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# Reproductive biology of female Pacific bluefin tuna *Thunnus orientalis* from south-western North Pacific Ocean

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***ABSTRACT:*** Pacific bluefin is a highly valuable pelagic species that inhabits a broad range in the North Pacific Ocean. The reproductive biology, especially for the spawning aggregation in the south-western North Pacific Ocean, is not well understood. Thus, a total of 119 paired ovary specimens were collected from the Taiwanese longline fleet during the 1999 fishing season (late April through June) to gain a better understanding of important reproductivity-related stock parameters associated with this species. The following conclusions were made: (i) condition factor decreased from late May to early June; (ii) the sex ratio might be 1:1 for spawners; (iii) the gonadosomatic index stayed at a relatively high level and markedly increased from late May to early June; (iv) histological examination of oocytes indicated that all specimens were sexually mature; (v) spawning activity appeared to start in May and peak in late May to early June; (vi) batch fecundity increased with fork length; and (vii) preliminary estimates of spawning frequency between batches ranged 2–4.5 days based on analysis of postovulatory follicles.

***KEY WORDS:*** **batch fecundity, oocyte stage, Pacific bluefin tuna, sex ratio, spawning frequency, spawning season, *Thunnus orientalis*.**

## INTRODUCTION

Pacific bluefin tuna *Thunnus orientalis* Temmincks and Schlegel 1844 is a large highly migratory pelagic species mostly found in the North and western South Pacific Oceans.[1] This species represents an important economic resource to a host of countries, including Japan, Taiwan, USA, and Mexico. Since the early 1990s, from late April through June each year, small-scale Taiwanese longline vessels have targeted bluefin tuna that aggregate and undergo spawning migrations in south-western North Pacific Ocean waters from the Philippines to Taiwan. Historically, annual catches by Taiwanese vessels have ranged approximately 1300–2700 t; total annual catches by all nations have ranged 13 000–25 000 t.[2]

Biological characteristics of this stock, including population status determinations, have been generally defined by Japanese and American scientists since the 1960s, and by the International Scientific Committee for Tuna and Tuna-like Species in the North Pacific Ocean (ISC) since the late 1990s.[2] However, details regarding critical biological parameters, such as maturity, have not been examined in a systematic manner, which confounds conducting timely evaluations on the status of the stock for management purposes. For example, a thorough database that includes results from specific biological studies is currently not readily available to researchers interested in Pacific bluefin population dynamics.

Members of the stock have been reported to move between the western and eastern North Pacific Ocean; however, spawning activity is more constrained in distribution, and is believed to occur only in the western North Pacific Ocean,[1,3–6] especially from waters around the Ryukyu Islands to the Sea of Japan from June to August. Reproductive studies have addressed the Pacific bluefin tuna sex ratio, spawning ground distribution, maturity-at-age, spawning fraction, and fecundity.[3,6–9] Recently, Tanaka[6] reported spawning season, spawning fraction, and batch fecundity of Pacific bluefin tuna around the Ryukyu Islands and in the

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Sea of Japan. Finally, bluefin tuna have been shown to be multiple spawners.[10,11]

There is little information available regarding spawning behavior for bluefin tuna in south-western North Pacific Ocean waters (i.e. the area of this study), where the fishery typically harvests very large (mature) adults.[12] The primary objectives of this study are to examine reproductivity-related biological aspects, including spawning season, sex ratio, batch fecundity, and length frequency distribution, from critical spawning habitats of bluefin tuna in the North Pacific Ocean.

## MATERIALS AND METHODS

### Sample collection

In total, 241 Pacific bluefin tuna were randomly sampled from 17 different trips of small-scale Taiwanese longliners (Table 1) that operated in south-eastern waters off Taiwan (Fig. 1) during April and June 1999. Among those, there were 123 females, and 119 ovary specimens were collected onboard the vessels (four ovaries were discarded by fishers). For Pacific bluefin tuna harvests, fish were typically eviscerated immediately onboard the vessel and subsequently chilled. Ovary samples were removed, numbered, and chilled during onboard procedures, with each sampled fish tagged for later identification associated with measurements (length and weight) collected in an ongoing port-side sampling program in Tungkang. Finally, field-related data regarding the sampled catch included fishing latitude and longitude, as well as other general fishing information gained through interviews with the captains at the ports following the fishing trip.

