmed, with a mean spawning interval of 1.99 days from fish taken by surface and sub-surface gear types. Length at 50% maturity for equatorial samples was estimated at 104.6 cm with no significant difference in length at maturity estimates between samples taken by surface and sub-surface gears. However, spawning frequency estimates varied according to school and harvest gear type. Reproductively active fish are vulnerable to troll, shallow handline, shallow-set longline and purse seine gear. Mature, but reproductively inactive fish are predominant in the catches of deep-set longline gear. Histological evidence suggests alternating periods of near daily spawning interspersed with non-spawning periods, with rapid development into and out of spawning condition. Equatorial areas subject to strongly reversing monsoonal weather patterns may experience related seasonal patterns in yellowfin spawning. However, yellowfin spawning in the oceanic regions of the tropical central and western Pacific takes place throughout the year, while peak areas and times were noted that varied between sampled years. A positive relationship was noted between intense feeding activity of mature yellowfin, a high reproductive condition of the fish and an increased vulnerability to surface fisheries. Localized areas of elevated forage abundance that vary both seasonally and by area may help to explain spatio-temporal variations in spawning activity. In particular, the ocean anchovy (*Encrasicholina punctifer*) appears to be a major forage source for western Pacific yellowfin, occupying a significant ecological role in the region. The spawning season for yellowfin in Hawaiian waters occurs from April through September/October, peaking in June, July and August when daily or near-daily spawning rates were noted. Hawaii based fisheries that target large yellowfin also peak during the northern summer and appear to be based on an in-shore spawning run when the highest potential for gear conflict and interaction occurs.

INTRODUCTION

Yellowfin tuna are a major component of central and western Pacific (CWPO) tuna landings, varying from 284,000–414,000 metric tonnes (mt) during the years 1990–1998 (Hampton et al., 1999). During the height of sampling for this project (1995) more than 335,000 mt of yellowfin was landed. (SPC, 1996) Purse seine and longline vessels of distant water fishing nations operating in the western tropical Pacific account for over seventy five per cent of the catch, although a combination of small and medium scale fisheries in the Philippines and eastern Indonesia land approximately twenty per cent of the annual yellowfin catch. Total landings of yellowfin in Hawaii are minor in comparison but are an economically important segment of Hawaii's longline, handline and troll fisheries (Anon, 1996; Boggs and Ito, 1993).

Semi-independent sub-populations of yellowfin tuna in the eastern, central and western Pacific have been proposed, although rates of exchange are poorly understood (Suzuki, et. al. 1978). However, observations of the distribution of yellowfin tuna larvae support the existence of a common central and western Pacific spawning stock as does a recent Pacific-wide genetics study, which proposed the existence of eastern and western Pacific sub-populations separated at around 150W (Ward, et. al., 1994). Tagging data also show widespread eastwest movement of yellowfin between 120E to 160W. The main area of interest described in this paper includes the central and western Pacific Ocean that lies westward of approximately 150W.

Within this region, several studies on different aspects of the reproductive biology of yellowfin tuna have been conducted (reviewed in Suzuki, 1994a; Anon., 1992), but the resulting information is incomplete and often conflicting. It is accepted that some degree of spawning takes place throughout the year within a zone at least ten degrees north and south of the Equator, with seasonal spawning at higher latitudes. Prior studies have proposed different peak spawning areas and seasons in the equatorial region as well as widely differing estimates of size at maturity, spawning frequency, batch and total fecundity and sex ratios in the population (Sun and Yeh, 1992). Other studies have noted intriguing differences in the apparent size at maturity of yellowfin caught by surface and sub-surface fishing gears suggesting that different gear types (purse seine and longline) may exploit different segments of western Pacific yellowfin populations.

The possibility of differential vulnerability of yellowfin to surface and sub-surface gear types due to reproductive condition is extremely important to catch and effort and interaction studies. This is particularly true as the project study area is believed to encompass the major spawning ground and recruitment source for western and central Pacific yellowfin that are experiencing significant exploitation by several gear types and fisheries. Central and western Pacific yellowfin tuna are known to spawn at higher latitudes, such as close to the Hawaiian Islands and off the east coast of Australia but the relative importance of these spawning areas is poorly understood.

In order to address these subjects, the reproductive parameters of the fish over a broad area must be accurately correlated to data on fishing methodology, school aggregation,

feeding behavior and environmental conditions at the time and area of capture. Links between spawning activity and areas of productivity and forage that may influence temporal and areal spawning distributions, vulnerability and catch rates by fisheries should be examined.

The present study was designed to address these issues and is an investigation of the reproductive biology of yellowfin tuna in the central and western Pacific region and how maturity and reproductive condition may influence their vulnerability and interaction between relevant tuna fisheries.

The main objectives were these:

- A. To define the spatio-temporal and size-related patterns in reproductive parameters for yellowfin in the central and western Pacific Ocean. The specific parameters of interest were (1) length at 50% maturity; (2) spawning frequency; (3) batch fecundity; (4) peak spawning distributions.
- B. To compare and contrast the major region of yellowfin tuna spawning along the Equator, to the Hawaii region (approximately 20N), representing a sub-tropical area of seasonal spawning activity.
- C. To compare the reproductive parameters of surface and sub-surface caught yellowfin, to investigate their role in gear vulnerability and interaction between surface and sub-surface tuna fisheries.

MATERIALS AND METHODS

EXPERIMENTAL DESIGN

Study Area

The study area encompassed the region of major yellowfin tuna fisheries and landings of the central and western Pacific as indicated in Figure 1. The equatorial region contains the major tuna fisheries of the western Pacific stretching from the Philippines and Indonesia in the west to an area including the Line Islands of Kiribati in the east, and within 10 degrees of the equator. The catch distribution of yellowfin tuna within the study area for the study period 1994–1996 by major gear type is indicated in Figure 2. Significant landings of yellowfin were made by handline, purse seine and a mix of small seine gear in the southern Philippines and northern Indonesia. Most of the purse seine catch was taken between 140–160E with lower catches extending eastward to 160W. Some degree of yellowfin spawning has been noted to occur in this area throughout the year as inferred by the presence of tuna larvae with a presumed lower temperature tolerance of 26°C although some larvae have been noted to occur in waters as low as 24°C (Ueyanagi, 1969; Nishikawa et al., 1985). To compare this area to a region characterized by seasonal yellowfin tuna spawning, the waters surrounding the Hawaiian island chain were included.

Sampling Period

Simultaneous sampling and data collection from all areas spanned a two year period, from May 1994 through April 1996. The two year sampling period was chosen to at least partially address the limitations of a single year of biological sampling i.e. to mitigate inter-annual variations in reproductive activity that may be related to shifts in large scale oceanographic conditions within the study area. The CWPO tuna fisheries exhibit significant inter-annual longitudinal variability in catch rates and productive fishing areas for skipjack and yellowfin tuna. These variations have been correlated to El Niño Southern Oscillation (ENSO) events that have a significant influence on the spatial distribution of sea surface temperatures, productivity and weather related indices for this region (Lehodey et al., 1997).

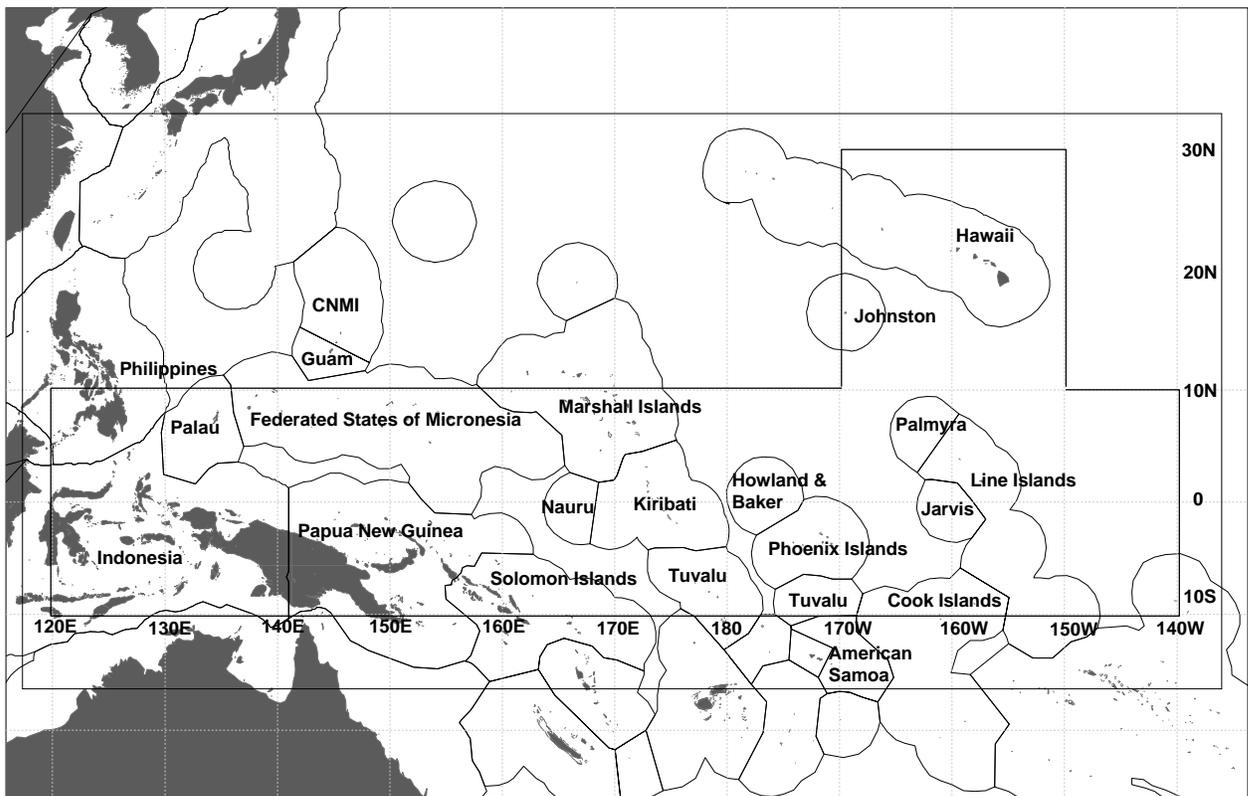


Figure 1. Project study area in the central and western Pacific Ocean.

Sampling Stratification

Project objectives were addressed through the collection of biological samples and related fishery data from both surface and sub-surface tuna fisheries over a broad spatial and temporal range. The target size classes for sampled yellowfin were established with respect to ten-centimeter categories between 50 and 150 cm in fork length. Some of the sampled fisheries land either small or large sized yellowfin, but samplers were instructed to sample fish from each 10 cm size class available during a sampling session. Male and

female yellowfin were measured but only ovaries from immature and mature yellowfin were sampled.

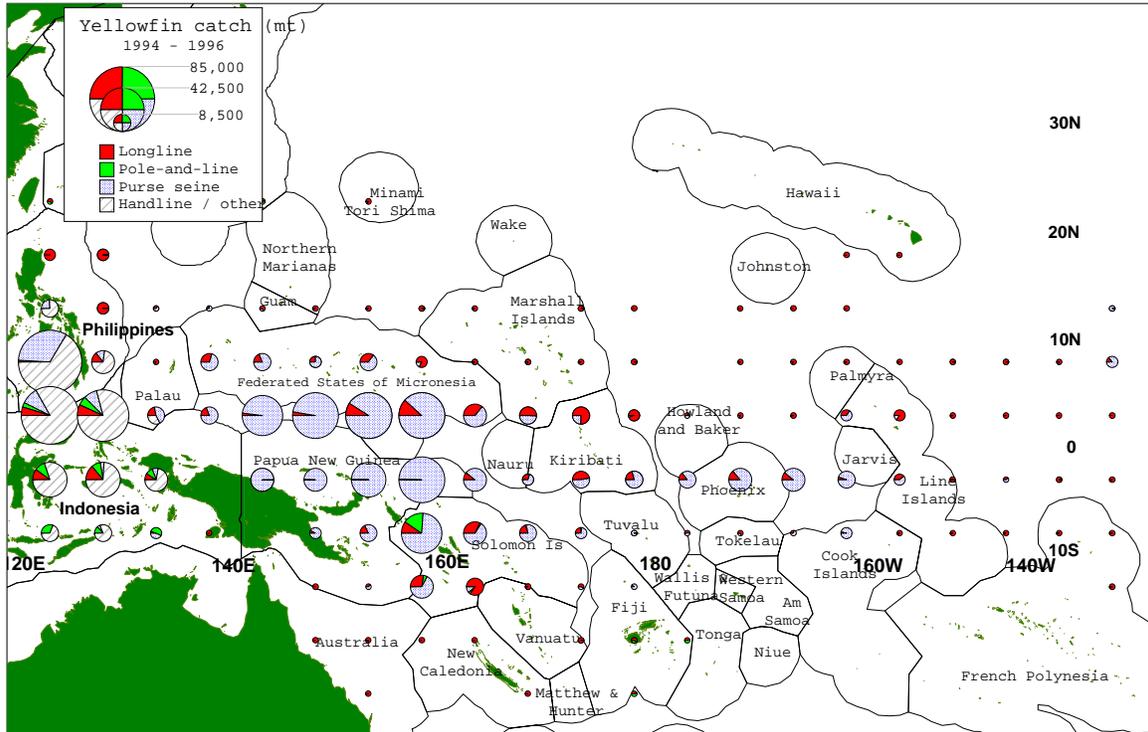


Figure 2. Yellowfin catch distribution by gear type for years 1994–1996 combined (mt). source SPC 1999.

DESCRIPTION OF SAMPLED FISHERIES

Western Pacific Region

General

Annual catches of yellowfin by large-scale gear types in the western Pacific region, excluding the Philippines and Indonesia were reported to be 263,393 and 215,809 mt during 1994 and 1995 respectively (SPC, 1996). Most of the catch by volume was produced by purse seine fisheries within ten degrees of the equator and within the boundaries of the proposed study area. Purse seine, longline and pole and line gear took 77.9%, 20.1% and 2.1% of the yellowfin catch with similar proportions reported in 1995 and 1996. Project sampling in this region reflected the relative magnitude of these commercial harvests, deriving mostly from purse seine and longline fleets of several domestic and distant water fishing nations.

Western Pacific Purse Seine

The purse seine fishery of the western Pacific is a relatively recent development, begun in the early to mid 1970s by Japanese vessels fishing mainly on tuna schools found in asso-

ciation with floating objects (Watanabe, 1983). American vessels expanded into the region in the late 1970s and became a major participant in the fishery by the early 1980s, successfully developing techniques to fish on free schools not associated with floating objects (Doulman, 1987). The fishery is now dominated by vessels of Japan, the Republic of China (Taiwan), the Republic of Korea and the United States, with some participation from purse seine vessels of the Federated States of Micronesia, the Solomon Islands and the Philippines (SPC, 1996).

These fleets generally employ one of two distinct fishing techniques to capture tuna schools in this region. 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 (Hampton and Bailey, 1993). These “log sets” can be accomplished before dawn when the tuna can not see to avoid the nets and the majority of sets are successful.

So called free schools or unassociated schools are also set on—these 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 large concentrations of forage fish. 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.

Western Pacific Longline

Longline activity targeting yellowfin and bigeye tuna within the study area is carried out primarily by distant water Japanese and Korean vessels and smaller Japanese, Taiwanese and mainland Chinese vessels operating out of transshipment ports throughout the western Pacific (SPC, 1996). Smaller domestic longline ventures are or have recently been active in the study area from the Federated States of Micronesia, the Marshall Islands, Papua New Guinea, Palau and Guam (USA).

Tuna longline vessels sampled by the project in the tropical western Pacific consistently employed one of two basic styles of longline fishing to take mostly mature sized yellowfin tuna. Fishing methods were highly consistent within fleets. Japanese longline vessels sampled for this study set 15 to 20 hooks between floatlines of 20 to 40 meters in length and set the mainline with a line shooter to throw additional line in the set to sink the gear deep in the water column. Their gear was normally set shortly after dawn and soaked during daylight hours to target large bigeye tuna that frequent deep waters during the day near the base of the thermocline. In sharp contrast, Taiwanese and mainland Chinese longline vessels sampled by the project utilized shallow-set gear with only four or five hooks per basket hung from 10 to 25 meter floatlines and fished their gear at night. Both styles of longline gear use single hook branchlines of 25 to 30 meters in length. Setting the shallow Taiwanese and Chinese gear normally began between 1700 and 1900 hours with line hauling commencing between 0600 and 0700 the following morning. These vessels also target bigeye, but by deploying gear close to the surface at night and concentrating effort during full moon periods (Williams, 1995)

Suzuki et al. (1977) estimated from 1974 and 1975 data that hooks of regular Japanese longline gear with an average of six hooks per basket fished at a depth of approximately 50 to 120 meters while deep-set gear with an average of 13 hooks per basket could normally fish to a depth of about 250 meters. Longline vessels sampled for this project apparently fished slightly shallower and deeper than these examples, with an average of five hooks per basket used by the shallow gear and 17 hooks set by vessels using deep-set gear. The shallow-set Taiwanese and Chinese gear is believed to fish very shallow as no line shooter is employed in the set. Observers estimated the gear was fishing at approximately 40 to 80 meters. The deep-set gear was estimated to fish between 50 and 300 meters.

Philippine and Indonesian Handline

The domestic fisheries of the Philippines and Indonesia reported yellowfin tuna landings of 123,210 and 119,821 mt during 1994 and 1995 from a variety of gear types (SPC, 1996). Approximately 35% of the catch, or over 40,000 mt of yellowfin was taken annually by simple handline gear targeting mature sized fish aggregated to anchored fish aggregation devices (FADs). Philippine vessels sampled for the study were diesel powered, double outrigger *bancas* with an average crew size of six making 6 to 10 day fishing trips in the Moro Gulf and northern Celebes Sea. These vessels deploy single hook handlines baited with small tunas or scads (*Decapterus* spp.) during the daytime as described by de Jesus (1982) and Yamanaka (1990) at depths of approximately 100 to 180 meters. Indonesian samples came from small handline vessels fishing on FADs anchored in the southern Molucca Sea utilizing similar gear and methods. Yellowfin and bigeye are targeted by both fisheries, iced whole and processed at the unloading sites.

Hawaii Region

General

Landing statistics for Hawaii domestic pelagic fisheries reported approximately 1860 mt and 2087 mt of yellowfin tuna for 1994 and 1995 taken by longline, pole and line, troll and handline gear (Anon, 1996). While these landings are small in comparison to the western Pacific fisheries, they contribute significantly to the economic viability of Hawaii based pelagic fisheries. Longline gear accounted for 34.1% and 45.7% of the reported yellowfin catch during these years, with the remaining catch reported by troll, handline and pole and line gear. Troll and handline landings, particularly from the sport and recreational sectors of the fishery are believed to be significantly under-reported.

Hawaii Troll and Handline

Small vessels of 5-8 m engage in trolling for yellowfin in Hawaii with a mixture of recreational, subsistence or part-time commercial motivations (Boggs and Ito, 1993). Slightly larger vessels are used by sport charter or full-time commercial trollers. Heavy sport tackle is used almost exclusively. The majority of yellowfin taken by surface troll,

handline and pole and line gear are juvenile fish estimated at a mean weight of 13.6 kg in 1995 (Anon, 1996). The troll catch of large yellowfin peaks during the summer months.

Yellowfin are also taken by a variety of small boat handline fisheries for small and large sized fish. *Palu ahi* handline gear is a modern adaptation of an ancient Polynesian fishing technique for handlining sub-surface tuna of medium to large sizes during the daytime. A recently developed offshore handline fishery employs a variety of handline and troll techniques to catch juvenile tuna aggregated to productive offshore seamounts and moored buoys. The *ika shibi* handline fishery targets large sized fish and takes place at night, having evolved from a squid fishery off the windward coast of the island of Hawaii (Yuen, 1979). The technique has spread to the other populated Hawaiian islands and concentrates on large yellowfin tuna during the summer months. Vessels are 6–9 meters in length and normally operated by one to two persons (Boggs and Ito, 1993). An underwater light is set to attract squid and baitfish with two to four baited lines set at approximately 20 to 40 meters (Rizutto, 1987). These fishing depths suggest it is a night-time surface fishery in contrast to the sub-surface daytime handline fisheries of the Philippines and Indonesia.

Hawaii Longline

Hawaii based longline vessels have been categorized into three size classes: less than 56 feet in length (17.1 m), 56 to 74 feet in length (17.1–22.6 m) and vessels over 74 feet (22.6 m) that target either tuna, swordfish or a mixed assemblage of swordfish and tuna species (Anon, 1996; Dollar, 1994). Both fisheries have a substantial utilized bycatch of other billfish and pelagic species. In a similar fashion to the western Pacific longline fisheries, Hawaii based longliners use either deep-set gear fished during the day or shallow-set gear fished at night. Gear configurations fall into two categories. The deep-set tuna gear deploys 15–40 hooks per basket set in the morning around 0700 hours with gear hauling beginning between 1600 and 1700 hours. Shallow-set gear consists of an average of 5 hooks per basket set around 1900–2000 hours with gear retrieval around 0700–0800 hours. The deep-set daytime gear targets bigeye and albacore tuna while shallow-set gear is typically used to target swordfish by setting at night with chemical light sticks, although the gear also takes bigeye and bluefin tuna. Both gear configurations harvest yellowfin tuna and project samples were obtained from both shallow and deep-set gear. Shallow-set gear is also used by some vessels to target yellowfin during the summer months when high catch rates are possible.

FISHERY SAMPLING PROCEDURES

Western Pacific Region

Purse Seine and Longline Fisheries

Project samples were obtained directly from capture fisheries, with the exception of ovary samples collected by Japanese longline fishery training vessels. Sampling by both surface and sub-surface gear types for all areas was conducted whenever possible.

Sampling of these fisheries was conducted through cooperation with regional and Pacific Island fishery observer programs. At-sea observer programs were used by the study whenever possible to obtain detailed fishery data and fresh biological samples of high quality. Observers from the Forum Fisheries Agency (FFA) collected biological samples and data from U.S. purse seine vessels operating under conditions of the multi-lateral South Pacific Tuna Treaty. Observers from the Micronesian Maritime Authority (MMA) and the South Pacific Commission–Oceanic Fisheries Programme (SPC-OFP) collected samples from purse seine and longline vessels of Japan, the Republic of China (Taiwan), the Republic of Korea, the United States and the Federated States of Micronesia. Longline vessels of the Peoples Republic of China (mainland China) were also sampled by these organizations.

Project sampling was conducted on Japanese prefectural longline training vessels through cooperation with the National Research Institute of Far Seas Fisheries (NRIFSF). These vessels operated mostly in areas adjacent to the proposed study area but also in important regions within the study area not sampled by other means between 10EN–15EN and 30EN–35EN; areas to the south and north of the main Hawaiian Islands.

Philippine and Indonesian Handline Fisheries

The handline fisheries of the Philippines and Indonesia are not monitored by domestic or regional observer programs, eliminating the possibility of sampling at sea. An assessment of yellowfin ovarian material landed by the Philippine handline fishery suggested it to be suitable for histological analysis. These vessels normally make fishing trips of five to ten days, with fish held whole on ice. The fish are weighed and eviscerated at the landing site, which provides a good opportunity for port sampling.

Project sampling in the Philippines took place at Lion Beach, General Santos City on the southern Philippine island of Mindanao. Lion Beach is the major landing site for Philippine handline vessels that operate in the Moro Gulf and northern Celebes Sea, and land yellowfin and bigeye tuna for fresh sashimi export or lower grade domestic markets. A port sampling program for the project was established at Lion Beach through the cooperation of the Bureau of Fisheries and Aquatic Resources (BFAR) of the Philippine government. Approximately 100 female yellowfin tuna were sampled per month over a two year period.

Samples from Indonesia came from coastal handline vessels operating in the south Molucca Sea. Single day fishing trips were conducted with fish held in whole condition on ice, which produced samples in excellent condition at the time of unloading. A port sampling program was established at a large tuna landing site at Panamboang, near Labuha, Bacan through cooperation with the Research Institute for Marine Fisheries and the national fishing company P.T. Usaha Mina. Figure 3 indicates the port sampling sites and fishing grounds sampled in the Philippines and Indonesia. Approximately 100 female yellowfin tuna were sampled per month over a two year period in Indonesia.

Hawaii Region

Hawaii Longline Fishery

Sampling in Hawaii concentrated on the longline fishery throughout the year and the surface troll and *ika shibi* handline fisheries that operate primarily during the summer months. Hawaii based longliners normally do not process their target catch at sea making access to tuna ovary samples prior to sale very difficult. Vessels in this fishery make trips of one to three weeks duration, maintaining whole tuna in a fresh, iced condition. Tests were performed on yellowfin ovarian material from this fishery and most samples were in suitable condition for histological interpretation. Gonad sampling of landed catch was conducted through cooperation with fish processors after the fish had been landed and sold at the United Fishing Agency auction in Honolulu.



Figure 3. Project port sampling sites in the Philippines and Indonesia.

Hawaii Troll and Handline Fisheries

Troll and handline catches were sampled at unloading sites or shore based processing facilities after single day fishing operations. Some sampling was conducted by small boat handline and troll fishermen who processed their catch at sea and were supplied with formalin, containers, sampling instructions and training.

GONAD SAMPLING AND PROCESSING

Histological Samples

The determination of maturity stage, spawning frequency and periodicity was based on the histological interpretation of preserved ovarian material. Other methods, such as the visual assessment of ovaries, gonosomatic index analysis (GSI) or the measurement of oocyte diameters are considered far less precise indicators of reproductive condition (West, 1990).

Ovary sampling procedures included the selection of fish within the required size classes and the recording of fork length to the nearest centimeter using a calibrated 1.6 meter calliper. Specimens were identified to sex by visual examination of the gonads and ovary pairs were removed from all female yellowfin and weighed to the nearest 10 grams using 1000 gram capacity T-2 Accu-Weigh Tubular spring scales.

A central section of the larger ovary approximately 1.5 centimeters in thickness was excised and placed in a 60 ml plastic vial pre-filled with 10% phosphate buffered formalin as per Roe (1985). For large ovaries greater than 3.0 cm in diameter, a pie shaped portion of the cross section was cut away and preserved to allow rapid formalin penetration and fixation of the sample. Preserved specimens were stored in a sheltered, dry location until the end of the sampling trip. The remainder of the ovarian material was discarded.

An exception to immediate formalin fixation of ovary samples took place on Japanese longline training vessels. These vessels offset expenses through revenue generated from fishing operations and would not allow formalin on board due a concern over possible contamination of the catch. However, the vessels were equipped to freeze catch at -60C to preserve sashimi quality in tuna. Tests were conducted by freezing yellowfin tuna ovarian material to this temperature which were later thawed and preserved in formalin. The stained and mounted specimens were judged to be in a less than ideal but adequate condition for histological analysis. Therefore, samples collected by Japanese longline training vessels were frozen and later transferred to 10% buffered formalin after the completion of the trip.

A portion of each preserved ovarian sample, which included several ovigerous lamellae with tissue extending from the outer ovarian wall to the inner lumen was embedded in Paraplast, sectioned to approximately 4 μ m and stained with Harris' hematoxylin followed by Eosin counter stain. Three serial sections were mounted on standard 25 by 75 mm microscope slides for examination by light microscopy. A Nikon Diaphot-TMD mi-

croscope with 10x Nikon eyepieces was used for all histological interpretations under 4x and 10x Nikon objectives. Light photo microscopy was conducted with a Nikon FE 35 camera body fitted to the microscope loaded with 100 ASA film.

Batch Fecundity Samples

Accurate batch fecundity estimates for yellowfin tuna can only be made from ovaries in a hydrated but pre-ovulatory condition, as any loss of oocytes would bias fecundity estimates. Yellowfin tuna is recognized to be a serial spawner (Schaefer, 1996; 1998). Fecundity estimates based on non-hydrated ovaries can significantly over-estimate batch fecundity as successive spawning batches can not be clearly differentiated until the onset of hydration (Schaefer, 1996). Previous studies and field observations have noted yellowfin spawning to occur in the evening or early morning hours with hydration presumed to occur a few hours prior to ovulation. Therefore, samplers were instructed to watch for tuna with hydrated ovaries during the late afternoon. The best opportunity to obtain fish in this condition came from troll and purse seine fisheries. Hydrated ovary pairs were carefully excised, placed in a labeled plastic bag and frozen on the vessel and maintained in a frozen condition until fecundity estimates were conducted.

Batch fecundity estimates were made using the hydrated oocyte method as described in Hunter et al. (1985). Frozen samples were partially thawed and ovary pairs were weighed to the nearest 0.1 g. Sections of ovigerous lamellae weighing approximately 0.04 to 0.05 g were taken from the anterior, middle and posterior region of the same ovary for fecundity counts. The samples were removed from the mid-section of one intact ovigerous lamellae and weighed to the nearest 0.01 mg. The sample was then evenly spread over a microscope slide etched longitudinally to assist counting, saturated with a glycerine solution and covered with a 25 mm x 60 mm slide cover. The number of hydrated oocytes present in each sample was counted three times and the numeric mean applied to the known weight of the sample and the total weight of the whole ovary sample to yield an estimate of batch fecundity. Estimates from the anterior, middle and posterior sections of the ovary were averaged to yield an estimate representative for the entire sample.

Gut Content Samples

Stomach contents of female yellowfin were examined at the time of ovary sampling. Stomachs were characterized as to fullness and major food items were preserved in 10% phosphate buffered formalin.

DATA COLLECTION

General

Fork length measurements to the nearest cm were recorded for each fish selected for sampling. After identification of the fish to sex by visual examination of the gonads, the sex was noted and the total weight of both ovaries was recorded for sampled females. Additional information recorded for all fisheries included the sampler name, vessel name, date, capture area or position, and sea surface temperature. The tuna school type and school association was noted in addition to any interesting comments specific to that tuna school.

Purse Seine and Longline Fisheries

Gonad Sampling

The date, individual set number, set start time, set end time, set start position and sea surface temperature was recorded for purse seine sets. Samplers on longline vessels recorded the date and start time of setting, date and start time of hauling and the position at the start of line hauling. To categorize the type and capture depth range of longline gear used, the floatline length, number of hooks between floatlines (hooks per basket) and an estimate of targeted fishing depth were recorded. All observers were instructed to note unusual or significant observations, such as fish in running ripe condition or feeding behavior and to note the sex ratio of the sample in the comments section.

The fork length, gonad weight and a unique sample number for the trip was noted. The vessel name, date, fork length, gonad weight and the corresponding sample number was recorded on a label placed inside the sampling vial with the formalin and sample. At the conclusion of purse seine and longline cruises, the samples were sorted, drained of formalin, placed in leak-proof specimen bags and shipped to Hawaii for processing and analysis.

Gut Contents

Data collectors on purse seine and longline vessels were instructed to note information on the feeding behavior and stomach contents of yellowfin sampled for the project. The observers noted stomach fullness according to a simple four point scale of empty, slight, half or full. Stomach contents were placed in labeled sample vials filled with 10% buffered formalin and shipped to Hawaii with their corresponding gonad samples.

Philippine and Indonesian Handline Fisheries

Similar data collection forms were designed for handline caught yellowfin sampled in the Philippines and Indonesia. Information on the catch area, trip length and sample date were noted as the port samplers could not determine exactly when and where a particular fish was caught. However, the short trip lengths and limited range of the vessels allow for

reasonable estimates of catch area and location. The estimated depth of capture was also noted. Fish are landed whole in both fisheries, and the whole weight of each fish was recorded in both sampling locations. Philippine and Indonesian samples were assigned the capture positions of 5N, 123E and 1S, 127E respectively for database purposes.

Hawaii Based Fisheries

Hawaii troll and handline caught samples were usually preserved within a day of capture. Some handline and troll caught samples were preserved immediately after capture by suitably trained and equipped fishermen. Sampling and data collection was conducted as for other fisheries. Fork length measurements were taken and if necessary, converted to estimated weights according to Nakamura and Uchiyama (1966) giving length/weight relationships for central Pacific yellowfin tuna.

Data collection procedures for Hawaii based longline vessels varied slightly from western Pacific sampling due to landing and marketing characteristics of the fishery. Sampling took place after the fish were sold at auction. Fork length measurements could not be obtained from these samples as the caudal fin is removed from all large longline caught tuna immediately after the fish are delivered and weighed at the United Fishing Agency. To resolve this problem, an alternate length measurement of upper snout to the insertion of the second dorsal fin was taken to the nearest mm and later converted to fork length using a linear regression derived from morphometric studies and field sampling¹. Capture date and position for Hawaii longline samples were estimated from federal logsheet data made available by the National Marine Fisheries Service, Honolulu Laboratory. Data from lengthy or geographically wide-ranging fishing trips and trips that ventured south of 15N latitude were not used in the analysis of reproductive parameters.

MATURITY STAGES

Histological criteria from ovary samples were used to classify the maturity stage of yellowfin based on characteristics and classification systems described by Hunter and Macewicz (1985) and Schaefer (1987; 1996; 1998). Each sample was assigned to one of ten maturity stages defined for this study which defined the degree of oocyte development and condition, spawning condition and degree of atresia. Stages 1–3 describe immature females and stages 4–10 represent mature samples with varying degrees of atresia of oocytes and spawning activity. Maturity was defined by the presence of fully yolkeed oocytes or atresia of fully yolkeed oocytes indicating that the fish had reached a stage with a potential to spawn.

The most advanced or developed group of oocytes present in the samples were described as (1) unyolkeed; (2) partially yolkeed; or (3) fully yolkeed. An oocyte was considered partially yolkeed if any eosinophilic (red) staining yolk spherules were observed or if yolk granules or globules were observed to extend from the cell periphery inward to within three quarters of the distance to the perinuclear zone. Fully yolkeed oocytes contain well

¹ FL = 2.1622X - 11.88 where X = snout to insertion of second dorsal fin in centimeters derived by the author from morphometric data from Hawaiian yellowfin tuna between 80 and 160 cm in Schaefer (1952).

developed yolk globules evident from the perinuclear zone to the outer periphery of the oocyte. Fully yolked oocytes were categorized as (1) normal; (2) coalescent (3) migratory nucleus stage; or (4) hydrated. In the second category (coalescent), lipid droplets around the nuclear periphery combine with each other, forming noticeably larger oil droplets. In the migratory nucleus stage, all lipid droplets coalesce into a single, large oil droplet with the nucleus in some stage of migration toward the animal pole. These stages correspond to the early and late migratory nucleus stages as described by McPherson (1991). Hydration was characterized by the fusion of yolk globules into platelets, a significant enlargement in oocyte diameter due to fluid uptake, and with full hydration, a homogenous and hyaline appearance within the cell boundary as the cell contents fuse. Samples were further categorized as to the type and degree of atresia of oocytes and the presence or absence of postovulatory follicles in the sample. Alpha and beta atresia of oocytes was categorized as (1) zero; (2) less than 50%; (3) greater than 50% or (4) 100%.

Postovulatory follicles degenerate rapidly, and at a regular rate, particularly in warm waters (Hunter and Macewicz, 1985). Previous studies have assumed a regular rate of follicular degeneration in yellowfin that is complete within 24 hours, based on observations of the condition of postovulatory follicles relative to capture time, the presence of follicles in the most advanced stages of degeneration in association with hydrated oocytes, and the consistent absence of two degenerating stages of postovulatory follicles within the same ovary (Nikaido, 1988; Schaefer, 1996).

Table 1 describes the ten maturity stages with Figure 4 indicating immature ovary samples in stages 1, 2 and 3, with oocytes progressing from unyolked to partially yolked condition. Figure 5 indicates yellowfin oocytes classified as mature in this study and assigned to stages 4–7. Stage 4 ovaries contain unyolked or partially yolked oocytes with atresia of fully yolked oocytes indicating the potential to spawn had been reached (Figure 5a). Stage 5, 6 and 7 describe ovaries with fully yolked oocytes and zero or minor atresia (Figure 5b, 5c, 5d). Stages 6 and 7 describe fish in active spawning condition due to the presence of postovulatory follicles or oocytes in migratory nucleus or hydrated condition.

Table 1. Yellowfin maturity stages used by the study

Stage	Maturity classification	Oocyte condition	Atresia	Comments
1	Immature	Majority of oocytes in late diplotene or early perinucleus stage	No atresia	Densely packed oocytes darkly stained with Hematoxylin
2	Immature	Mix of early and late perinucleus stage oocytes. No yolk granules present	No atresia or minor atresia of unyolked oocytes	Early developing stage
3	Immature	Partially yolked	No atresia or minor atresia of unyolked oocytes	Red staining yolk granules or globules evident from cell periphery inward to within 3/4 of distance to perinuclear zone
4	Mature	May be unyolked or partially yolked	Atresia of fully yolked oocytes evident	Considered to have reached a fully yolked and potentially reproductive state but regressed to a reproductively inactive state
5	Mature	Fully yolked oocytes present but no post ovulatory follicles observed	Zero or less than 50% atresia of fully yolked oocytes	A mature, potentially reproductive fish
6	Mature	Fully yolked oocytes present. Oocytes may be in migratory nucleus or hydrated condition and/or post ovulatory follicles present	Less than 50% atresia of fully yolked oocytes, generally zero or minor atresia	An actively spawning fish with zero or minor atresia. A typical, actively reproductive and spawning fish
7	Mature	Fully yolked oocytes present. Oocytes may be in migratory nucleus or hydrated condition and/or post ovulatory follicles present	Atresia of 50% or more of fully yolked oocytes	An actively spawning fish with significant atresia.
8	Mature	Some fully yolked oocytes present but none in migratory nucleus or hydrated condition. No POFs present	Atresia of 50% or more of fully yolked oocytes	A potentially reproductive fish with significant atresia
9	Mature	No fully yolked oocytes but atresia of fully yolked oocytes evident	100% atresia of fully yolked oocytes	A mature fish in non-spawning phase
10	Mature	No fully yolked oocytes present. Oocytes resemble Stage 1 or 2	Advanced atresia of oocytes	A mature fish in advanced atretic, post spawning phase

Figure 6 indicates fully yolked oocytes in advancing stages from a normal (resting) condition to full hydration, immediately prior to ovulation. Figure 6a indicates a typical, mature sample with a mix of unyolked, partially yolked and fully yolked oocytes. Lipid droplets combine to form larger oil droplets surrounding the nucleus during the stages prior to hydration (Figure 6b). At the migratory nucleus stage (Figure 6c), the oil droplets combine into one large oil droplet with the nucleus in some stage of migration toward the

animal pole. Figures 6d and 6e show yellowfin oocytes in early and late stages of hydration. Post ovulatory follicles in advanced stages of resorption are evident between the hydrated oocytes, suggesting a daily spawning periodicity.

Stage 8 ovaries have some fully yolked oocytes but contain greater than 50% atresia of fully yolked oocytes and are typical of spawning yellowfin that are either shutting down a reproductively active period (Figure 7a). Stage 9 fish have 100% α and/or β atresia of fully yolked oocytes and are typical of post spawning, or reproductively inactive but mature fish (Figures 7b, 7c). Figure 7d shows a Stage 9 sample in advanced stages of α and β atresia.

Figure 8a shows a Stage 10 sample, classified in this study as a mature, reproductively inactive fish. Stage 10 samples exhibit such advanced atresia of yolked oocytes that they may be difficult to distinguish histologically from immature Stage 1 samples. However, these samples were classified as mature in this study due to the presence of advanced oocyte atresia, large and well developed ovigerous lamellae, thick ovarian walls and large fish size. This classification scheme was supported by the observation of mature, reproductively active yellowfin progressing rapidly from stage 7 through 10 in Hawaii at the end of the spawning season (September–October). The reverse situation occurred at the beginning of the spawning season, when ovary samples from large yellowfin progressed from Stage 10 to reproductively active Stage 6 fish. Figure 8b shows a Stage 10 sample with unyolked, but developing oocytes.

REPRODUCTIVE CLASSIFICATIONS

The **immature** category consisted of Stage 1, 2 or 3 fish with unyolked or partially yolked oocytes and no atresia of fully yolked oocytes. Samples in Stages 4-10 were classified as **mature** fish due to the presence of fully yolked oocytes or atresia of fully yolked oocytes indicating at least the potential to reproduce. The ovary samples of **reproductively active** fish contained fully yolked oocytes with zero or minor atresia or evidence of recent or imminent spawning activity (Stages 5, 6 and 7). **Actively spawning** fish in Stage 6 or 7 with postovulatory follicles evident in the sample were used to calculate the fraction spawning per day while peak spawning areas and seasons included samples with oocytes in migratory nucleus or hydrated condition. Stage 4, 8, 9 and 10 were considered **mature**, but **reproductively inactive** fish (Table 2).

Table 2. Maturity classification system

Category	Stage	Fully yolked oocytes present	POF present	Comments
Immature	1,2,3	No	No	Oocytes have never reached fully yolked condition
Mature	4 to 10	Yes for St. 5 - 8	Yes for St. 6, 7	Having developed fully yolked oocytes
Reproductively active	5, 6, 7	Yes	Yes for St. 6, 7	Fully yolked oocytes present
Spawning	6, 7 ²	Yes	Yes for St. 6, 7 No for St. 5	Histological evidence of recent or imminent spawning
Reproductively inactive = atretic = post spawning	4, 8, 9, 10	Yes for St. 8	No	Had developed fully yolked oocytes but now regressed to partially or completely inactive condition

Estimates of the age in hours of postovulatory follicles were used to estimate time of spawning (ovulation) from samples with a known time of capture (mortality) and sample preservation. The age of postovulatory follicles was based on the relative size and folded appearance of the structure and the appearance of the granulosa and thecal cell layers and granulosa cells as described by Hunter and Macewicz (1985) and Schaefer (1996). Figures 9a–9d indicate post-ovulatory follicles of advancing age in various stages of degeneration and resorption. Degenerating post ovulatory follicles can also be seen in Figures 6b, 6c, 6d and 6e.