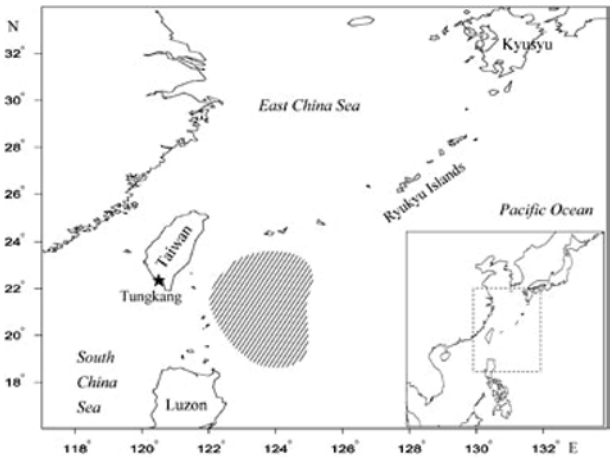


**Fig. 1** South-western North Pacific where Taiwanese small-scale longline fleet operated to target bluefin tuna and collect female gonad specimens, shaded area.

**Table 1** Sampling information and binomial test data for statistical differences in Pacific bluefin tuna sex ratio from fishing-trip data collected from the Taiwanese longline in the south-western North Pacific Ocean in 1999. Null hypothesis was based on a sex ratio hypothesis of 1:1

| Trips | Dates | Females (No.) | Males (No.) | Total (No.) | Probability of female occurrence (*P*) | Test results |
|---|---|---|---|---|---|---|
| 1 | 9 May | 7 | 1 | 8 | 0.0313 | * |
| 2 | 17 May | 8 | 4 | 12 | 0.1208 | ns |
| 3 | 19 May | 2 | 6 | 8 | 0.1094 | ns |
| 4 | 22 May | 6 | 2 | 8 | 0.1094 | ns |
| 5 | 23 May | 7 | 7 | 14 | 0.2095 | ns |
| 6 | 26 May | 8 | 9 | 17 | 0.1855 | ns |
| 7 | 27 May | 7 | 10 | 17 | 0.1484 | ns |
| 8 | 27 May | 16 | 14 | 30 | 0.1354 | ns |
| 9 | 27 May | 6 | 6 | 12 | 0.2256 | ns |
| 10 | 31 May | 6 | 10 | 16 | 0.1222 | ns |
| 11 | 31 May | 6 | 6 | 12 | 0.2256 | ns |
| 12 | 01 June | 7 | 9 | 16 | 0.1746 | ns |
| 13 | 03 June | 4 | 7 | 11 | 0.1611 | ns |
| 14 | 06 June | 14 | 12 | 26 | 0.1439 | ns |
| 15 | 08 June | 6 | 3 | 9 | 0.1641 | ns |
| 16 | 12 June | 10 | 9 | 19 | 0.1762 | ns |
| 17 | 13 June | 3 | 3 | 6 | 0.3125 | ns |
| Sum | | 123 | 118 | 241 | 0.0487 | * |
| Sum† | | 116 | 117 | 233 | 0.0521 | ns |

ns, not significant ($P > 0.05$); *significant ($P < 0.05$).
†data excluded the first trip.