Figures 4-9 may be viewed full size and in color at <http://www.soest.hawaii.edu/PFRP/biology/itano/oocytes.html>

² Considered spawning only if oocytes observed in migratory nucleus or hydrated condition

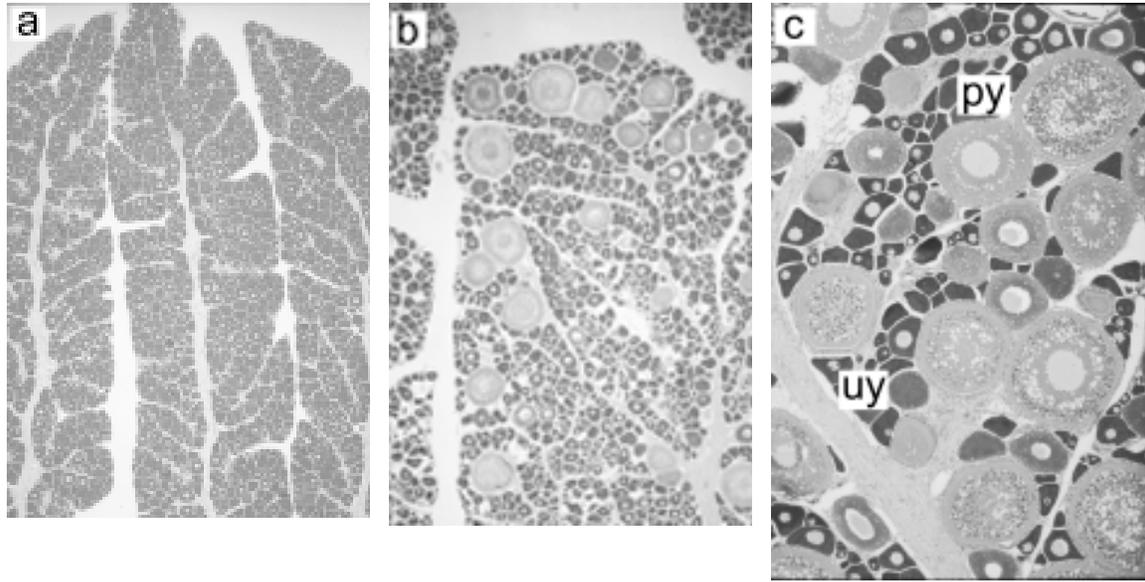


Figure 4. Transverse section of immature ovaries of yellowfin tuna indicating oocytes in advancing developmental stages. (a) Stage 1 - immature with early stage, unyolked oocytes @ 40x (b) Stage 2 - immature, unyolked but developing oocytes @40x. (c) Stage 3 - immature, mix of unyolked (uy) and partially yolked (py) oocytes @40x.

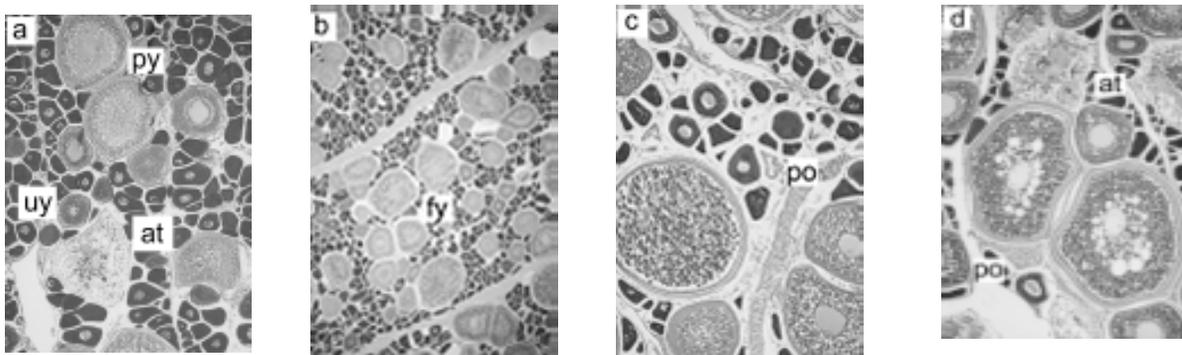


Figure 5. Transverse section of mature yellowfin ovaries in different stages. (a) Stage 4 – mature reproductively inactive tuna with unyolked (uy), partially yolked (py) and alpha atresia of fully yolked (at) oocytes @100x. (b) Stage 5 – mature, potentially reproductive with fully yolked (fy) oocytes present @40x. (c) Stage 6 – reproductively active, fully yolked oocytes and post ovulatory follicles (po) present @ 100x. (d) Stage 7 – reproductively active, fully yolked oocytes and post ovulatory follicles (po) present with significant atresia of fully yolked oocytes (at) @100x.

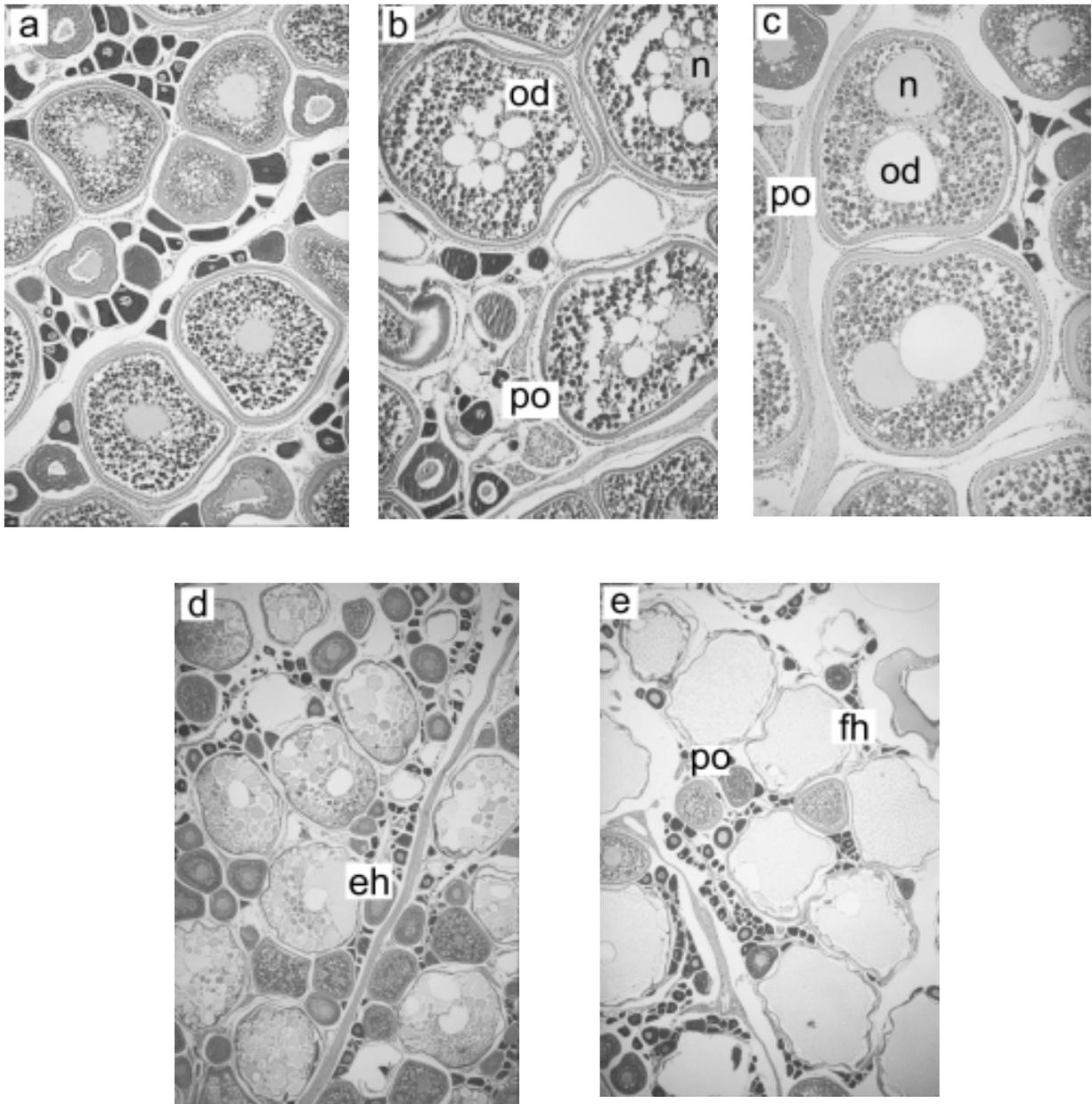


Figure 6. Fully yolked yellowfin oocytes in stages advancing toward ovulation. **(a)** Normal, fully yolked oocyte with well developed yolk globules @100x. **(b)** Coalescent stage oocytes with lipid droplets combined into larger oil droplets (od) surrounding the nucleus (n). Degenerated post ovulatory follicles (po) are evident @100x. **(c)** Migratory nucleus stage oocyte with lipid combined into one large oil droplet with the nucleus (n) migrating toward the animal pole @100x. **(d)** Early hydrated (eh) oocytes showing disintegration of the nucleus and fusion of yolk globules into larger yolk platelets @40x. **(e)** Fully hydrated (fh) oocytes with a degenerated post ovulatory follicle (po) evident indicating daily spawning periodicity @40x.

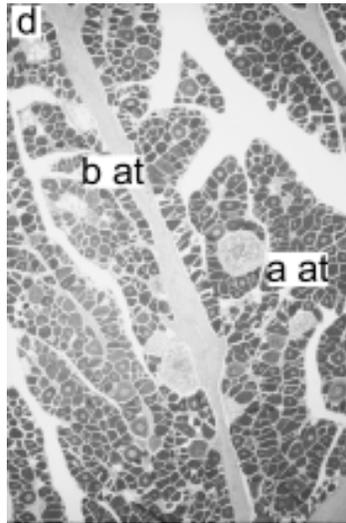
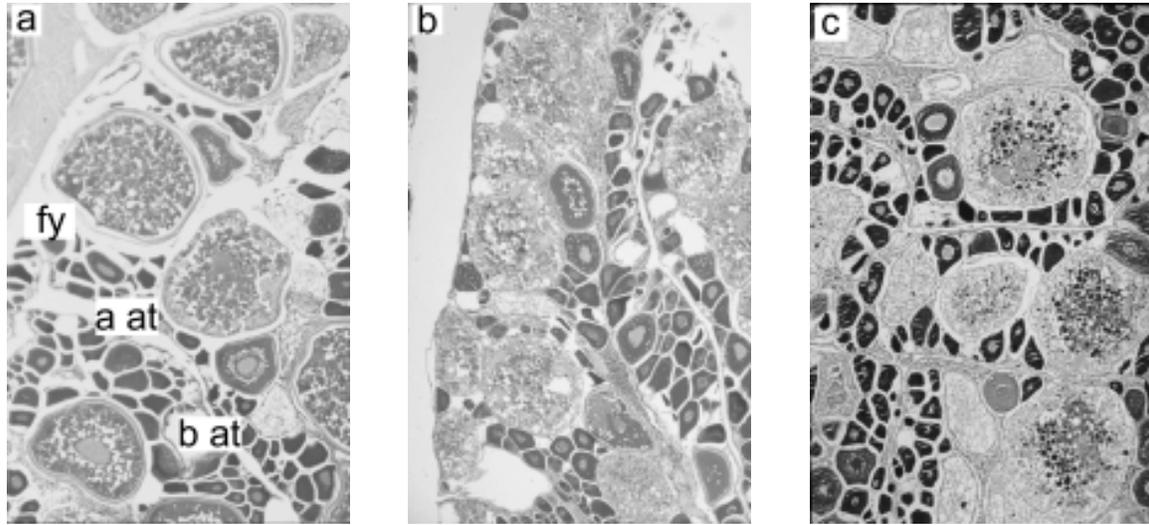
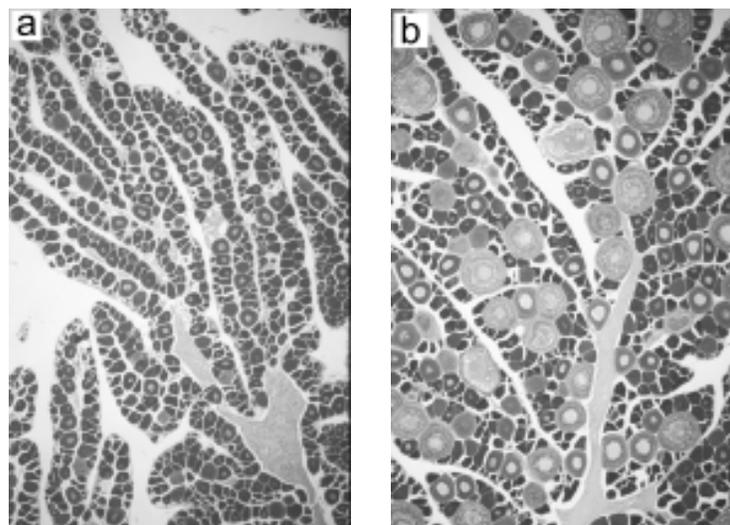


Figure 7. Ovary samples from the Hawaii region (Area F) progressing from a fully yolked to fully atretic, post spawning condition. **(a)** Stage 8 – some fully yolked oocytes (fy) with significant α (α at) and β (β at) atresia of fully yolked oocytes @100x. **(b)** Stage 9 – 100 per cent α atresia of fully yolked oocytes @40x. **(c)** Stage 9 – 100 per cent alpha and beta atresia of fully yolked oocytes @40x. **(d)** Stage 9 – advanced α (α at) and β (β at) atresia @40x.

Figure 8. Ovary samples progressing from a fully atretic to reproductively active condition. **(a)** Stage 10 sample @40x. **(b)** Stage 10 sample with unyolked but developing oocytes @40x.



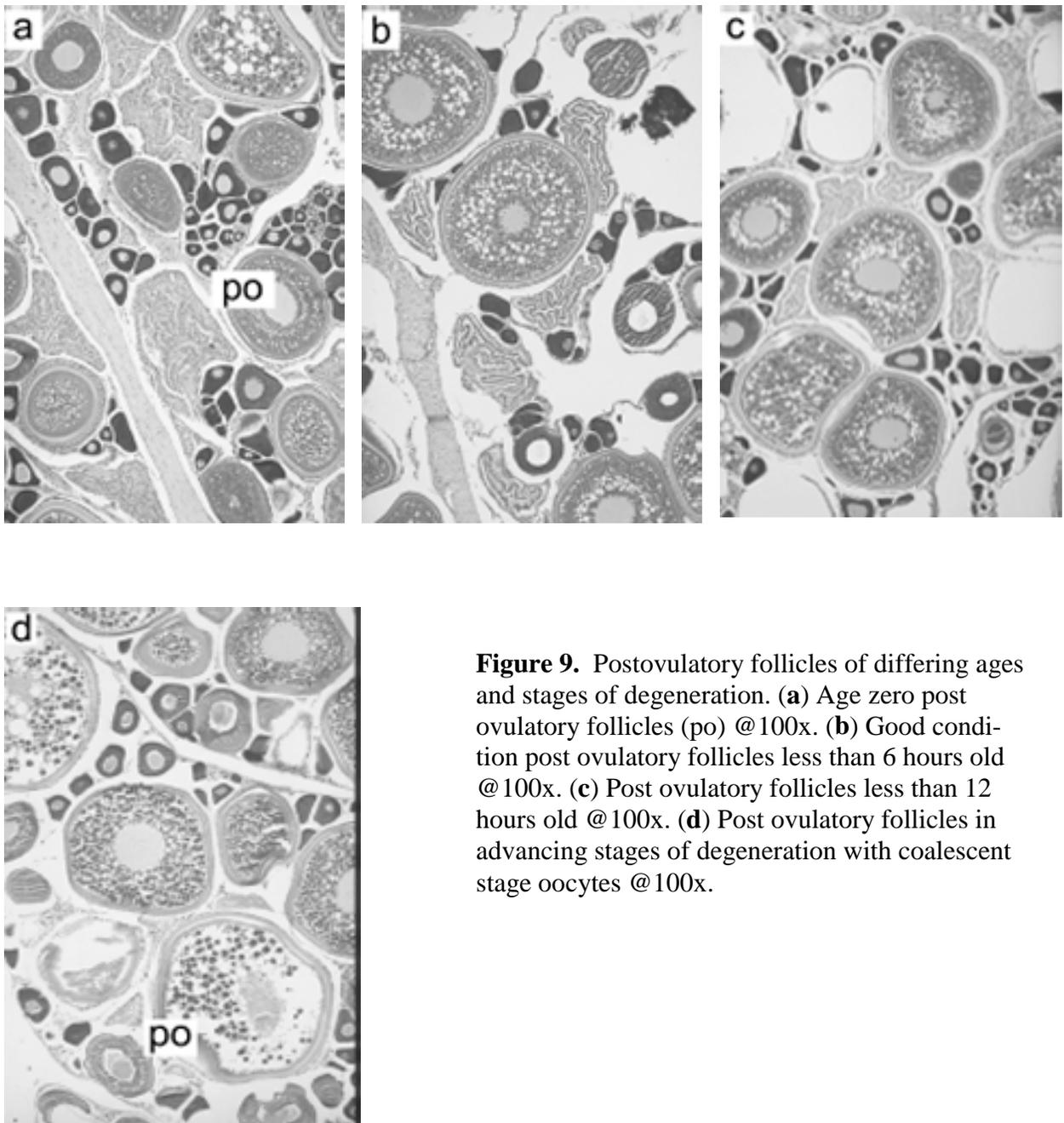


Figure 9. Postovulatory follicles of differing ages and stages of degeneration. (a) Age zero post ovulatory follicles (po) @100x. (b) Good condition post ovulatory follicles less than 6 hours old @100x. (c) Post ovulatory follicles less than 12 hours old @100x. (d) Post ovulatory follicles in advancing stages of degeneration with coalescent stage oocytes @100x.

POST-COLLECTION STRATIFICATION OF SAMPLES

The proposed study area was stratified into six areas to examine peak seasons and areas of yellowfin spawning and to address interaction and vulnerability aspects between the different fisheries (Figure 10). Areas A, B, C and D lie within 10 degrees of the equator. Area A included all sampling from the Philippine and Indonesian handline fisheries, with areas B, C and D comprising samples collected from purse seine, shallow-set longline and deep-set longline gear. Most of the samples from area E came from Japanese training vessels running deep-set longline gear at 10°–15° N latitude. Area F included samples from the Hawaii region collected from several different fisheries and gear types.

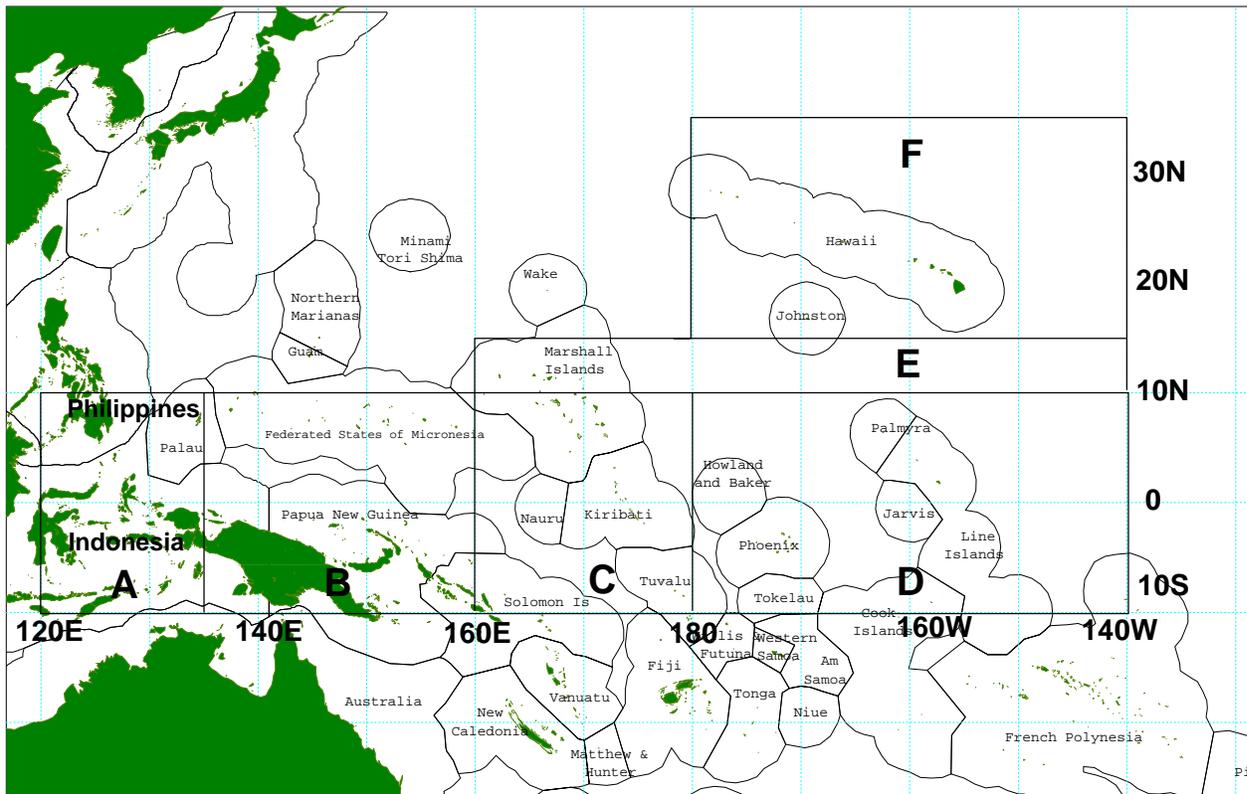


Figure 10. Post-stratification of samples by area and fishery.

SAMPLING DISTRIBUTION

A total of 10,898 yellowfin ovary samples were collected and preserved during the project and shipped to Hawaii for analysis. The sampling density by five degree square areas by gear type is given in Figure 11. Generally, sampling density mirrored catches from this region as indicated in Figure 2. Area A samples were taken by simple handline gear only while purse seine, shallow and deep-set longline gear was sampled from areas B, C and D. Area E is represented only by deep-set Japanese longline gear. Area F is the Hawaii region where samples were collected by longline, *ika shibi* handline, troll and sport pole gear. The exact positions of sample collection in the Philippine and Indonesia were

not known but were assigned the capture positions of 5°N, 123°E and 1°S, 127°E respectively. These positions were considered adequate considering the limited operational range of these fisheries.

Table 3 summarizes sampling levels for different regions of the study area. Of the total number of samples, 10,063 were classified to reproductive condition. Figure 12 indicates the length frequency distribution of female yellowfin sampled from all areas from fish measuring between 50 and 161 cm fork length in two centimeter length classes, including 23 fish that measured greater than 161 cm (n=10,850).