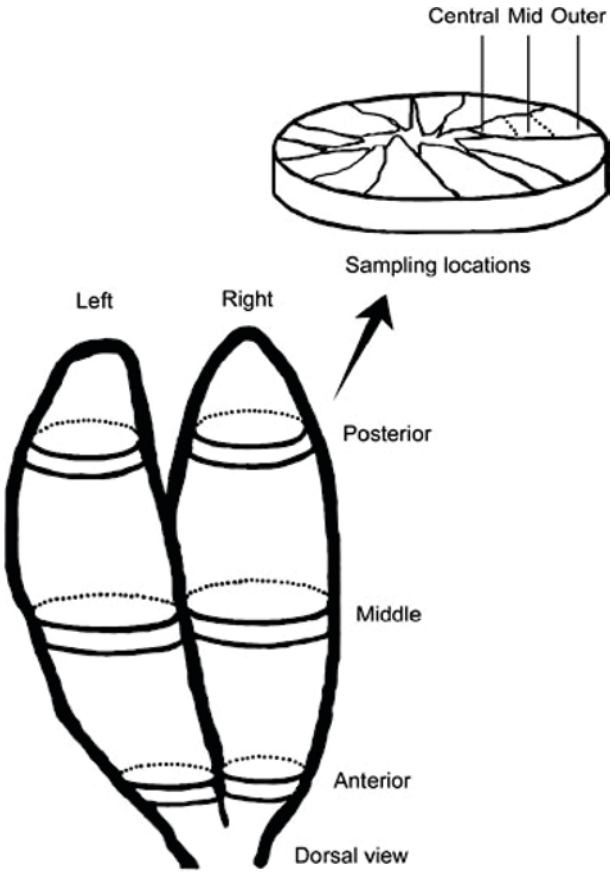


**Fig. 2** Schematic of Pacific bluefin tuna ovary, showing the location (anterior, middle and posterior) and layer (central, mid and outer) where samples were taken.

Ovary samples were immediately transported from the landing site to the laboratory, wiped clean of moisture, and weighed to the nearest 20 g. Small pieces (~50 g) were subsampled from the anterior, middle, and posterior regions of both lobes of each ovary (Fig. 2), and subsequently fixed in 10% seawater-diluted formalin for further histological examination and analysis.

## Morphological descriptions

Since 1993, nearly all fish commercially harvested by the Taiwan longline fishery that operates in the south-western North Pacific Ocean have been measured for fork length (FL). Hsu *et al.*[12] presented length distributions associated with this fishery until 1998, and updated length distributions sampled after 1999 are reported here.

To investigate indices of condition of sampled fish, the following classical Fulton-type condition factor ($C$) was used:

$$C = \frac{W}{L^3} \times 10^5, \quad (1)$$

where $W$ is eviscerated weight (kg) and $L$ is fork length (FL) (cm).

## Sex ratio

Sex ratio was calculated as the proportion of females in all samples collected in this study (Table 1). Under the assumption that vulnerability (probability of capture) to the fishery is equal between sexes, a simple binomial distribution test was conducted to statistically evaluate sex ratio estimates from the sampled fishing trips. If the test generated non-significant findings among trips (i.e. failed to reject the null hypothesis), the samples were pooled and the test repeated on the total, combined sample.

## Analysis of ovaries

The gonadosomatic index $I$ was calculated following Yabe *et al.*[3]

$$I = \frac{W_{ov}}{L^3} \times 10^4, \quad (2)$$

where $W_{ov}$ is ovary weight (g) and $L$ is FL (cm).

The developmental stages of oocytes of Pacific bluefin tuna were classified by histological examination. First, to examine the relationship between diameter and developmental stage of oocytes, a 0.03-g sample was removed from each lobe of a sampled ovary, and immersed in a 33% glycerin solution for 10–20 min[13] to maintain the equal pressure inside and outside the eggs. Second, oocytes were detached from ovarian tissue by needles, and diameter (random axis) measurements were taken to the nearest 18 μm at 40× magnification using a dissecting microscope with an ocular micrometer. A representative diameter for non-spherical oocytes was calculated as the mean of short and long axes.[14–16] Oocytes smaller than 0.2 mm were not measured.

Ovaries with hydrated oocytes were randomly selected to evaluate the extent to which these oocytes were homogeneously distributed within an ovary. A nested, one-way analysis of variance (ANOVA) was used to evaluate differences in numbers of hydrated oocytes among different layers and locations within an ovary.

Estimates of batch fecundity were derived from the ovary sample using the gravimetric method:[17] a cork borer (5 mm) was used to obtain a core sam-

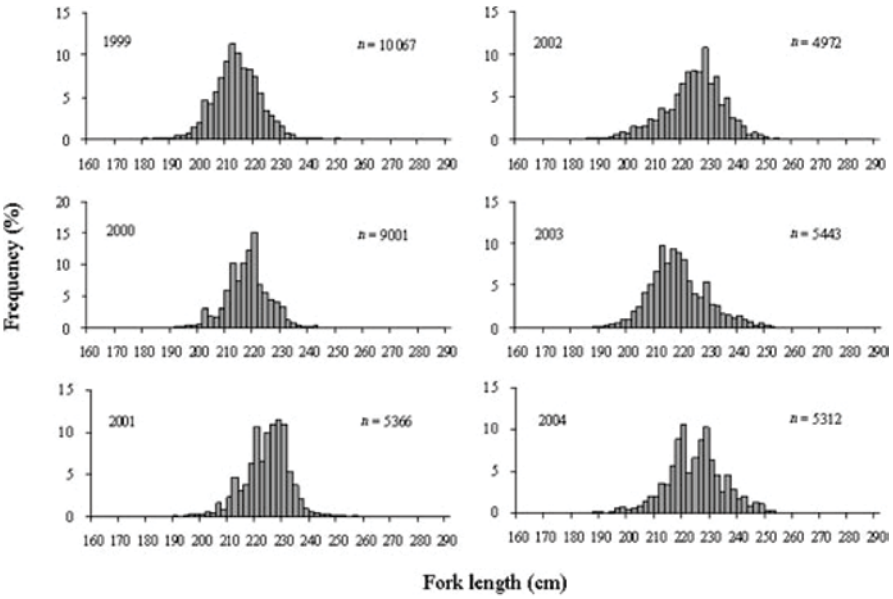


**Fig. 3** Length frequency distributions for Pacific bluefin tuna caught from the south-western North Pacific by Taiwanese small-scaled longliners, 1999–2004.

ple that included tissue from the outer surface of the ovary to the centrally located lumen. The core was further partitioned into the three areas associated with the lumen (outer, middle, and central layers). Separate cores were taken from the anterior, middle, and posterior regions of both lobes of each ovary and thus, 18 locations were sampled from the ovary of each fish (Fig. 2). Four subsamples (0.03 g) of ovarian tissue were taken from each of the 18 locations within the ovaries and weighed to the nearest 1 mg. Finally, the diameters and numbers of oocytes present in advanced size mode were recorded.

Spawning frequency can be estimated as the inverse of the ratio of spawning females, which is defined as the number of females with identifiable postovulatory follicles divided by the total number of mature females.

The spawning season was determined by examining the spatio-temporal distribution of spawners sampled with the most advanced group of oocyte (MAGOs), and examination of postovulatory follicles associated with the ovary samples.

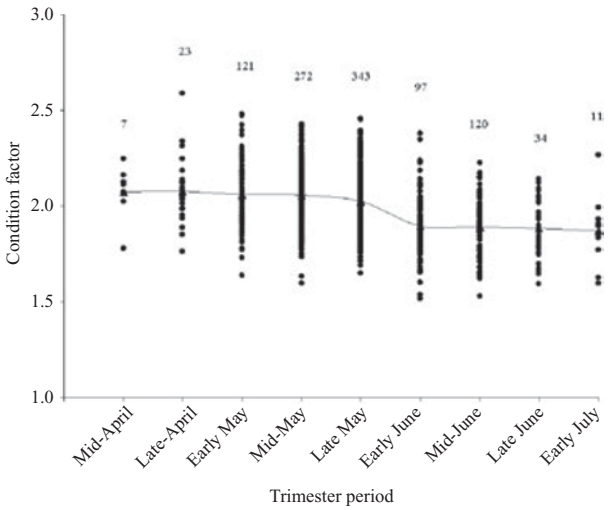


**Fig. 4** Changes in mean condition factor of female bluefin tuna from the south-western North Pacific by trimester periods from mid-April to early July in 1999; observed data (●) and means during trimester period (▲); numbers above bars are sample sizes.

## RESULTS

### Morphological aspects

Sex-combined FL distributions from 1999 to 2004 illustrated that most fish from this fishing area were larger than 180 cm (Fig. 3), indicating that the fishery harvests almost mature fish. Examining the samples collected in 1999, the condition factor of females decreased slightly from the beginning of the fishing season in mid-April to the end of the fishing season in early July (Fig. 4). The decline in condition factor might result from increased reproductive effort of spawning activity.

### Sex ratio

In total, 241 fish were randomly sampled from 17 fishing trips operating in the study area in the 1999

fishing season, for purposes of sex determination (Table 1). Based on a binomial test, the null hypothesis that the expected probability of female occurrence was 0.5 (50%) within each fishing trip failed to be rejected, i.e. no significant difference in sex ratio was found within fishing trips ($P > 0.05$). However, pooled fishing trip data across all samples resulted in a significant ($P = 0.0487$) difference from the hypothesized 1:1 sex ratio (Table 1). Moreover, the first trip showed different results from the other 16 trips. Hence, if excluding data obtained in the first trip, the test resulted in a non-significant difference from the hypothesized 1:1 ratio.