Different subsets of the collected samples were used depending on the area and analysis conducted. Sampling in Indonesia and the Philippines was conducted at a steady level over the two year period and almost all samples were processed and histologically interpreted. However, all of these samples were taken by handline fisheries and consisted of medium to large sized fish well above the observed size at first maturity for yellowfin from these areas. The length frequency distributions of female yellowfin in two centimeter length classes sampled in the Philippines and Indonesia are given in Figures 13 and 14.

Table 3. Yellowfin ovary samples collected by area and gear type (Forum Fisheries Agency, FFA; Australian Observer Program, AUS; Micronesian Maritime Authority, MMA; National Fisheries Corporation, NFC; South Pacific Commission, SPC; National Research Institute of Far Seas Fisheries, NRIFSF; National Marine Fisheries Service, NMFS)

Source	Sampling area	Gear types	No. female samples collected	Reproductively classified
Indonesia	Molucca Sea	Handline	1917	1912
Philippines	Moro Gulf, Celebes Sea	Handline	1740	1733
FFA	WTP	Purse seine	1194	1191
AUS	WTP	Purse seine	105	105
MMA	WTP	Purse seine, longline	2077	2010
NFC	WTP	Longline	18	18
SPC	WTP	Purse seine, longline	209	209
NRIFSF	Western and central Pacific	Longline	2929	2179
Processors	Hawaii	Longline, troll, handline	576	575
Fishermen	Hawaii	Troll, handline	129	127
NMFS	Hawaii	Longline	4	4
Total			10898	10063

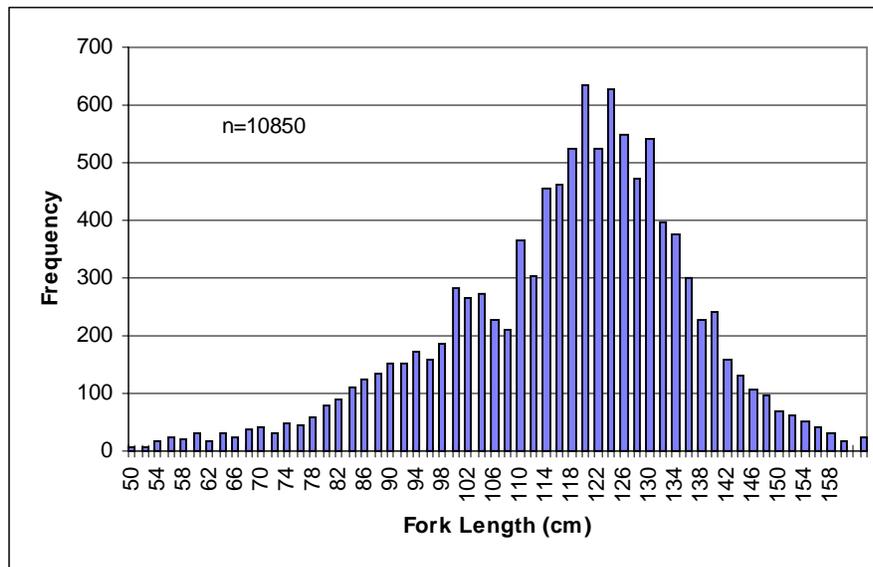


Figure 12. Length frequency distribution of female yellowfin sampled from all areas from fish measuring between 50 and 161 cm fork length (n=10,850).

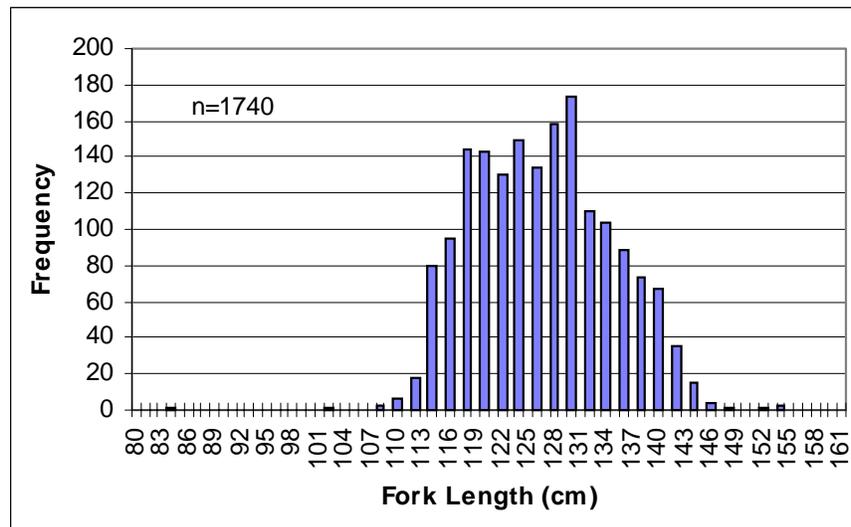


Figure 13. Length frequency distribution of female yellowfin sampled from the southern Philippines. (n=1740)

Sampling in the western tropical Pacific region of the study area east of the Philippines and Indonesia (Areas B, C, D) contributed 3811 samples from purse seine and longline vessels of several distant water and Pacific island domestic fleets. Figure 15 shows the length frequency distribution of samples collected in Areas B, C and D having fork lengths between 50 and 160 cm (n=3807).

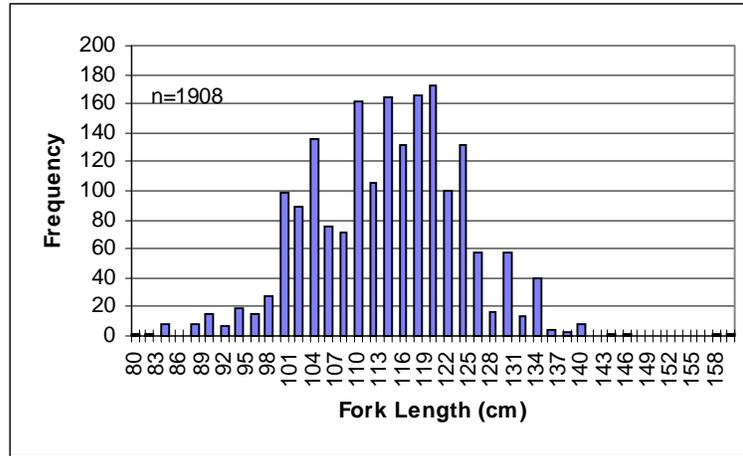


Figure 14. Length frequency distribution of female yellowfin sampled from Indonesia. (n=1908)

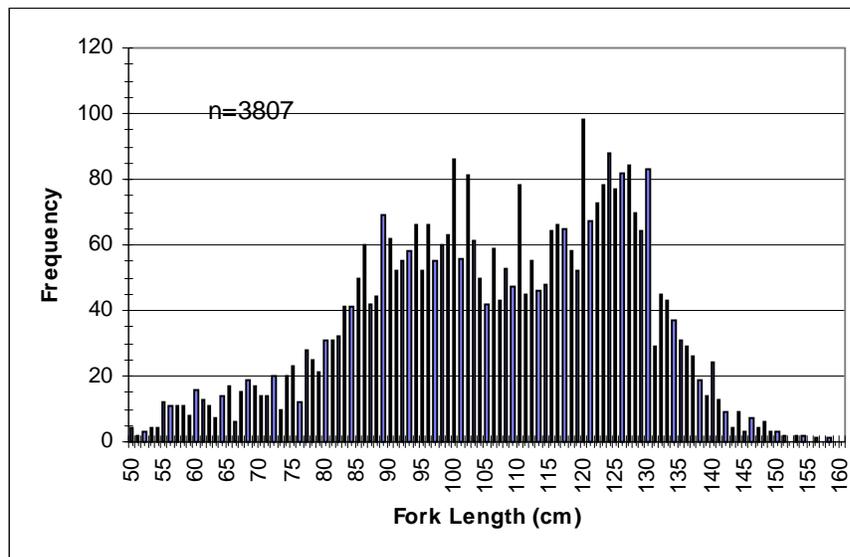


Figure 15. Length frequency distribution of samples collected from Areas B, C and D having fork lengths between 50 and 160 cm (n=3807).

The majority of samples collected by Japanese longline training vessels were collected in Area F, north of 10°N latitude and southwest of Hawaii. Most of the samples collected in Hawaii came from Hawaii based longline vessels fishing within 300 nmi of the main Hawaiian islands. Figures 16 and 17 give length frequency distributions of sampled yellowfin with recorded fork lengths between 50 and 160 cm from Areas E and F.

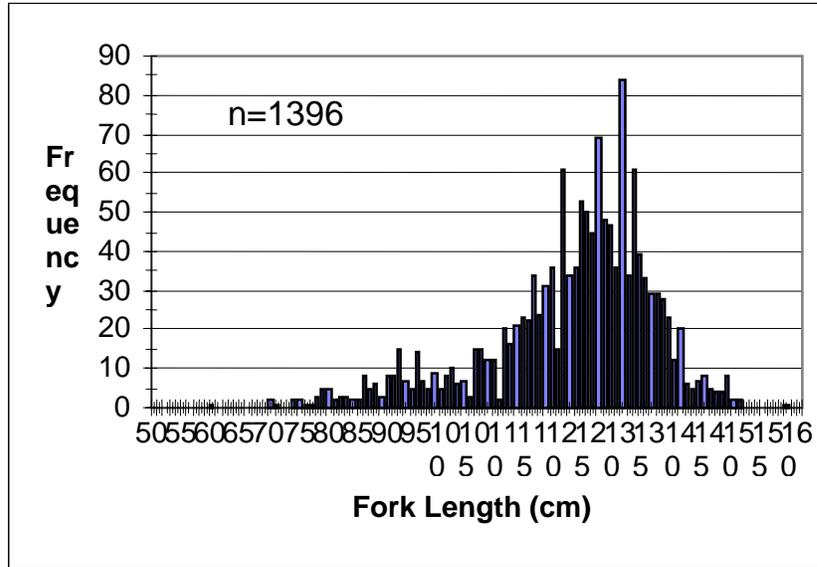


Figure 16. Length frequency distribution of samples collected from Area E having fork lengths between 50 and 160 cm (n=1396).

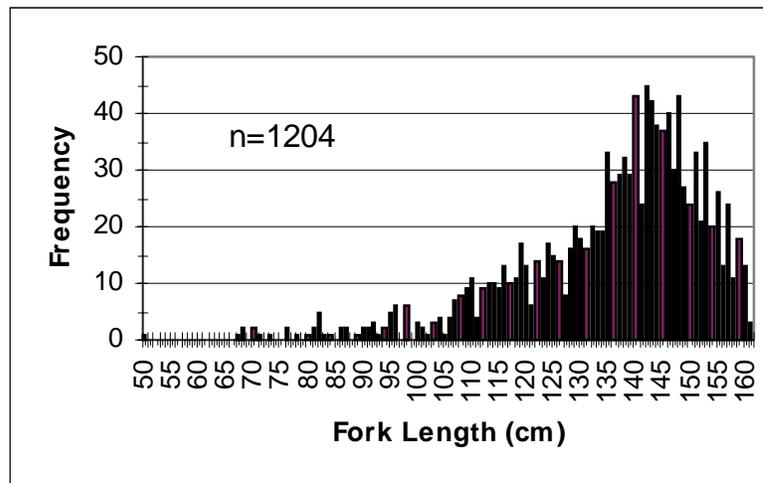


Figure 17. Length frequency distribution of samples collected from the Hawaii region (Area F) having fork lengths between 50 and 160 cm (n=1204).

RESULTS

DIURNAL SPAWNING PERIODICITY

The time of spawning was estimated by the observation of oocyte condition and the estimated age of postovulatory follicles in relation to fish mortality and sampling time. The observed presence of postovulatory follicles of age zero or less than twelve hours can be useful to estimate the actual time of spawning. Prior to ovulation, oocytes pass through an initial stage when lipid droplets coalesce into larger fatty droplets before progressing to

the migratory nucleus stage and hydration. The times these stages occur can also be useful in estimating the time of spawning. Handline or troll samples with short fight times and known time of capture and mortality are more useful and accurate to estimate time of spawning. Purse seine collected samples are less precise due to the uncertainty of time of mortality and the lengthy period in which sampling could have taken place. Longline collected samples were not used for the estimation of spawning time.

The time of mortality and sample fixation was estimated for purse seine samples from the set start and end times and notes made by samplers. Samples with coalescent oocytes were observed from 1000 to 2115 h, with a mean time of 1728 h. Migratory nucleus stage oocytes were observed in purse seine samples between 0913 and 2251 h (mean 1748 h). Ovary samples with the most advanced group of oocytes in a hydrated state were observed between 1120 and 2128 h, with a mean time of 1852 h. Ovulation would occur soon after hydration suggesting the majority of yellowfin spawning commences around 1900 to 2000 h.

Eight purse seine caught yellowfin in Area B had new postovulatory follicles classified as less than six hours in age that were sampled between approximately 0650 and 0800 h (mean 0739 h) with an estimated spawning times of 0050 to 0200. Purse seine samples with postovulatory follicles estimated at age six to twelve hours were collected between 0632 and 2009 (n=127) with a mean time of 0952 h, indicating an approximate spawning range 2152 and 0352 h. Mean estimated times of spawning for fish with postovulatory follicles of age twelve to sixteen hours (n=200) and sixteen to twenty four hours (n=266) were 1427 h and 1627 h yielding estimated spawning ranges of 2017 to 0217 and 1627 to 2227 hours respectively.

Samples collected from the Hawaiian *ika shibi* handline fishery, which takes place at night, provided the most accurate estimates of the actual time of spawning. Twenty seven samples had postovulatory follicles estimated at age zero or less than six hours. Exact capture times were recorded for eight of these samples that were fixed on board soon after capture (2345, 2350, 0045, 0045, 0052, 0245, 0330 and 0345). Spawning time estimates for these samples range from approximately 1800 to 0300. Ten other samples had postovulatory follicles estimated to be less than twelve hours old that were caught between 0130 and 0530 h. Based on these observations, yellowfin in both the equatorial western Pacific and around the Hawaiian islands appear to spawn almost completely between the hours of sunset and sunrise with peak spawning periods estimated to occur between 2000 and 0300 hours.

LENGTH AT MATURITY

Logistic regression analysis³ of data on the proportion of mature female yellowfin in one cm length classes between 50 and 150 cm produced estimates of length at 50% maturity for fish taken in different areas or by different gear types. The logistic model can be ex-

³ From SYSTAT, v. 7.0, LOGIT module based on Cox (1970)

pressed as $\ln[p/(1-p)] = \alpha + \beta L$ where p is a probability that a tuna was mature, α and β are linear regression parameters of the model and L is the fish length (cm). The predicted values for length at 50% maturity with 95% confidence limits for western and central Pacific yellowfin are listed in Table 4. The predicted length at 50% maturity for all samples collected within 10 degrees of the equator (Areas A, B, C and D) which were taken by handline, purse seine and longline gear was 104.6 cm. Figure 18 indicates the predicted and histologically observed per cent maturity of female yellowfin between 50 and 150 cm by one centimeter size classes from the equatorial samples ($n = 7565$).

Table 4. Predicted lengths at 50% maturity

Description	Area	Gear Type	n	Fork Length	Lower 95%	Upper 95%
All Equatorial western Pacific	A, B, C, D	PS, LL, HL	7565	104.57	104.08	105.05
Philippines and Indonesia	A	HL	3630	98.13	96.47	99.54
Equatorial western Pacific	B, C, D	PS, LL	3935	107.86	107.24	108.47
Equatorial western Pacific	B, C, D	PS	2836	108.38	107.64	109.13
Equatorial western Pacific	B, C, D	LL	1099	107.22	105.89	108.40
10-15 N	E	LL	1208	105.66	104.07	107.06
Hawaii	F	LL, HL, TR	899	112.54	110.10	114.61

Predicted lengths at 50% maturity for female yellowfin taken by purse seine and longline gear from the equatorial region (Areas B, C, D) were not significantly different, ranging between 107 and 108 cm. An estimate of length at 50% maturity from fish sampled from both gear types from Areas B, C and D is 107.9 cm.

The estimated length at 50% maturity for handline caught yellowfin from the Philippines and Indonesia was significantly lower than other estimates at 98.1 cm. The highest length at 50% maturity estimate of 112.5 cm came from the Hawaii region (Area F).

Figures 19 through 22 indicate the predicted and observed maturity of female yellowfin between 50 and 150 cm from (1) the Philippines and Indonesia; 2) Areas B, C and D for equatorial purse seine and longline region and 3) the Hawaii region.

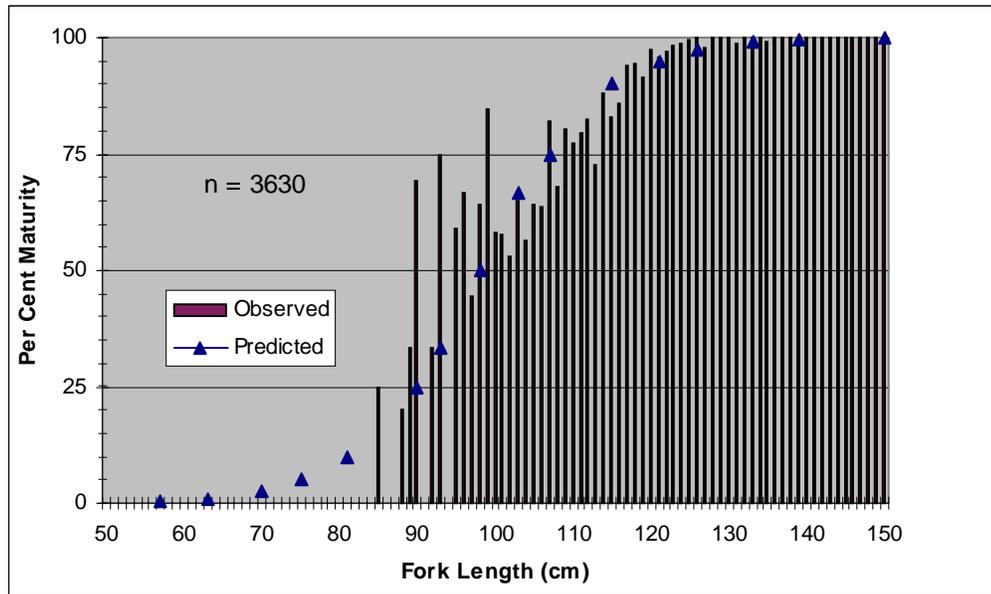


Figure 19. The observed and predicted per cent maturity by length of female yellowfin taken by handline gear between 50 and 150 cm fork length sampled from the Philippines and Indonesia.

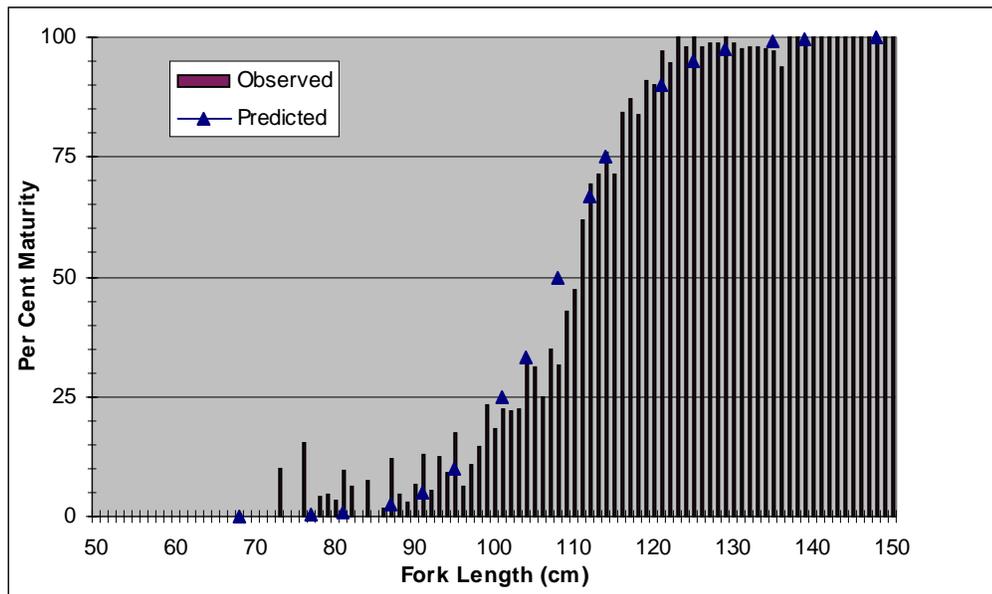


Figure 20. The observed and predicted per cent maturity by length of female yellowfin taken by longline and purse seine gear between 50 and 150 cm fork length sampled from Areas B, C and D.

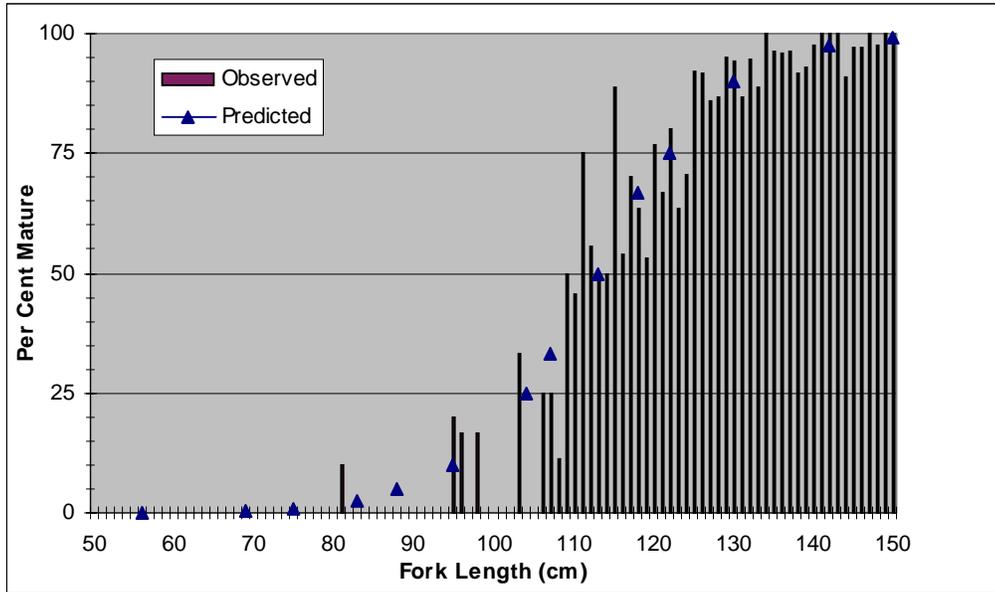


Figure 21. The observed and predicted per cent maturity by length of female yellowfin taken by longline, troll and handline gear between 50 and 150 cm fork length sampled from Area F (Hawaii).

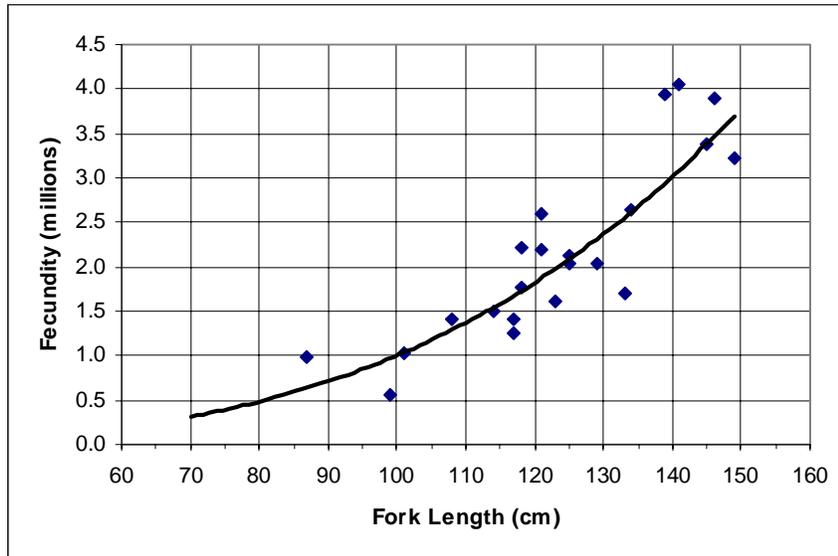


Figure 22. The relationship between fork length and batch fecundity for yellowfin tuna from Area B.

The minimum observed length at maturity for female yellowfin from all project sampling was 73 cm. The fish was taken with purse seine gear from a log associated school in Area B. However, the fish was not reproductively active (Stage 8) having fully yolked oocytes but exhibiting significant alpha and beta atresia of fully yolked oocytes. The minimum observed length of an actively spawning fish was 78 cm taken from a surface feeding

school by the same vessel during the same fishing trip in Area B. In the Hawaii region (Area F), the smallest mature fish sampled was 81 cm for a reproductively active fish taken close to the island of Hawaii with *ika shibi* style handline gear.

SPAWNING FREQUENCY

Estimates of spawning frequency were based on the fraction of actively spawning fish with postovulatory follicles noted in relation to (1) the total number of reproductively active fish, and (2) the total number of fish histologically classified as mature including reproductively inactive individuals.

Spawning frequency within ten degrees of the equator was relatively high, where yellowfin in spawning condition can be found throughout the year (Table 5). The mean fraction of actively spawning fish collected along the equator (Areas A, B, C, D) was slightly over 0.50^4 (95% CI 0.49-0.52) equivalent to a mean interval between spawning events of 1.99 days⁵ (approximate 95% CI 1.94-2.04 d). The mean spawning interval in the western Pacific purse seine and longline grounds (Areas B, C, and D) was estimated to be 1.93 days (approximate 95% CI 1.86-2.02 d).

Table 5. Spawning frequency estimates for yellowfin tuna within ten degrees of the equator

Gear Type	Area	Number of females			Spawning fraction and spawning interval of reproductively active females				Spawning fraction and spawning interval of all mature females			
		Spawning	Active	Mature	Fraction	95% CI	Interval	95% CI	Fraction	95% CI	Interval	95% CI
HL	A	1618	1943	3272	0.83	0.82-0.85	1.20	1.18-1.22	0.49	0.48-0.51	2.02	1.95-2.09
PS	B, C, D	642	756	1101	0.85	0.83-0.87	1.18	1.15-1.21	0.58	0.55-0.61	1.71	1.63-1.81
LL	B, C, D	391	450	897	0.87	0.85-0.89	1.15	1.12-1.18	0.44	0.40-0.47	2.29	2.14-2.48
PS + LL	B, C, D	1033	1206	1998	0.86	0.84-0.87	1.17	1.15-1.19	0.52	0.50-0.54	1.93	1.86-2.02
All equator	A, B, C, D	2651	3149	5270	0.84	0.83-0.85	1.19	1.17-1.20	0.50	0.49-0.52	1.99	1.94-2.04

Spawning frequency estimates for handline caught fish from the Philippines and Indonesia combined were similar while purse seine and longline caught fish were noted to have the highest (1.71 d) and lowest (2.29 d) spawning frequency estimates for this area.

⁴ i.e., $2651/5270 = 0.503$

⁵ i.e., $1/\{2651/5270\} = 1.99$

The estimated spawning frequencies of reproductively active fish were similarly high from all areas and gear types. The fraction of females with postovulatory follicles for handline (Area A), purse seine and longline (Areas B, C and D) caught samples were 0.83, 0.85 and 0.87, equivalent to mean spawning frequency estimates of 1.20, 1.18 and 1.15 d. Combined data for this region indicates 0.84 (95% CI 0.83-0.85) of reproductively active females are spawning per day, equivalent to a spawning interval estimate of 1.19 d (approximate 95% CI 1.17-1.20 d).

Spawning frequency estimates by gear and set types are summarized in Table 6. Purse seine estimates were derived for sets made on drifting objects (log associated) and for unassociated schools found actively feeding on baitfish. Longline data were examined separately for shallow or deep-set gear, with Philippine and Indonesian handline caught fish presented separately. The highest spawning fraction in this group was for purse seine caught yellowfin schools actively feeding on baitfish (0.68, 95% CI 0.64-0.71) or 1.47 d and was significantly higher than for log associated yellowfin or fish taken by longline gear. Samples from deep-set longline gear were the least reproductively active, with spawning fractions of 0.37 (Area B, C, D) and 0.34 (Area E) equivalent to mean spawning intervals of 2.68 and 2.91 d. A higher rate of spawning activity was estimated in the Philippines in comparison to Indonesia.

Table 6. Spawning frequency estimates by gear and set type.

Gear Type	Association or set type	Area	Number of females			Spawning fraction and spawning interval of reproductively active females				Spawning fraction and spawning interval of all mature females			
			Spawning	Active	Mature	Fraction	95% CI	Interval	95% CI	Fraction	95% CI	Interval	95% CI
Phil HL	FAD	A	954	1122	1679	0.85	0.83-0.87	1.18	1.15-1.20	0.57	0.54-0.59	1.76	1.69-1.84
Indo HL	FAD	A	664	821	1593	0.81	0.79-0.83	1.24	1.21-1.27	0.42	0.39-0.44	2.40	2.27-2.55
PS	Bait-fish	B, C, D	455	492	670	0.92	0.90-0.94	1.08	1.06-1.11	0.68	0.64-0.71	1.47	1.40-1.55
PS	Log	B, C, D	132	142	291	0.93	0.90-0.96	1.08	1.04-1.11	0.45	0.40-0.51	2.20	1.96-2.52
LL	Shallow-set	B, C, D	186	216	348	0.86	0.82-0.90	1.16	1.11-1.21	0.53	0.48-0.59	1.87	1.70-2.07
LL	Deep-set	B, C, D	205	234	549	0.88	0.85-0.90	1.14	1.11-1.18	0.37	0.33-0.41	2.68	2.42-3.00
LL	Deep-set	E	325	384	947	0.85	0.82-0.87	1.18	1.15-1.21	0.34	0.31-0.37	2.91	2.68-3.20

Spawning frequency estimates in Hawaiian waters are only meaningful during the spawning season. Table 7 indicates the reproductive condition of yellowfin in the Hawaii region during the spawning (April–September) and non-spawning seasons (October–March) by gear type. Only 2.3% of mature fish sampled during the non-spawning season (13/556) were found to be reproductively active (fully yolked oocytes with minor atresia).

Table 7. Reproductive condition of yellowfin tuna taken in the Hawaii region (Area F) north of 15EN during the spawning (S = April to September) and non-spawning (N = October to March) seasons by various gear types.

Gear Type	Ika Shibi HL		Troll		Shallow-set Longline		Deep-set Longline		All Longline		All Hawaii	
	S	N	S	N	S	N	S	N	S	N	S	N
# Active spawners with POFs	42	-	87	1	72	2	21	4	93	6	222	7
# Reproductively active (fully yolked, low atresia)	43	-	93	4	74	3	26	6	100	9	236	13
# inactive, atretic, post spawning	2	-	20	0	67	154	73	389	140	543	162	543
# Classified mature (with reproductively inactive fish)	45	NA	113	4	141	157	99	395	240	552	398	556

During the spawning season, the spawning rates of reproductively active fish were high from all surface fisheries, ranging from 1.02 d to 1.07 d indicating near daily spawning for fish taken by *ika shibi* handline, surface troll and shallow-set longline gear (Table 8). The spawning fraction of reproductively active fish taken by deep-set longline gear was slightly lower, equivalent to a spawning interval of 1.24 d. This pattern is repeated when computing the spawning frequency for all mature samples by gear type, with inshore, surface fisheries having the highest spawning rates. The spawning rates of longline caught fish were significantly lower, with the spawning fraction of mature yellowfin taken by deep-set longline gear the lowest of all (0.21, 95% CI 0.13-0.29) equivalent to a mean spawning interval of 4.71 d.

Table 8. Spawning frequency estimates for the Hawaii region north of 15°N during the spawning season (April - September).

Gear Type	Area	Number of females			Spawning fraction and spawning interval of reproductively active females				Spawning fraction and spawning interval of all mature females			
		Spawning	Active	Mature	Fraction	95% CI	Interval	95% CI	Fraction	95% CI	Interval	95% CI
Ika shibi HL	Inshore	42	43	45	0.98	0.93-1.02	1.02	0.98-1.07	0.93	0.86-1.01	1.07	0.99-1.16
Troll	Inshore	87	93	113	0.94	0.89-0.98	1.07	1.02-1.12	0.77	0.69-0.85	1.30	1.18-1.44
Shallow LL	Off-shore	72	74	141	0.97	0.95-1.00	1.03	1.00-1.06	0.51	0.43-0.59	1.96	1.69-2.34
Deep LL	Off-shore	21	26	99	0.81	0.73-0.89	1.24	1.13-1.37	0.21	0.13-0.29	4.71	3.42-7.60
All LL	Off-shore	93	100	240	0.93	0.90-0.96	1.08	1.04-1.11	0.39	0.33-0.45	2.58	2.23-3.07
All Hawaii	All	222	236	398	0.94	0.92-0.96	1.06	1.04-1.09	0.56	0.51-0.61	1.79	1.65-1.96

BATCH FECUNDITY

Western Pacific

Accurate batch fecundity estimates for yellowfin can only be made from ovaries that are within a few hours of ovulation, after the migratory nucleus or early stages of hydration have begun but before any hydrated oocytes have been released. During the early stages of hydration, the mean oocyte diameter increases above 700 µm and the formation of a large, single oil droplet becomes obvious (McPherson, 1991). Batch fecundity estimates derived for this study followed the methods outlined by Hunter et al. (1985). With a presumed commencement of spawning in the early evening, troll and purse seine fisheries provided the best opportunity to obtain samples suitable for batch fecundity estimates. However, the window of sampling opportunity for both gear types is usually limited to a few hours during the late afternoon.

Batch fecundity counts were made from twenty-two purse seine caught samples along the equator. The samples were collected between April 1995 and March 1996 within five degrees of the equator and between 145°–167°E longitude (Areas B, C). Fork length of samples ranged from 87 to 149 cm with total ovary weights ranging from 310 to 1840 g for a mean of 739 g. Estimates from the entire sample ranging from 0.550 to 4.061 million ova for yellowfin of 99 and 149 cm respectively (Table 9). The mean fork length from the 22 sampled fish was 123.2 cm with a mean batch fecundity estimate of 2.160 million. Mean relative batch fecundity in oocytes per gram body weight ranged from 22.2 for a 123 cm female to 77.6 oocytes per gram of body weight for an 87 cm yellowfin. The

mean relative batch fecundity for the 22 samples was 54.7 oocytes per gram of body weight.

Table 9. Estimates of batch fecundity and mean number of oocytes per gram body weight from Area B.

Fork Length (cm)	Fish Weight (kg)	Gonad weight(g)	BF estimate	Oocytes/g
87	12.62	310	978,899	77.6
99	18.74	300	549,865	29.3
101	19.92	300	1,031,829	51.8
108	24.45	500	1,417,748	58.0
114	28.84	550	1,493,223	51.8
117	31.23	492	1,248,746	40.0
117	31.23	652	1,408,318	45.1
118	32.05	525	2,209,177	68.9
118	32.05	530	1,766,667	55.1
121	34.61	714	2,185,237	63.1
121	34.61	620	2,602,254	75.2
123	36.39	742	1,612,528	22.2
125	38.23	660	2,030,247	53.1
125	38.23	774	2,126,393	55.6
129	42.10	653	2,045,880	48.6
133	46.22	600	1,691,974	36.6
134	47.29	826	2,643,318	55.9
139	52.89	964	3,933,117	74.4
141	55.26	1840	4,061,420	73.5
145	60.19	950	3,370,225	56.0
146	61.47	1600	3,890,449	63.3
149	65.42	1150	3,221,983	49.3

The relationship between fork length and estimated batch fecundity can be described by a power function equation in the form $Y=cL^b$, where Y is the batch fecundity estimate from a fish of fork length L in cm. The resulting formula that describes Figure 22 is $Y = 0.2934L^{3.2673}$ ($r^2=0.7646$)

The relation between batch fecundity and estimated body weight for the samples can be expressed by the linear regression

$$Y = 62,173W + 225,310 \quad (r^2=0.7829)$$

where Y is the resulting batch fecundity and W is the weight of the fish in kilograms (Figure 23).

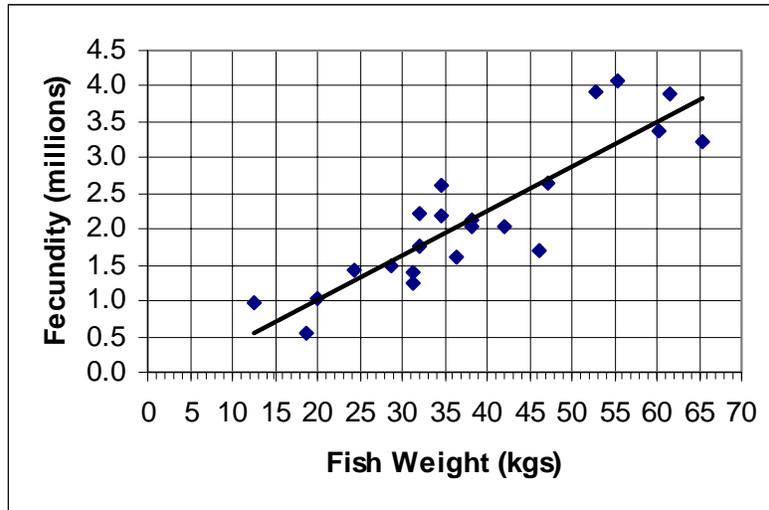


Figure 23. The relationship between total body weight and batch fecundity for yellowfin tuna from Area B.

Hawaii

Batch fecundity counts were made on fifteen hydrated ovary pairs collected from longline and troll catches within the Hawaii region (Area F). Batch fecundity estimates for this sample ranged from 0.435 to 10.612 million oocytes for 144 and 154 cm yellowfin respectively (Table 10). Total gonad weights ranged widely from 210 to 3901 g. There is a high degree of variability in this small data set, with two fish with very low fecundity and one example of very high fecundity.

Table 10. Estimates of batch fecundity and mean number of oocytes per gram body weight from the Hawaii region (Area F).

Fork Length (cm)	Fish Weight (kg)	Gonad weight (g)	BF estimate	Oocytes/g
116	30.42	982	2,299,484	75.6
127	40.37	710	2,647,270	65.6
134	47.17	580	1,693,884	35.9
135	48.08	1129	1,825,389	38.0
135	48.08	559	1,532,074	31.9
136	49.27	1393	3,557,529	72.2
137	50.60	975	2,148,849	42.5
141	55.34	1217	3,174,169	57.4
141	55.34	620	4,145,279	74.9
143	57.15	365	630,136	11.0
143	58.06	913	2,195,085	37.8
144	54.43	210	425,354	7.8
146	61.24	1452	4,800,968	78.4
147	63.05	1565	4,286,223	68.0
154	72.12	3901	10,611,913	147.1

The two fish with very low fecundity estimates equivalent to mean relative batch fecundity estimates of 7.8 and 11.0 oocytes per gram body weight were sampled early and very late respectively in the spawning season. Excluding these two samples, the mean fork length of the remaining 13 samples was 137.8 cm with a mean batch fecundity estimate of 3.455 million. Mean relative batch fecundity ranged from 31.9 to 147.1 oocytes per gram of body weight with an average value of 63.5 oocytes per gram of body weight for the 13 samples.

The whole body weight yellowfin sampled for batch fecundity estimates in Hawaii was accurately measured with weights converted to fork length, thus weight data were considered more accurate for Hawaii samples. Fecundity by fish weight was calculated which was also done for Hawaii yellowfin by June (1953). The relationship between fecundity and fish weight is described by the linear regression functions of

$$Y = 163,048W - 5,062,591 \quad (R^2 = 0.5141)$$

where Y is the resulting batch fecundity and W is the weight of the fish in kilograms (Figure 24).

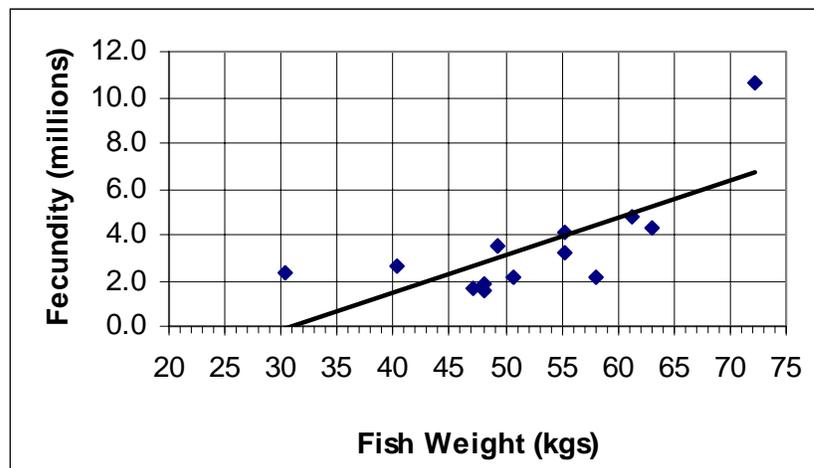


Figure 24. The relationship between total body weight and batch fecundity for yellowfin tuna from the Hawaii region (Area F).

SPAWNING SEASONALITY

Spawning seasonality was assessed by comparisons of reproductive state of all mature samples in an area by monthly time periods. Mature fish were categorized as (1) fully yolked but not spawning (Stage 5), (2) actively spawning (Stage 6, 7) or (3) atretic (Stages 4, 8, 9, 10) being mature but reproductively inactive.

Area A (Philippines and Indonesia)

The most pronounced seasonal pattern of spawning activity along the equator was noted in the southern Philippines. Figure 25 plots the percentage of mature fish in fully yolked, spawning or atretic condition by month during the sampling period. Significant declines in the proportion of spawning fish occurred from February to June 1995 and February to May 1996. During the remainder of the sampling period, 80% to 90% of all mature fish were actively spawning or exhibited fully yolked oocytes with low atresia. The figure also plots monthly means of sea surface temperature from the region of the sampled Philippine handline fishery from satellite derived data⁶.

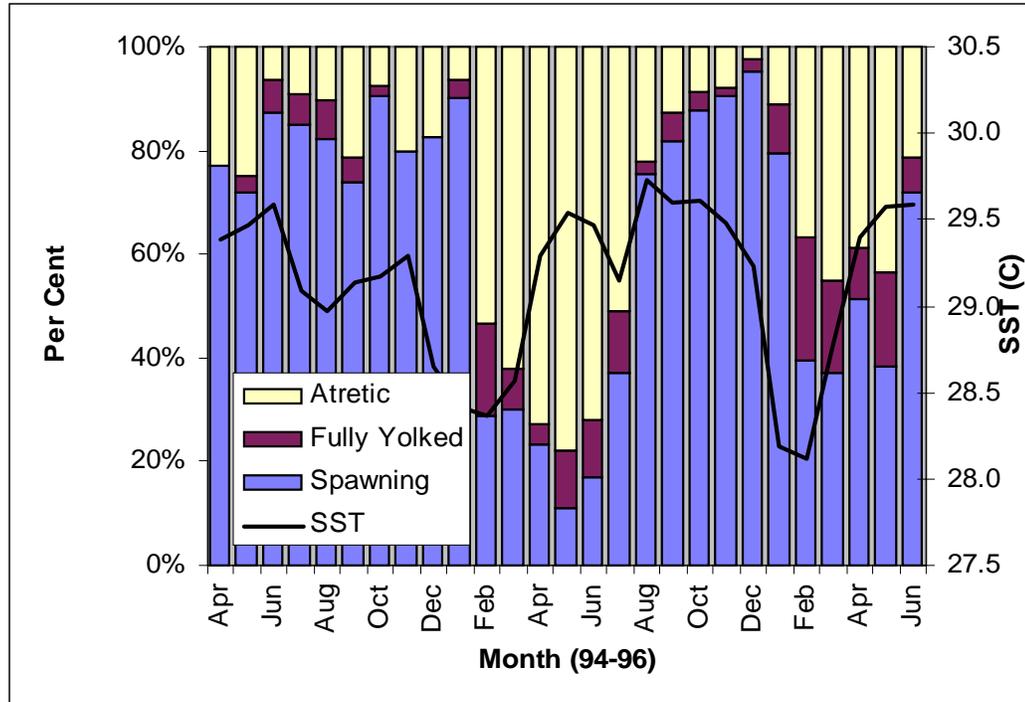


Figure 25. Proportion of mature yellowfin in fully yolked, spawning and atretic condition by month for samples from the Philippine handline fishery with mean monthly SST (EC).