### Analysis of ovaries

Weights of 119 sampled ovaries ranged 1.7–19.4 kg. Ovary weight generally increased with length (Fig. 5). The estimated gonadosomatic indices were greater than 2.1, with a high value of 18.7 for one fish (Fig. 6). In general, the gonadosomatic indices stayed consistent over the study period, with a slight increase from early in the fishing season to later in the season.

The developmental process of oocytes for Pacific bluefin tuna were classified into seven stages based on histological examination and diameter measurements: (i) chromatin nucleolus stage oocytes (Fig. 7a) were strongly basophilic, with one larger and several smaller nucleoli in the nucleus (oocyte diameters <56 μm); (ii) perinucleolus stage oocytes (Fig. 7b) with several small nucleoli in the periphery of the nucleus (diameter 37–131 μm); (iii) yolk vesicle stage oocytes (Fig. 7c) with yolk vesicles in the cytoplasm (diameter 112–243 μm); (iv) early yolk stage oocytes (Fig. 7d) with small yolk granules in the periphery (diameter 318–336 μm); (v) advanced yolk stage oocytes (Fig. 7e) with large yolk granules distributed in the cytoplasm (diameter 375–598 μm); (vi) migratory nucleus stage oocytes (Fig. 7f) had small lipid droplets fused to each other to form larger lipid droplets, with a nucleus that had migrated to the periphery (diameter 616–655 μm); and (vii) mature or hydrated stage oocytes (Fig. 7g) that were irregular in shape because of dehydration and had a single, large oil droplet (diameter 673–991 μm). Finally, postovulatory follicles from a recently spawned female are illustrated in Figure 7h.

Three paired ripe ovaries were subsampled (Fig. 2) for enumerating most advanced group oocytes (MAGOs). A homogeneity test based on ANOVA revealed no significant ($P > 0.05$) findings for numbers of MAGOs among locations or layers, i.e. the null hypothesis that MAGO numbers were equal across locations and layers of an ovary was rejected (Table 2). Significant ($P < 0.001$) differences were found between fish used in this analysis. Therefore, it was concluded that hydrated oocytes were uniformly distributed within ovaries; however, levels of MAGOs were not statistically similar between the sampled fish.

Oocytes at different stages were found simultaneously in the hydrated ovaries, with no large hiatus present between non-yolk and early yolk oocytes (Fig. 8). Thus, the development of oocytes was asynchronous and the annual fecundity was indeterminate.

Most specimens were characterized by ovaries with advanced yolk and advanced-developed

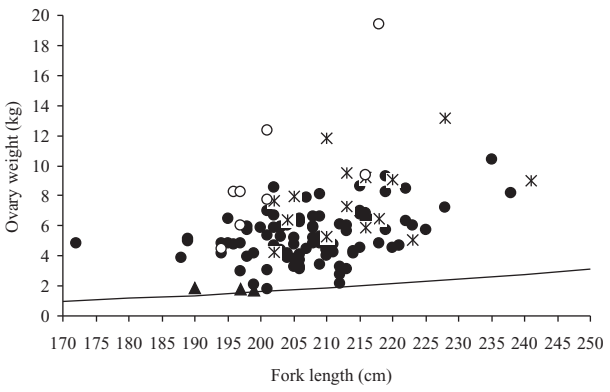


**Fig. 5** Ovary weight *vs* fork length of bluefin tuna from the south-western North Pacific during 1999. Ovaries in early yolk stage (▲), ovaries in advanced yolk stage (●), ovaries in migratory nucleus stage (*), and ovaries in mature stage (○). The line represents gonadosomatic index = 2.