The Indonesian samples collected during the study period did not indicate any clearly seasonal patterns of spawning activity, with the possible exception of a decrease in spawning activity noted during the December to February 1996 period. Sampling during June and September 1994 was not conducted due to logistical problems at the sampling site but fishing effort was reported to be low from July to September 1994. Overall, the proportion of mature fish in spawning condition was lower in comparison with Philippine samples, with approximately 50% of sampled fish either in spawning condition or fully yolked per month (Figure 26). Climate data indicates some seasonal fluctuations of sea

⁶ Weekly mean SST in degrees C for 5EN, 123EE from http://ferret.wrc.noaa.gov/fbin/climate_server DATA SET: /home/fe3/data/reynolds_sst_wk.cdf

surface temperature ranging from 27.0 to 30.0°C with declining SST noted during the June to September periods for both 1994 and 1995⁷.

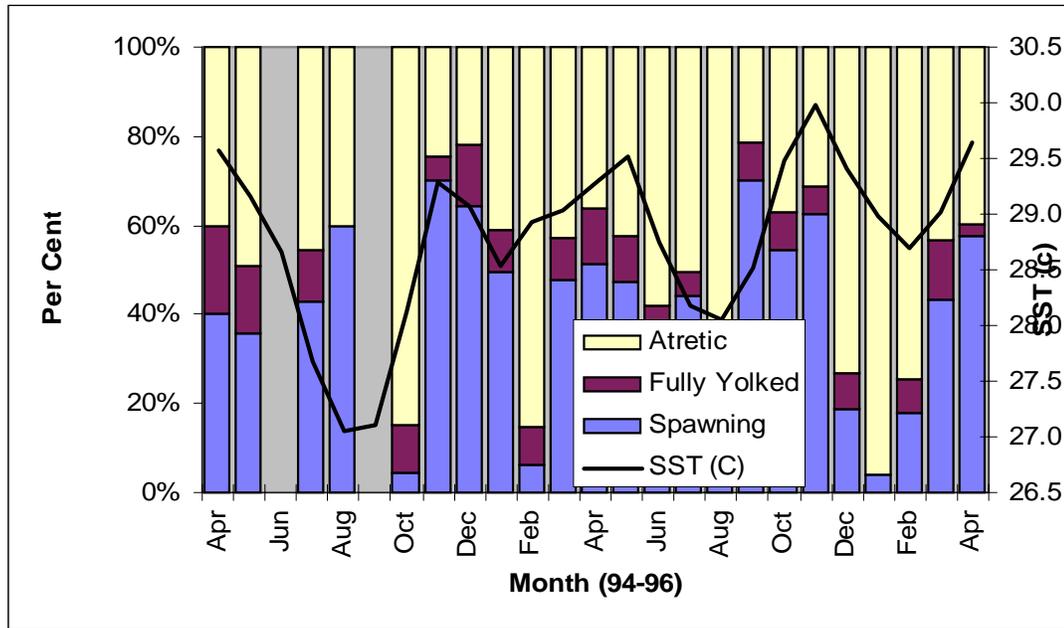


Figure 26. Proportion of mature yellowfin in fully yolked, spawning and atretic condition by month for samples from the Indonesian handline fishery with mean monthly SST (EC).

Areas B, C, D (Western Pacific Purse Seine and Longline)

The spatio-temporal distribution of sample collection from purse seine and longline gear along the Equator was not uniform due to the uneven distribution of fishing effort and observer coverage during the sampling period. As a result, some regions were not adequately sampled for the examination of spatial and temporal patterns in spawning activity throughout the study period. Sampling in Areas C and D was relatively low in comparison to Area B. Area D, east of 180E longitude was sampled only during the latter half of 1994 when US flag purse seine vessels were active in that region and carried observers trained and equipped to sample for the project.

Area B, particularly between 140°E to 160°E had continuous sampling from April 1994 to March 1996 and 1,266 purse seine and longline samples in this area were classified as mature. A high percentage of mature fish sampled during this period were actively spawning from April to November 1994 and during the third and fourth quarters of 1995 (Figure 27). A period of reduced spawning activity is apparent from December 1994 to June 1995 when less than 30% of mature fish sampled were actively spawning. This

⁷ Weekly mean SST in degrees C for 0EN, 127EE from http://ferret.wrc.noaa.gov/fbin/climate_server DATA SET: /home/fe3/data/reynolds_sst_wk.cdf

trend was apparent in both purse seine and longline samples. The sampling carried out in Area D east of the Date Line indicated a high rate of spawning of mature yellowfin from samples collected during the third and fourth quarter of 1994 (Figure 28).

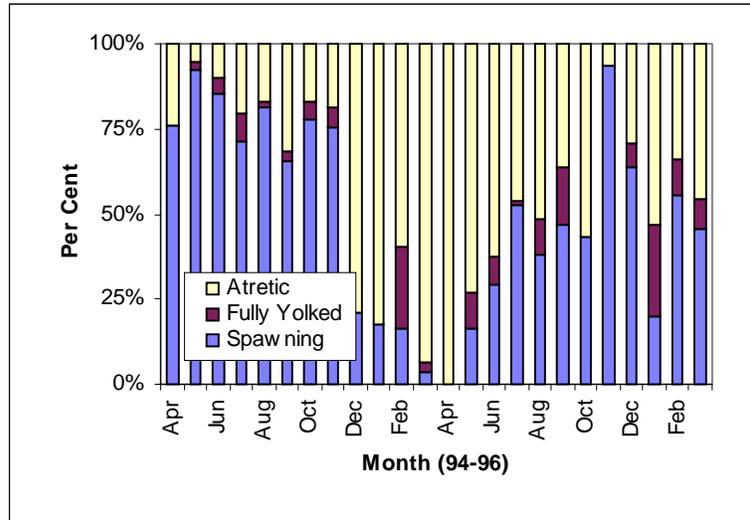


Figure 27. Proportion of mature yellowfin in fully yolked, spawning and atretic condition by month for purse seine and longline samples from Area B.

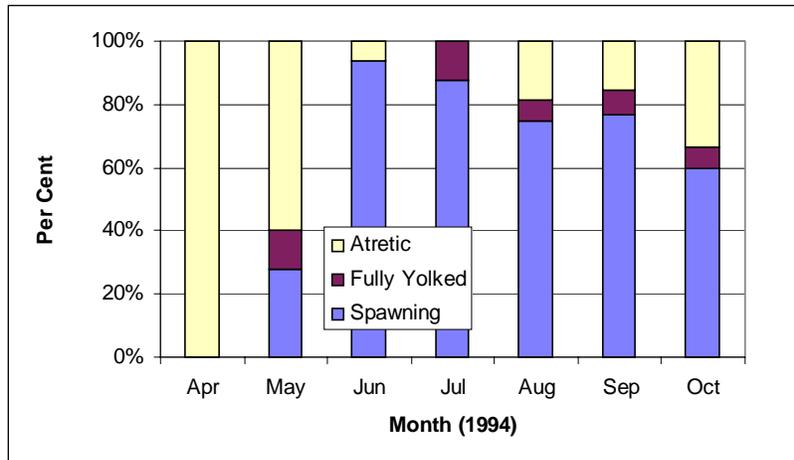


Figure 28. Proportion of mature yellowfin in fully yolked, spawning and atretic condition by month for purse seine samples from Area D.

Areas E and F (Hawaii)

In Area E, between 10° and 15°N, 956 samples were assessed as mature. Almost all of these samples were taken from Japanese longline training vessels. The vessels operate seasonally in the region which contributed to an uneven sampling distribution concentrated during the May to July and January to February periods. However, the available data supports spawning seasonality peaking with the northern hemisphere spring and summer months (Figure 29).

The examination of spawning seasonality of yellowfin in the Hawaii region (Area F) was confined to samples collected north of 15°N by all gear types. Histologically confirmed development to a fully yolked condition and spawning activity was clearly a spring to fall activity with peak spawning occurring from June to August (Figure 30). The main spawning season takes place from April through September, though limited spawning activity was noted to occur in March and October during some years. Figure 31 plots spawning activity with bi-weekly sea surface temperatures as recorded by a NOAA weather buoy moored south of Oahu and east of the island of Hawaii⁸. Spawning was noted to commence in the spring when sea surface temperatures rose above 24.5°C and continued throughout the period of highest SST.

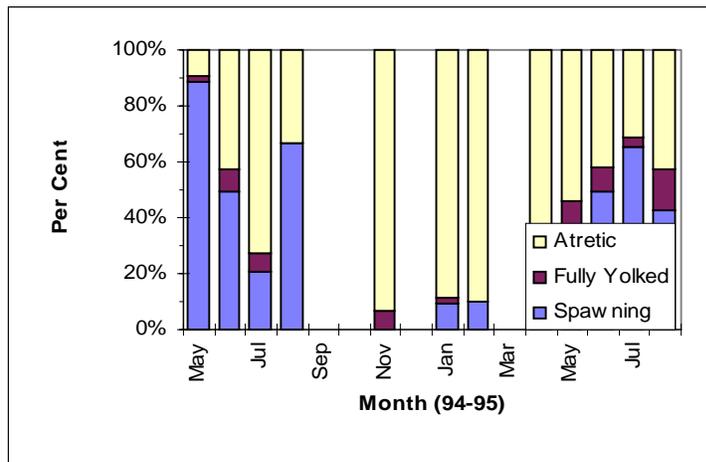


Figure 29. Proportion of mature yellowfin in fully yolked, spawning and atretic condition by month for longline samples from Area E.

⁸ Recorded SST in EC at NOAA moored weather buoy 51003 located at 19E8' N, 160E48' W for the first and fifteenth day of every month at 1200 UTC.

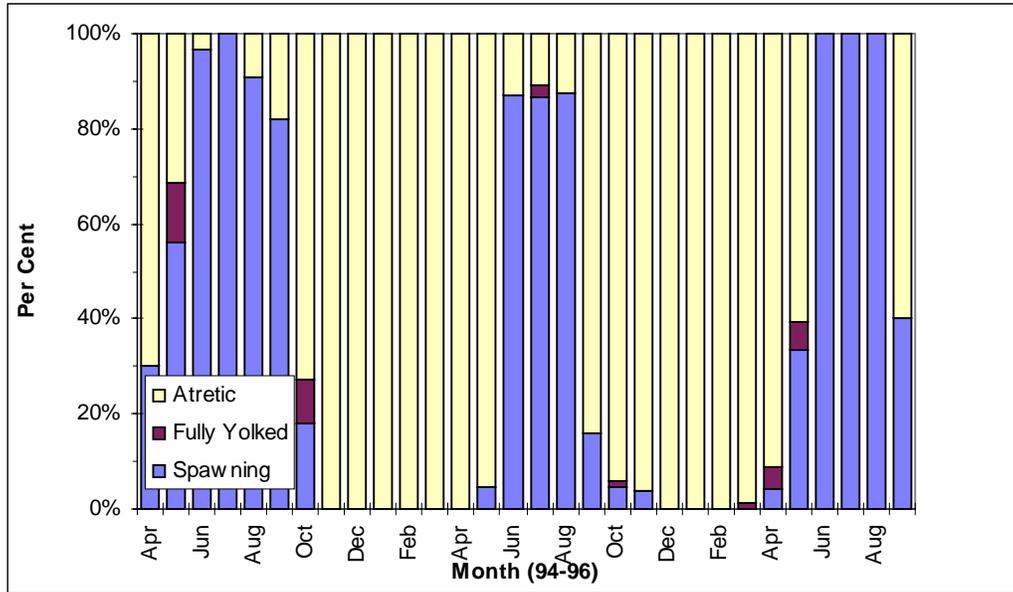


Figure 30. Proportion of mature yellowfin in fully yolked, spawning and atretic condition by month for longline, handline and troll samples from Area F.

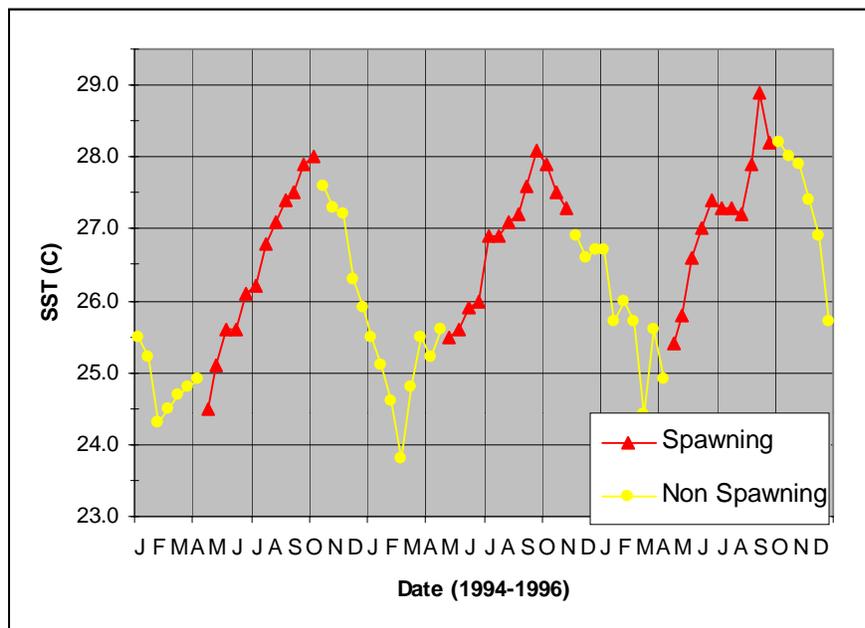


Figure 31. Sea surface temperatures near the main Hawaiian Islands and the spawning season for 1994 - 1996. Dark triangles indicate months in which yellowfin

Spawning activity ceased shortly after maximum SSTs around 28°C were recorded in October and surface temperatures declined by less than one degree centigrade. The northernmost yellowfin confirmed to be actively spawning (Stage 6) was an 118 cm fish caught on November 23, 1994 at 26°32' N, 154°44' W by a Japanese longline training vessel.

GUT CONTENTS

Stomach contents of ovary sampled yellowfin were examined and preserved on purse seine and longline vessels in Areas B, C and D. Yellowfin tuna feed opportunistically on a wide variety of prey, including several classes of crustaceans, cephalopods and fish in all stages of development (Alverson, 1963) and as reviewed in Cole (1980) and Suzuki (1994a).

The most common diet item by degree of occurrence and volume of stomach contents were anchovies (Engraulidae) that were often completely filling the stomachs of purse seine caught yellowfin. Specimens were in progressive stages of digestion with several in excellent condition that had apparently been consumed shortly before capture and sampling. Early juvenile through adult phases were observed from different stomachs, i.e. adult and juvenile specimens were not recorded from the same fish. Sizes ranged from approximately 25–65 mm SL and were positively identified as the ocean anchovy (*Encrasicholina punctifer*⁹) using standard keys and references (Lewis et al., 1983; Ozawa and Tsukahara, 1973; Whitehead et al., 1988). This species of anchovy was consistently found in yellowfin stomachs sampled from purse seine sets recorded as unassociated, free school or baitfish associated sets. The stomach contents of well preserved ocean anchovies in good condition were found to contain an assortment of copepods and other crustacean zooplankton. A single fish larvae, tentatively identified as a *Thunnus* sp. was noted. Hida (1973) examine stomach contents of *E. punctifer* collected in the western Pacific and found the majority of diet items to consist of calanoid and cyclopoid copepods and other crustaceans.

PARASITES WITHIN THE OVARY

Nematode parasites were observed in histological sections of yellowfin ovaries from all areas at a mean rate of 8.7% from 8841 samples where the presence or absence of parasites was noted. The rate of observed infection of parasites from different areas and fisheries ranged from 4.35% for Hawaii handline caught yellowfin to 11.87% for Hawaii based deep-set longline gear (Table 11). These differences were likely been due to the decreased likelihood of encountering a parasite when sectioning a large, fully yolked ovary as were typical of the Hawaii handline samples compared to the increased likelihood of encountering a parasite in an atretic ovary typical from deep-set longline gear at higher latitudes. The overall rate of infection was probably much higher than observed here, but entire ovaries were not examined. Yuen and June (1957) found yellowfin ovaries from the central equatorial Pacific to be infected with low numbers of a nematode parasite, but at a high rate of 88%.

⁹ *Stolephorus buccaneeri* and *S. zollingeri* are junior synonyms

Table 11. Nematode parasites observed in yellowfin tuna ovary samples by area and gear type.

Fishery	Area	Nematodes observed in sample	Number of samples observed	% observed
Philippine HL	A	138	1733	7.96
Indonesia HL	A	198	1912	10.36
All PS	B, C, D	199	2868	6.94
Deep-set LL	B, C, D, E	115	1200	9.58
Shallow-set LL	B, C, D, E	43	420	10.24
Hawaii deep-set LL	F	26	219	11.87
Hawaii shallow-set LL	F	34	316	10.76
Sport rod	F	1	7	14.29
Troll	F	13	120	10.83
Hawaii HL	F	2	46	4.35
Total		769	8841	8.70

The nematode observed in sampled ovaries was assigned to the genus *Philometra* (Order Spirurida) by examination of both whole specimens preserved in formalin and histological preparations (Overstreet, pers. obs.¹⁰). A positive identification to the species level was not possible from the available material. Female and male specimens were identified using standard keys and information on the genera (Chabaud, 1975). The most developed specimen measured between 153 and 261 Φ m in diameter. Simmons (1969) found *Philometra* sp. in the ovaries of approximately 90% of mature skipjack examined from the tropical Atlantic and the genus has been reported from several scombrid species.

Philometrid nematodes brood larvae that are normally released when the host organism spawns. It is not known in the case of yellowfin tuna if the larvae infect other tuna directly or if an intermediate host is required. The rate of infestation noted was considered slight and relatively benign to the host (Overstreet, pers. comm.). These parasites normally die or degenerate after spawning and most specimens were collected from atretic ovaries in various stages of degeneration. Lester et al. (1985) noted *Philometra* sp. in the ovaries of skipjack tuna from the western equatorial Pacific, Australia, New Zealand, California, Ecuador and the Atlantic. The presence of *Philometra* sp. showed some association within schools in New Zealand which was assumed to be linked to the uniform state of maturity within schools. The presence of the genus in yellowfin ovaries appears to be so widespread and common in the Pacific as to eliminate useful applications to stock discrimination, migration or movement.

¹⁰ Robin M. Overstreet, Gulf Coast Research Laboratory, Institute of Marine Sciences, University of Southern Mississippi.

DISCUSSION

LENGTH AT MATURITY

Many different methods and criteria have been used to assess yellowfin maturity, resulting in a wide range of maturity estimates for western Pacific yellowfin. Different authors have reported lengths at first observed maturity ranging from 56.7 to 112.0 cm based either on external features of the ovaries, the microscopic examination of oocyte diameters or GI analysis (Wade, 1950; Buñag, 1956; Yuen and June, 1957; Sun and Yang, 1983). These methods tend to overestimate length at maturity by incorrectly classifying mature fish that are reproductively inactive, as immature.

Several studies cite observations of length at first maturity, but this parameter is of limited use to population studies, as a single observation may represent a rare and biologically insignificant event. Length at observed or predicted 50% maturity is a more useful parameter but it is important to know how the value was calculated when making comparisons between studies. Yuen and June (1957) estimated an approximate length at 50% maturity for central Pacific yellowfin by observing that at a length between 120 and 129 cm, 47% of the sampled fish were classified as sexually active with ovaries containing fully yolked or hydrated oocytes. Kikawa (1962) noted from the central and western tropical Pacific that a few longline caught yellowfin were reproductive at 80–110 cm and estimated a length at 50% maturity between 110 and 120 cm from GI analysis.

Sun and Yang (1983) reported size at first maturity for western Pacific yellowfin of 106 cm and 112 cm for fish taken by longline gear between 0°–10°N and 10°–23°N respectively. These estimates are far higher than reported by other authors and highlight the problem of using gonad indices on longline caught yellowfin to assess maturity which can not accurately discriminate immature samples from mature but reproductively inactive (atretic) ovaries. However, their study was correct to report findings by latitudinally defined areas as fish in higher latitudes may exhibit delayed maturity and longer periods of reproductive inactivity. Their estimates of size at first maturity likely equate to observed lengths of reproductively active yellowfin with fully yolked oocytes, equivalent to maturity Stage 5, 6 or 7 as described in Table 1.

The results of a study by McPherson (1991) are more comparable in relation to western Pacific yellowfin, as similar criteria for histologically assessed maturity and spawning frequency were used. The study estimated from logistic regression analysis that 50% of yellowfin matured at 107.9 cm in the traditional handline fishing area of the Coral Sea compared to 120.0 cm for fish taken from offshore longline areas. Differential maturity was also noted between these areas by Hisada (1973) who proposed that the difference may be due to delayed warming of subsurface waters exploited by the longline gear. In addition to the consideration of temperature at depth, the longline areas were generally at higher latitudes compared to handline areas. These Coral Sea estimates compare favorably with the estimate of 107.9 cm for length at 50% maturity from the main purse seine and longline fishing grounds of the tropical western Pacific made by this study.

Schaefer (1998) used histological analysis of a large data set and a general regression model to predict a length at 50% maturity for Eastern Pacific yellowfin of 92 cm and observed first maturity of females at 59 cm. These values are significantly lower than estimates from this study of western tropical Pacific yellowfin predicting a length at 50% maturity of 108 cm with an observed length at first maturity of 73 cm (inactive) and 78 cm (spawning). The two studies did not use identical methods to predict length at 50 % maturity but results suggest a lower length at maturity in the Eastern Pacific Ocean, which may be related to the generally oligotrophic environment of the western Pacific in comparison to the more productive and forage rich waters of the eastern Pacific (Longhurst, 1998).

An explanation for differential maturity between regions is supported in Cole (1980) citing studies that indicate that yellowfin close to high islands or land masses attain sexual maturity sooner than fish in offshore areas, presumably due to enhanced productivity. Wade (1950) and Buñag (1956) noted relatively low lengths at first maturity for Philippine yellowfin which has contributed to theories of differential maturity between coastal and offshore populations; e.g. yellowfin inhabiting coastal areas attain sexual maturity at a smaller size. Whether they were actually noting differential maturity or smaller sized mature and reproductively active fish at inshore locations is debatable, but the observation of relatively small yellowfin in advanced yolked or spawning condition has also been made in the coastal waters of Central America (Orange, 1961). The available data from this study for Area A suggests that yellowfin in the archipelagic waters of the Philippines and Indonesia reach maturity and reproductive activity sooner than those from the oceanic environment of Areas B, C and D, with an estimated length at 50% maturity of 98.1 cm.

Suzuki (1988) noted in an area of the western tropical Pacific corresponding to Area B in this study that female yellowfin caught by purse seine gear (n=72) had a higher sexual maturity compared to those taken by longline gear (n=3027) using GI analysis. Koido and Suzuki (1989) noted the same situation from a similar data set and assumed that these differences were due to a shift in habitat of maturing yellowfin tuna toward surface waters for spawning. Theories of differential vulnerability and exploitation by purse seine and longline fisheries have led some sources to propose that two sub-populations/segments of populations of yellowfin exist side by side in the western Pacific: a subsurface group vulnerable to longline gear and a surface group that is more reproductively active and vulnerable to purse seine gear.

The results of this study do not support a differential maturity of yellowfin taken by purse seine and longline gear in the oceanic region of the central and western Pacific (Areas B, C and D). Predicted lengths at 50% maturity for fish sampled from both gear types from the same area were not significantly different, falling between 107 and 108 cm. The combined estimate from purse seine and longline caught samples of 107.9 cm for length at 50% maturity is proposed for the oceanic regions of the western equatorial Pacific. The proportion of mature, reproductively active fish was found to be much higher from purse seine catches, in agreement with higher gonad indices noted by previous studies. Mature, but reproductively inactive (post-spawning) yellowfin predominate in the catch of deep-

set longline gear suggesting an ongoing cycle of vulnerability to surface and sub-surface fisheries depending on reproductive condition.

The highest length at maturity estimate of 112.5 cm came from the Hawaii region. This appears reasonable as lower mean sea surface temperatures and a relatively short spawning season may delay maturity.

SPAWNING FREQUENCY

The spawning frequency of small tuna or tuna-like species (Scombridae) include studies by Dickerson et al. (1992) for chub mackerel (*Scomber japonicus*) and Schaefer (1987) for black skipjack (*Euthynnus lineatus*) in the eastern Pacific. Studies on larger tuna species in tropical waters have estimated a mean interval between spawning events of 1.18 d for south Pacific skipjack (Hunter et al., 1986), 1.11 d for bigeye from Indonesia and from an area south of Hawaii (Nikaido et al., 1991). Schaefer (1996) estimated a spawning frequency of 1.27 d for eastern tropical Pacific yellowfin and 1.52 d in a large scale study of yellowfin in the Eastern Pacific Ocean (1998). Spawning frequency estimates of Atlantic yellowfin taken by longline fisheries ranged from 2.2 to 2.8 d (Batalyants, 1992). Of particular relevance for the western Pacific are estimates from the Australian Coral Sea of 1.54 d (McPherson, 1991) from handline and longline samples and an estimate of 1.7 d from Japanese purse seine samples collected within Area B of this study (Nikaido, 1988). All of these studies support high spawning frequencies for tropical tunas that approach a daily spawning periodicity for some species.

Results from this study are in general agreement with previous studies for yellowfin tuna, with estimates from Areas A, B, C, D and E ranging from mean intervals of 1.08 to 2.89 days between spawning events (Tables 5, 6 and 7). Spawning frequency estimates for purse seine caught fish in Areas B, C and D was 1.71 d in complete agreement with the findings of Nikaido (1988) who estimated the spawning frequency of western Pacific yellowfin sampled from Japanese purse seine vessels at 1.7 days. Spawning frequency estimates from longline caught yellowfin fall neatly within the ranges determined by Batalyants (1992) for longline sampled yellowfin in the Atlantic.

The fraction of mature female yellowfin spawning per day in the western tropical Pacific was estimated at slightly over 0.50 and equivalent to a spawning rate of every 1.99 days. A range of estimates resulted from samples taken by different gear or school types, supporting the importance of sampling from a variety of fisheries to obtain a representative picture of the entire population. This does not imply that individual fish spawn on alternate days in this region but represents an average estimate for the population.

Spawning frequency estimates for reproductively active yellowfin in this region are similarly high for fish taken by all gear and school types, ranging between 1.08 and 1.20 d with an estimate of 1.19 days from all samples combined (Tables 5 and 6). The large-scale study conducted by Schaefer (1998) found the same result, estimating the spawning rate of reproductively active yellowfin in the Eastern Pacific Ocean to be 1.19 d. Spawning appears to commence soon after a reproductively active, or fully yolked condition is

achieved, as 84.9% of fully yolked samples from all fisheries and areas were actively spawning as indicated by the presence of postovulatory follicles. Of 427 samples containing migratory nucleus or hydrated oocytes (indicating imminent spawning), 78% also contained postovulatory follicles from a previous spawning, indicating they were in a daily spawning mode. The actual percentage is probably higher as some regressed post-ovulatory follicles may have been overlooked. These observations imply that yellowfin tuna can progress rapidly to a fully yolked and spawning condition and that the majority of reproductively active fish are in a daily or near-daily spawning mode. It is not known for how long an individual fish can maintain daily or near-daily spawning activity but periods of weeks or months at a time are likely. Captive yellowfin tuna in the Achatines Laboratory of the Inter-American Tropical Tuna Commission in Panama have been observed to engage in 116 spawning events over a 155 day period (I-ATTC, 1997a).

Significant differences in spawning rate were noted between tuna in different school associations or taken by different gear and set types. The highest spawning frequency estimates from the equatorial areas came from purse seine sets on unassociated schools that were actively feeding on baitfish, with postovulatory follicles found in 68% of mature fish (95% CI 0.64-0.71) equivalent to a mean spawning interval of 1.47 d. Mature yellowfin taken in log associated sets were less reproductively active with a spawning fraction of 0.45 (95% CI 0.40-0.51) or 2.20 d, indicating a higher proportion of post-spawning or reproductively inactive fish found in association with drifting objects. The high spawning frequency of mature yellowfin caught from baitfish associated schools (1.47 d.) is very close to the 1.52 d estimate made by Schaefer (1998) in the Eastern Pacific Ocean. Discrete areas of abundant forage in the CWPO may emulate the productive, forage rich waters of the eastern Pacific producing similar reproductive conditions for yellowfin. The proportion of mature yellowfin spawning per month was significantly higher in the Philippines compared to Indonesian yellowfin caught by the same method, which may suggest a higher level of productivity in the southern Philippines.

Yellowfin catches sampled from deep-set longline gear had the lowest proportion of reproductively active and actively spawning fish and were lower than for fish sampled from shallow-set longline gear. This appears logical since the shallow-set longline gear is set close to the surface at night when mature and spawning tuna are more likely to be encountered. Deep-set longline gear that is set during the day appears to be more efficient at exploiting mature, reproductively inactive yellowfin that are dispersed over wide areas and not vulnerable to purse seine gear. Yellowfin spawning in Hawaiian waters occurs during the April to September period when 56% of mature fish sampled were found to be actively spawning (95% CI 0.51-0.61) and was noted to virtually cease during the remainder of the year. June, July and August can be considered the peak spawning season, when 89% of mature yellowfin sampled were in an active spawning mode as determined by histological means. The spawning fraction of reproductively active yellowfin in Hawaii was found to be very high at 0.94 (95% CI 0.92-0.96) suggesting daily or near daily spawning activity during the peak spawning season.

BATCH FECUNDITY

Western Pacific

Ovary samples for batch fecundity estimates were collected from purse seine vessels operating in Areas B, C and D and sent to Hawaii in whole, frozen condition. However, the majority of these were collected before the onset of hydration and could not be used to obtain accurate batch fecundity estimates. Therefore, batch fecundity sampling was not adequate for comparisons of batch fecundity by time and area strata. Estimates were made for one year of sampling in Area B and in Area F (Hawaii) from small data sets.

Estimates of mean relative batch fecundity from Schaefer (1996, 1998) and Joseph (1963) for eastern tropical Pacific yellowfin are 68.0, 67.3 and 106 oocytes per gram of body weight respectively. The estimate from this study for Area B of 54.7 oocytes per gram body weight is slightly lower than those of Schaefer but all estimates are significantly lower than the value derived by Joseph. Schaefer suggested the higher estimates of Joseph were not a reflection of spatial or temporal variability in fecundity but was the result of a different methodology that can significantly overestimate fecundity. In that study, estimates were based on counts of advanced yolked oocytes that had been separated from mature ovarian tissue in Gilson's fluid rather than specifically selecting ovaries with oocytes in the migratory nucleus or hydrated condition.

Hawaii

Batch fecundity estimates from Hawaii were highly variable compared to the equatorial estimates, ranging from 0.425 to 10.612 million ova per spawning event. The majority of estimates fell between 2 and 5 million with a singular outlier above 10 million and two samples with unusually low fecundity. The high estimate came from the largest fish in the sample that had very large ovaries (3901 g) that were in a state of full hydration. Replicate counts from different regions of both ovaries were made and found to be consistent with the high fecundity estimate.

The two low estimates were sampled at the beginning and end of the Hawaii spawning season (May and October). The cause of these low estimates are likely the result of two different situations as supported by an examination of their gonad weight and histological classification of the samples. The sample with lowest gonad weight (210 g) was taken in June, had no signs of ovarian atresia and very low relative fecundity of 7.8 oocytes per gram body weight with most oocytes in a partially yolked or developing condition. This may have been the first season the fish had spawned and was at the beginning of an initial spawning period with very small ovaries. The second fish was sampled in mid October at the end of the Hawaii yellowfin spawning season. While still actively spawning as evidenced by the hydrated condition, the fish was classified as Stage 7, with greater than 50% atresia of yolked oocytes and was in the process of absorbing yolked oocytes and shutting down reproductive processes. Schaefer (1998) noted an apparent high variation in batch fecundity estimates from a large data set of eastern Pacific yellowfin. He con-

cluded that the presence of atresia in hydrated ovaries was significantly correlated to below average batch fecundity estimates.

June (1953) examined the spawning characteristics of yellowfin tuna caught by longline vessels close to the main Hawaiian islands during 1950. Samples were divided into 11 maturity stages based on oocyte diameter and the observation of loose ova in the ovarian lumen. Batch fecundity estimates of eleven large (>47 kg) yellowfin sampled during the spawning season ranged between two and eight million ova. Adjusted estimates from this study from the linear regression from data not including the two samples of unusually low fecundity are comparable to the estimates made by June in the size range of 40 to 80 kg tuna. However, both data sets are characterized by low sample sizes. Both linear functions fail to predict fecundities of smaller sized fish that were not sampled by either study and calculate negative values for fish less than approximately 26 kg (Table 12).

SPATIAL AND TEMPORAL SPAWNING DISTRIBUTIONS

Continuous reproductive activity of yellowfin in the central and western Pacific was noted within ten degrees of the equator, with histologically confirmed spawning observed throughout the two year study period. Spawning in this region has been correlated to sea surface temperatures (SSTs) higher than 26°C as inferred by the presence of yellowfin larvae, although some larvae have been noted to occur at temperatures above 24°C (Ueyanagi, 1969). Continuous spawning in this tropical region has been confirmed by several studies and at higher latitudes when sea surface temperatures rise above 24°C (Suzuki, 1994a). Captive yellowfin have been observed to spawn at water temperature ranges above 24.4°C (I-ATTTC, 1997b). Schaefer (1998) noted a minimum sea surface temperature of 22°C for yellowfin spawning in the Eastern Pacific Ocean with 85.3% of spawning occurring at water temperatures between 26°C and 30°C. Water temperatures remained well above 24°C in Areas A, B, C and D throughout the study period but temporal variations in relative spawning activity were noted for these areas.

Area A (Philippines and Indonesia)

Wade (1950) proposed a peak spawning period for Philippine yellowfin tuna between May and August. However, this conclusion was based on a very small sample size of fish less than 84 cm in fork length with maturity stages estimated by macroscopic methods. Buñag (1956) observed no well defined spawning season through the examination of oocyte diameters from a limited data set. Yesaki (1983) using GI analysis observed spawning condition female yellowfin from September to May (1982). However, the remaining May to July period, proposed as a period of low spawning, was determined from a small sample size. His results indicated peak spawning in the March to May period with a secondary spawning period from October to December. The findings of his study suggested that the Moro Gulf and northern Celebes Sea was a major spawning region for the Philippines which coincides with the area sampled by the current study.

The results of this study indicate continuous spawning of yellowfin at a high rate in the southern Philippines, confirming the importance of the region to western Pacific yellow-

fin. However, peak seasonality noted for the area was in contrast to previously mentioned studies. Spawning was noted to occur at high rates throughout the year but with significant decreases in spawning activity noted during the February to June (1995) and February to May (1996) periods (see Figure 25). These periods of low spawning activity may be related to seasonal weather patterns. Yamanaka (1990) noted peak spawning periods from GI analysis of fish larger than 35 kg in the April to June and October to November (1987) periods from handline samples collected from the same region of the southern Philippines. She proposed that monsoonal weather patterns have a significant influence on the spawning and recruitment of yellowfin in the southern Philippines. Longhurst (1995) noted that seasonal alterations between eutrophic and oligotrophic biological systems can occur in tropical systems with strongly reversing monsoon driven weather patterns. The prevailing weather pattern consist of three seasons: (1) a northeast monsoon from November to March with the strongest winds and lowest SSTs; (2) a transitional trade wind period between April and May with low winds and rapidly rising SSTs; and (3) a southwest monsoon period from June to October during which the highest SSTs occur and winds increase in force (Dalzell and Ganaden, 1987) See Wyrski (1961) for a thorough review on the physical oceanography of this region. However, inter-annual variability in these seasons does occur.

During 1995 and 1996, the lowest sea surface temperatures occurred following sharp declines in SST during the January to February northeast monsoon periods which follows the normal pattern the southern Philippines (Figure 25). Decreases in spawning activity were noted to follow in February to May. However, SSTs for both years ranged from 28°C to 30°C, well above the minimum temperature necessary for yellowfin spawning. This observation suggests the importance of additional factors in maintaining high reproductive rates in yellowfin. It is possible that the noted drops in sea surface temperatures brought on during the northeast monsoon coincide with decreases in productivity or food availability that subsequently inhibit spawning activity. Yamanaka (1990) noted low condition factors of yellowfin during the northeast monsoon, speculating that the strong winds may cause instability in the ocean environment and a decrease in the concentration of food items. Another possibility is that a sudden though small decrease in SST triggers a physiological reaction that temporarily shuts down spawning activity.

Spawning seasonality was less defined in Indonesia where sea surface temperatures ranged slightly lower, from 27°-30°C. Four slight declines in seasonal SSTs were noted during the study period; two during the June to September periods and two in the January to February periods (Figure 26). It is not clear if these patterns had any influence on spawning activity from the available data. The general proportion of mature fish spawning per month is significantly lower than for Philippine samples. This may be due to the fact that the Indonesian fishery harvests fish that are slightly smaller than the Philippine fishery or it may be the result of a real difference in productivity and spawning activity between the Molucca Sea (Indonesia) and the Moro Gulf (Philippines). The nutrient distribution and hydrography of this region varies seasonally in response to monsoonal influences (Gieskes et al. 1990; Zilstra et al. 1991). The mean sizes of Indonesian sampled yellowfin compared to Philippine fish were 114.8 and 126.6 cm respectively.

Areas B, C And D (Western Pacific Purse Seine and Longline)

Within this region, several different areas and seasons of peak spawning for yellowfin tuna have been proposed. Koido and Suzuki (1989) inferred from Japanese purse seine data that the main spawning season for yellowfin in the western tropical Pacific extends from November to April in an area roughly bounded by 10°N–5°S, 130°–170°E which is coincident with Area B. However, sample sizes were small and the date and position of catch had to be estimated as sampling was conducted at the time of unloading. The study also examined a large data set of longline samples collected during 1968–1970 but were not able to discern any seasonality to spawning activity in this region. This is not surprising as the paper stated that reproductively active yellowfin are rarely caught by Japanese longliners. However, Kikawa (1966) reported a December to January peak spawning potential in the western tropical Pacific (120°E–180°) and an April to May peak in spawning east of the Date Line (180°–140°W) from longline caught samples. These results are in agreement with a general consensus by some researchers of peak spawning for western Pacific yellowfin during the fourth and first quarter and in the central Pacific during the second and third quarter.

Spawning rates in both longline and purse seine samples examined by this study decreased in the western Pacific (Areas B and C) from December 1994 to May 1995 which contrasts to the proposal of peak spawning in this area during the first and fourth quarters. Spawning rates were high at all other times. However, purse seine sampling from the central Pacific region (Area D) east of the Date Line indicated an active spawning period between June and October in agreement with previous studies.

Peak spatial and temporal spawning rates for yellowfin in the equatorial western Pacific appear to be highly variable and subject to significant inter-annual variation. An explanation for this variability may be linked to the discontinuity and “patchiness” of surface productivity in the western tropical Pacific Ocean, which has been characterized as an oligotrophic environment with low primary productivity (Longhurst et al., 1995; Longhurst, 1998). However, areas of high productivity must occur as the region supports the largest tropical tuna stocks and fisheries in the world.

Lehodey et al. (1997) theorize that localized productivity in this environment is enhanced by the westward advection and convergence of nutrient rich waters of the central and eastern Pacific with the eastern edge of the Western Pacific Warm Pool (WPWP) which is the largest body of warm water in all oceans with surface temperatures consistently above 28°C (Yan et al., 1992). Large scale longitudinal displacements of the convergence apparently occur in response to ENSO cycles which are mirrored by significant zonal shifts in catch and effort by surface tuna fisheries: expanding to the east of 170°E during warm El Niño events and contracting west of 160–170°E during normal or La Niña events (Hampton, et. al, 1998). High CPUE of skipjack by the western Pacific purse seine fishery was found to be highly correlated to the location of the WPWP convergence zone, identified by a well-defined salinity front close to the 28.5°C isotherm (Lehodey et al., 1997). Tagging data suggested the zonal shifts in peak CPUE were a result of a true displacement of tuna in response to the location of the convergence zone. However, higher

catch rates occurred consistently westward of the apparent line of convergence, possibly due to a time lag necessary for enriched waters to develop into secondary and tertiary production, i.e. tuna forage or prey organisms. These concepts have been taken further by the development of predictive models based on preferred tuna habitat defined by optimal sea surface temperature and high densities of tuna forage (Bertignac et al. 1998; Lehodey et al., 1998).

Cole (1980) noted that “areas of high productivity and high standing crops of zooplankton are produced, in part, by upwelling, doming and converging surface waters of different densities. Yellowfin conceivably are drawn to these areas to feed on forage organisms also gathered there.”

Figure 32 indicates purse seine catch by quarter for 1994 on unassociated yellowfin surface schools, the majority of which consisted of medium to large sized yellowfin actively feeding on baitfish concentrations. Significant catches east of 180E occur during the second and third quarter. Mature sized yellowfin sampled by this study from actively feeding schools were found to be reproductively active with high spawning frequencies approaching a daily spawning rate. Project sampling in the region of 180°–140°W from June to October 1994 confirmed high spawning rates of mature fish from baitfish associated schools (Figure 25). Theoretically, significant levels of spawning would result in areas supporting concentrations of tuna forage, if the relationship between active feeding and reproduction is valid and the forage concentrations persisted for significant periods of time. High levels of purse seine effort on mature sized tuna in baitfish associated schools could be a means to estimate tuna spawning activity in the western equatorial Pacific.

The general consensus of a fourth and first quarter peak in yellowfin spawning in the western Pacific that shifts to the east during the remainder of the year, as was suggested from purse seine effort in 1994 has support from industry and field surveys, but the relationship is not well documented. Gillett and Taufao (1985) using data from the SPC Skipjack Survey and Assessment Programme (SSAP), documented the incidence of “foaming” tuna schools in the western and central Pacific that were actively feeding on baitfish and considered suitable for purse seining. They state that “Japanese fishermen have been aware for several years that foaming schools are especially common in the area to the north of Papua New Guinea during October to December”. Myers (1984) in a feeding study of pelagic gamefish reported ocean anchovy (*Engrasicholina punctifer*) as being more abundant in tuna stomachs sampled near Guam in the western Pacific in the October to November period. To the east, US purse seine fishermen recognize seasonally abundant foaming schools of yellowfin and skipjack in the eastern range of the fishery near the Phoenix and Line Islands (160°-175°W) reported to occur more frequently between May and August (Yamasaki, pers. comm.). Fishing on these concentrations of foaming schools can continue in the same general area for periods of two to three months at a time.

Other localized regions of productivity and high forage may result from upwelling or nutrient enhancement occurring near oceanic islands or along frontal boundaries that form between the westward flowing North and South Equatorial Currents and the eastward flowing Equatorial Countercurrent (reviewed in Cole, 1980). These discrete, and shifting

areas of productivity and subsequently derived forage could help to explain the inter-annual variability in observations of peak spawning areas and times of year or “seasons” for yellowfin in the tropical central and western Pacific region.

Areas E and F (Hawaii)

Seasonal spawning patterns were evident in Areas E and F where samples were collected at higher latitudes. Area E was sampled almost entirely by deep-set Japanese style longline gear which normally land reproductively inactive fish. However, higher proportions of fully yolked or spawning fish were evident during the northern hemisphere summer and fall periods. Yellowfin spawning shows a classically seasonal pattern in Hawaiian waters as was proposed by June (1953) who noted well developed ovaries in longline caught fish from mid-May to the end of October, 1950. Yellowfin larvae have been identified in the nearshore waters surrounding Oahu (Hawaiian Islands) in June and September but were absent in December and April (Boehlert and Mundy, 1994). The current study histologically verified active spawning of yellowfin north of 15E N between April and November during the 1994 to 1996 study period. June, July and August are clearly the major spawning months for this area when 89% of mature fish sampled were noted to be in an actively spawning condition verified by the presence of postovulatory follicles or oocytes in a hydrated condition (Figure 30).

An examination of yellowfin spawning activity around Hawaii relative to local sea surface temperatures is particularly interesting. Figure 31 plots bi-monthly mean SSTs and indicates months in which actively spawning yellowfin were sampled in the Hawaii area during the 1994–1996 period¹¹. Spawning was first noted in April or May with SSTs above 24.5°C and continued until the October/November period. The highest SSTs in this region consistently occur during September or October, with the cessation of spawning noted to occur at SSTs above 27°C; well above the temperature considered necessary for yellowfin spawning. Spawning activity consistently ceased in all three years shortly after the highest yearly SSTs occurred and slight declines of less than one degree centigrade were recorded, suggesting the importance of additional factor(s) for continued yellowfin spawning.

Miller (1979) conducted larval fish surveys near the main Hawaiian Islands, noting larval tuna abundance was frequently one or two orders of magnitude higher than for typical oceanic regions of the central Pacific Ocean with *Thunnus* larvae (most likely yellowfin) more common close to the main islands. Boehlert and Mundy (1994) observed differential distributions of scombrid taxa around Oahu, Hawaii, with the abundance of yellowfin larvae highest at inshore leeward areas, in contrast to skipjack larvae (*Katsuwonus pelamis*) which were more abundant at offshore stations. They did not agree with studies suggesting that high inshore abundance of tuna larvae were the result of a physical concentration of larvae by mesoscale eddies or onshore advection of larvae from offshore spawning events (Lobel and Robinson, 1988; Miller, 1979). Their conclusion was in closer agreement with Yesaki (1983) for the southern Philippines; that high concentra-

¹¹ Recorded SST in EC at NOAA moored weather buoy 51003 located at 19E8' N, 160E48' W for the first and fifteenth day of every month at 1200 UTC.

tions of yellowfin larvae at inshore, leeward locations were a natural consequence of aggregations of spawning adults at or close to these areas, coupled with rapid larval development. They proposed that concentrations of spawning tuna may be due to increased forage available to mature yellowfin near islands or a selective advantage that promotes subsequent larval growth and survival.

High catch rates of mature yellowfin by hook and line gear close to the main Hawaiian Islands during the summer strongly supports an inshore aggregation effect during the spawning season. Prior to exclusion from nearshore fishing grounds, the Hawaii based yellowfin longline fishery concentrated on inshore waters off the leeward (west) coast of Oahu and the leeward and windward sides of the island of Hawaii, with catch rates peaking during the summer season (June, 1950). The Hawaii yellowfin spawning season and peak landings by Hawaii based longliners so nearly coincided (c. 1950) that June (1953) concluded that the fishery was based on a spawning run. After 1991, longline gear was restricted from within 50 to 75 nautical miles of the main Hawaiian Islands to mitigate gear conflicts with handline and troll fisheries, primarily during the summer season when the small gear types are most active¹². Longline landings of yellowfin now occur throughout the year due to an expansion of fishing grounds to lower latitudes during the winter season, but catches and catch rates are still highest during the second and third quarters and appear to be island associated (Curran et al., 1996). Handline and troll catches of mature sized yellowfin in Hawaii also peak during the summer season. These fish are in an actively feeding mode as observed by fishermen and inferred by their positive biting response to hook and line gear, and are reproductively active as confirmed in this study. The highest spawning frequency estimates for Hawaiian yellowfin indicating daily spawning rates were sampled from the inshore *ika shibi* handline and troll fisheries during the second and third quarters.

High catch rates and spawning frequencies were also noted for some offshore areas in the Hawaii region; in particular the five degree square south of the main Hawaiian Islands and southwest of 20°N, 155°W. This area encompasses several productive offshore seamounts targeted by Hawaii based longline vessels for large yellowfin and bigeye tuna and offshore handline vessels fishing for juvenile tunas. This area is at the eastern edge of two counter-rotating gyres separated by an eastward flowing countercurrent set up by the influence of the main Hawaiian Islands on the westward flowing North Equatorial Current (Qiu et. al, 1997). Research interest in this area is strong, as the interaction of bottom contours, current gyres and a location in the lee of the main Hawaiian Islands contribute to enhanced productivity and may play an important role in the retention and return of pelagic eggs and larvae of coastal and pelagic resources to the Hawaiian Islands. An enhanced productivity and concentration of forage in this area would also promote spawning conditions for pelagic fish, including yellowfin tuna.

¹² Amendment 5 to the Fishery Management Plan (FMP) for the Pelagic Fisheries of the Western Pacific Region of the Western Pacific Regional Fishery Management Council.

AGGREGATION, PRODUCTIVITY, AND VULNERABILITY

Nearshore Environment

Blackburn (1969) noted, “the availability of forage organisms in areas of optimum temperature is an important factor in determining where yellowfin tend to aggregate.” The “island mass effect” with elevated primary production close to islands (Doty and Oguri, 1956), rich zooplankton communities (Jones, 1962) and coral reef associated and pelagic fish larvae (Leis and Miller, 1976; Miller, 1979; Leis, 1982) which contribute to elevated forage levels may contribute to differential maturity or elevated spawning activity close to high islands and archipelagos. A positive relationship between discrete areas of local productivity and tuna reproduction has also been noted. Grimes and Lang (1992) sampled fish larvae in the vicinity of the nutrient rich Mississippi River discharge plume in the Gulf of Mexico and suggested that the area supported significant levels of yellowfin spawning. Tuna larvae aged at 2 to 14 days were concentrated in frontal zones where mixing of river plume and oceanic waters occurred. The productive waters of the Gulf of Mexico, enhanced by nutrient input from the Mississippi River could be considered analogous to the Moro Gulf, surrounded by the Philippine and Indonesian archipelagos and enriched by seasonal monsoon runoff and wind driven upwelling of nutrient rich waters (Munro, 1986; Yamanaka, 1990).

The strong association of juvenile and adult yellowfin to islands and seamounts has been well recognized (Murphy and Shomura, 1972; Petit et al. 1989; Fonteneau, 1991). Yesaki (1983) suggested that large sized yellowfin aggregate to the archipelagic waters of the Moro Gulf region of the Philippines to feed and spawn, as inferred by high catch rates of mature fish, active feeding behavior and high reproductive condition. Intermediate sized yellowfin of 60 to 110 cm, which are common from other areas of the western Pacific are noticeably absent from Moro Gulf fishery landings further suggesting that larger, mature sized yellowfin actively aggregate to this area. In addition, larval and juvenile yellowfin less than 30 cm in fork length are very abundant in the Moro Gulf that are the likely result of elevated local spawning.

The relationship between high catch rates, increased forage and temporal and spatial spawning distributions of yellowfin is clearly evident in the hook and line fisheries of Hawaii. The highest catch rates of large yellowfin taken by troll and handline gear close to the main islands coincide so precisely with the peak spawning season that the fisheries could be considered to be based on an inshore spawning run. Longline catches also peak during the summer spawning season. Prior to the exclusion of longline effort from inshore waters, the Hawaii based tuna longline fishery operated very close to the shore during the summer season, apparently targeting an inshore spawning aggregation (June, 1953).

High catch rates of mature yellowfin also occur during the spawning season in a productive area directly south of the longline exclusion zone that surrounds the main Hawaiian Islands. A segment of the Hawaii longline fishery appears to concentrate on reproductively active yellowfin during the summer months to compensate for exclusion from in-

shore fishing grounds and to offset seasonally poor fishing for bigeye tuna. During the winter season, longline effort shifts to swordfish, bigeye and albacore tuna when the nearshore vulnerability of yellowfin tuna decreases.

Offshore Environment

The vulnerability of large yellowfin tuna to purse seine gear is also related to aggregation, feeding and spawning behavior. Spawning events are a surface oriented activity, which greatly increases the vulnerability of concentrations of schools of mature fish to surface gear. Successful purse seining for large yellowfin as it developed in the Eastern Tropical Pacific (ETP) depends on schools associated with marine mammals or is restricted to areas with a relatively shallow thermocline and sharp temperature gradient between the 15° and 23°C isotherms (Sharp, 1978). The central and western tropical Pacific is characterized by nutrient poor waters of high clarity with a relatively deep thermocline. Successful purse seining in this region was first developed on tuna schools found aggregated to natural floating objects which allowed setting on stabilized schools before dawn when the tuna can not see to avoid the seine (Doulman, 1987; Watanabe, 1983). Subsequent gear developments and methods have lead to successful purse seine operations on unassociated schools which are actually feeding schools aggregated to surface concentrations of baitfish. Tuna schools engaged in this activity are termed “boilers” or “foamers” by the fishermen due to the choppy, frothing white appearance of the water (Scott, 1969). Setting and pursing of the seine is completed while the tuna are distracted by their feeding activity, which temporarily increases their vulnerability to purse seine gear. These feeding tuna schools have been observed on several research cruises and the baitfish prey species positively identified as the ocean anchovy, *Engrasicholina punctifer* (Hida, 1973; Ozawa and Tsukahara, 1973).

The ocean anchovy is broadly distributed throughout the Indo-Pacific region and has been reported from several locations, including the east coast of Africa, India, the Persian Gulf, southeast Asia, Japan, the Philippines, the central tropical Pacific and Hawaii (Strasburg, 1961; Whitehead, 1967). The species is well known from coastal locations (Sreekumari, 1977; Young et al. 1995) but appears to be primarily an offshore species and the only member of the anchovy group capable of completing the life cycle in the oceanic environment (Gorbunova, 1973; Orlov, 1995). Ozawa and Tsukahara (1973) concluded from large-scale larval fish surveys that *E. punctifer* is dominant and widely distribute in the surface waters of the tropical western Pacific, comprising over 45 % of all fish larvae obtained by the examined surveys. The anchovy larvae were evenly distributed between the westward flowing North and South Equatorial Currents and the eastward flowing Equatorial Countercurrent, leading them to propose widespread spawning of ocean anchovy throughout the region. Five years of pelagic trawl survey in the tropical western Pacific targeting skipjack larvae found all stages of ocean anchovy to be widespread and highly abundant in surface waters during the day and night (Ogura et al., 1999).

The species is a major prey item of juvenile and adult tuna in this region (Buckley and Miller, 1994; Hida, 1973; Itano and Williams, 1992; Ozawa and Tsukahara, 1973; Myers,

1984). The South Pacific Commission conducted intensive surveys of the western tropical Pacific between 1977 and 1980 in conjunction with tuna tagging operations of the Skipjack Survey and Assessment Programme. During this period, the majority of yellowfin tuna schools sighted by program vessels were free swimming schools actively feeding on *E. punctifer* (Itano and Williams, 1992). This situation was repeated by tuna school sightings recorded during the SPC Regional Tuna Tagging Project that surveyed the same region between 1988 and 1992 (Itano and Lewis, 1990). Tanabe et al. (1999) conducted gut analysis of larval skipjack and *Thunnus* spp collected by pelagic trawl in the tropical western Pacific. The larvae fed primarily on fish larvae, and ocean anchovy larvae was a dominant component of the identified samples.

The examination of gut contents of yellowfin sampled by the current study found *E. punctifer* to be the dominant food item by frequency and volume for fish taken on unassociated purse seine sets. The stomachs of yellowfin caught on baitfish associated schools were often filled exclusively with the ocean anchovy. These samples contained a high proportion of reproductively active females with high spawning frequency estimates approaching a daily spawning periodicity. This is not surprising, considering the high energy requirements necessary to support an output of millions of ova per day over prolonged periods (Schaefer, 1998). This proposed link between the ocean anchovy (*E. punctifer*), tuna feeding aggregations, vulnerability to surface fisheries and yellowfin reproduction highlights the importance of this single forage species to the central and western Pacific. Ozawa and Tsukahara (1973) proposed that the ocean anchovy, that feed primarily on copepods (Hida, 1973), may provide a critical link between zooplankton and larger pelagic fishes, such as skipjack and yellowfin tuna.

INTERACTION AND GEAR CONFLICT

Western Pacific

Categories of fisheries interaction relevant to western Pacific tuna fisheries are reviewed by Hampton (1994) and Kleiber (1994; 1996). Stock related interactions and gear conflict issues are most relevant to this study due to the influence of reproductive condition on the vulnerability of mature yellowfin to different gear types.

The sequential, or growth interaction issue specific to purse seine harvests of juvenile yellowfin on the subsequent catch rates of large fish by longline has been considered the most important interaction issue facing western Pacific tuna fisheries in recent years. Specific studies on this issue include Suzuki (1988) and Medley (1994) and the subject is reviewed in Suzuki (1994b). Concerns are based on the common perception that purse seine gear harvests juvenile yellowfin. This has been a feature of the Japanese fishery, particularly in the early years when purse seiners were noted to take fish smaller than about 70 cm while Japanese longline gear harvests fish larger than 90 cm (Suzuki, 1988).

This generalization is accurate for the fishery as a whole, although an increased targeting of large yellowfin by some fleets has occurred over time resulting from advances in gear technology and accumulated fishing experience. In comparison to the Japanese fleet, US

purse seiners in the western Pacific regularly land a higher percentage of large yellowfin with a mode between 80 and 120 cm but ranging to over 150 cm (Coan, 1994) and will target large yellowfin if available and vulnerable. Suzuki (1988) noted that size related vulnerability of yellowfin to purse seine gear was dependent on school type, with fish less than 70 cm characteristic of log associated sets and large fish over 100 to about 150 cm dominant in free swimming schools. As noted earlier, so called “unassociated” or “free swimming” yellowfin schools that are harvested by purse seine gear in the western Pacific are usually feeding intensively on the pelagic anchovy (*E. punctifer*). The other major distant water purse seine fleets of Korea and Taiwan have also adopted gear modifications and fishing techniques to target large yellowfin on baitfish associated schools. Results of the current indicate that actively feeding yellowfin schools often consist of reproductively active fish in near daily spawning modes. Therefore, the reproductive condition of yellowfin not only influences the vulnerability of large yellowfin to purse seine gear but has the potential to increase competition with other fisheries for large sized tuna, i.e., longline and handline fisheries.

Results of this study indicate that direct interaction between purse seine and longline gear is more significant with shallow-set longline gear that is fished at night. The shallow-set gear is technically simple and less costly to deploy and is utilized by many small to medium sized longline vessels operating from transshipment bases in the central and western Pacific region. A high proportion of reproductively active (fully yolked) fish with high spawning frequency estimates were noted in the catch of both purse seine and shallow-set longline gear from the same spatial and temporal strata. These observations suggest that the different gear types are potentially in direct competition for large, reproductively active yellowfin.

The degree of direct competition for large fish, inferred by spawning frequency estimates and reproductive condition, may be significantly less between purse seine and deep-set longline gear. Mature yellowfin taken from actively feeding schools by purse seine were often in a daily or near-daily spawning mode. A higher ratio of mature, but reproductively inactive fish were noted in catches of deep-set longline gear. Previous studies have noted a similar situation where purse seine fish were classified as “more matured” compared to fish taken by Japanese (deep-set) longline gear according to GI analysis (Suzuki, 1988; Suzuki and Koido, 1989). In some cases, these differences have been interpreted as evidence of a lower size at maturity for purse seine caught yellowfin and a differential vulnerability to gear types. In contrast, this study estimated similar lengths at 50% maturity for fish taken by both gear types; purse seiners landing higher proportions of spawning fish while deep-set longline gear takes a higher proportion of post-spawning tuna that can be incorrectly classified as immature if maturity is assigned by non-histological methods. It is proposed that mature yellowfin enter and leave periods of active spawning throughout their mature stage, exposing them to alternating cycles of vulnerability to different gear types and fisheries with related shifts in interaction rates.

Hawaii

Several user groups harvest yellowfin tuna in the Hawaii region, including domestic longline, pole-and-line, troll and handline fisheries motivated by a combination of subsistence, recreational, charter and commercial purposes. Interaction issues between commercial and recreational/subsistence fisheries have received the most attention in recent years.

Direct competition for mature sized yellowfin in Hawaii occurs between large-scale longline and small-scale troll and *ika shibi* handline fisheries. Different rates of fishery interaction between Hawaii pelagic fisheries have been proposed. Boggs (1996) examined the relationship between local catches and CPUE for Hawaiian bigeye and yellowfin fisheries and could not support a general conclusion that local catches influence CPUE for either species. In an earlier study, no statistically significant relationship between domestic yellowfin catches and yellowfin troll CPUE could be supported, although the data examined was considered incomplete (Boggs, 1994). However, local yellowfin CPUE was found to be closely related to seasonal effects and positively correlated to abundance estimates of yellowfin from the broader central and western tropical Pacific. A study by Lovejoy (1977), modeling interaction between Hawaii longline and troll fisheries for blue and striped marlin concluded that interaction rates, or at least the ability to discern them increases with the proximity of the fisheries. Squire and Au (1990) also proposed that localized fishing effort can significantly increase local interaction rates and depress CPUE over short time lags.

The rate of fishery interaction relevant to Hawaii yellowfin fisheries is uncertain, but there is no doubt that direct gear conflict can occur when different fisheries operate concurrently. Gear conflict problems between longline and troll fisheries became acute in Hawaii following a rapid influx of longline vessels from US mainland fisheries during the late 1980s which lead to the implementation of longline exclusion areas surrounding the main Hawaiian Islands (Dollar, 1992).

The findings of this study support an increased local abundance and vulnerability of mature yellowfin tuna close to the Hawaiian Islands when they are reproductively active, peaking during June, July and August. During this period, catch rates of mature sized yellowfin are highest for Hawaii based longline, handline and troll fisheries, and inshore fishing effort by small gear types reaches a seasonal maximum. Consequently, the potential for fishery interaction and gear conflict peaks during the summer spawning season.

SUMMARY

Results from this study confirm the high reproductive potential of yellowfin tuna in areas where sea surface temperatures remain above 24°C to 25°C. However, spawning activity was noted to decrease or temporarily cease in some areas where sea surface temperatures remained high, suggesting that trends in local water temperatures, forage availability or other factors may be important to maintain spawning activity. The current study examined peak spawning areas and seasons by school and capture gear type, noting a positive

relationship between high reproductive rates, localized areas of forage abundance and heightened vulnerability to surface fisheries.

This study does not support a differential maturity schedule for yellowfin that are harvested in the same time/area strata by surface and sub-surface fisheries. After reaching maturity, it is proposed that female yellowfin tuna cycle in and out of active spawning periods, characterized by near daily spawning rates and high fecundity. Increased vulnerability to surface gear may occur as the fish cycle into spawning condition. During post-spawning periods, their vulnerability to surface gear apparently decreases as the fish disperse from spawning aggregations. Deep-set longline gear appears to be more efficient at harvesting these post-spawning adults that may be spread out over greater distances.

Higher latitude regions, such as around Hawaii have well defined seasonal patterns of yellowfin spawning. Seasonal peaks in spawning may also be evident in equatorial areas subject to strongly reversing monsoon weather patterns. In the equatorial region of the central and western Pacific purse seine fishery (~ 145°E–150°W), consistently high sea surface temperatures and a relatively stable oceanographic environment suggest tropical tunas can reproduce independently of season. However, areas and times of elevated spawning activity appear to exist and vary between years. The current study found a positive relationship between intense feeding activity on the ocean anchovy (*Encrasicholina punctifer*) and high reproductive rates for yellowfin. It is suggested that discrete areas of elevated forage abundance that vary in time and space and between years could help to explain differences in proposed spawning areas and “seasons” in this region. Further study along these lines is encouraged.

In Hawaii, fisheries targeting large yellowfin appear to be based on an inshore spawning run during the spring, summer and early fall, when vulnerability to surface gear and the potential for gear conflict and interaction between fisheries increases. To mitigate gear conflict issues between large and small gear types, inshore longline area closures have been imposed. An unintended consequence of these measures is that reproductively active yellowfin close to the main Hawaiian Islands are exposed to reduced fishing pressure. However, the significance of this will require more information on the role of immigration, residence times, spawning site fidelity and recruitment of yellowfin to Hawaiian fisheries.

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