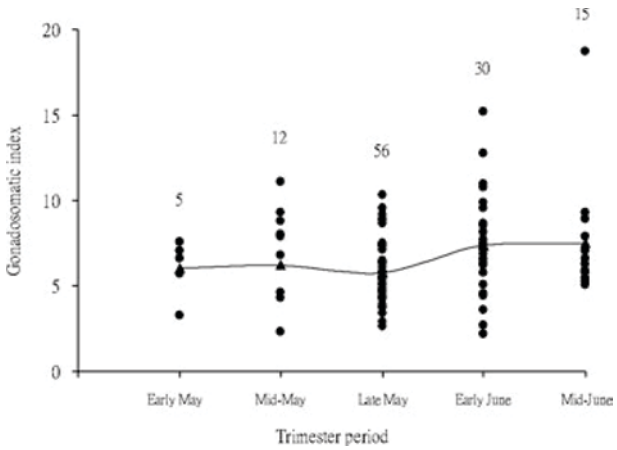


**Fig. 6** Seasonal changes in gonadosomatic index (GSI) of female bluefin tuna from the south-western North Pacific by trimester periods from May to June in 1999; observed data (●) and means during trimester period (▲); numbers above bars are sample sizes.

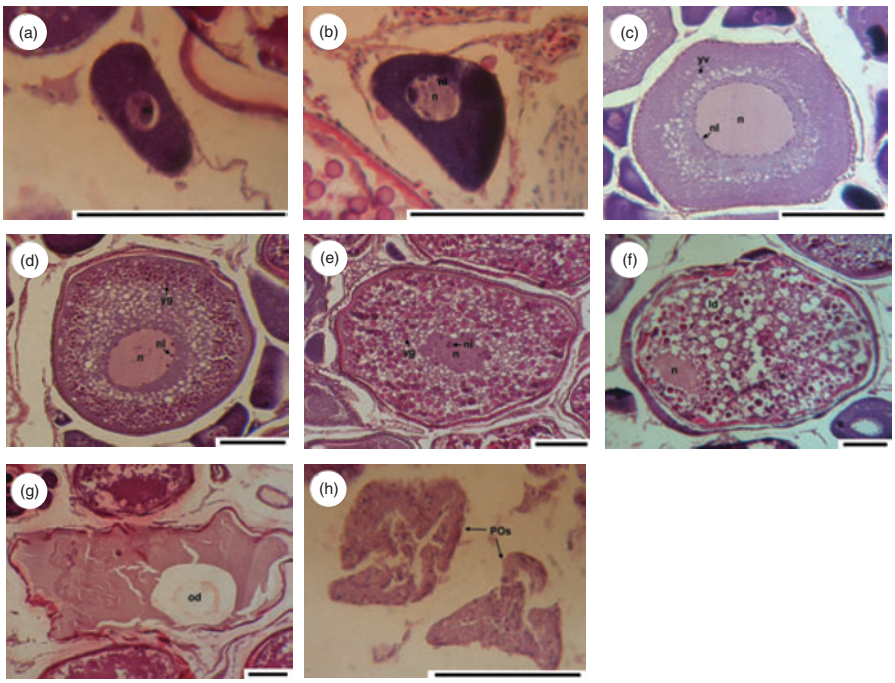


**Fig. 7** Oocyte development of bluefin tuna from the south-western North Pacific. (a) Chromatin nucleolus, (b) perinucleolus, (c) yolk vesicle, (d) early yolk, (e) advanced yolk, (f) migratory nucleus, and (g) mature or hydrated stages, and (h) postovulatory follicles shown in spent ovary. Mayer's hematoxylin–eosin stain. Bar = 0.1 mm. ld, lipid droplet; nl, nucleolus; n, nucleus; od, oil droplet; POs, postovulatory follicles; yv, yolk vesicle; yg, yolk granule.

**Table 2** ANOVA result of homogeneity test for the number of the migratory nucleus and hydrated oocytes (MAGO) in different regions of the ovaries for three Pacific bluefin tuna *Thunnus orientalis* sampled from south-western North Pacific

| Source of variation | d.f. | *SS* | *MS* | *F* | *P* |
|---|---|---|---|---|---|
| Fish | 2 | 10 747.24 | 5373.62 | 412.82** | <0.001 |
| Location | 5 | 88.38 | 17.68 | 1.36$^{ns}$ | 0.248 |
| Layer (Fish × Location) | 10 | 183.65 | 18.37 | 1.41$^{ns}$ | 0.188 |
| Error | 90 | 1 171.50 | 13.02 | | |
| Total | 107 | 12 190.77 | | | |

Lobe (right and left); Location (anterior, middle and posterior); Layer (outer, mid-layer and center).
**significant ($P < 0.01$).
ns, not significant ($P > 0.05$).

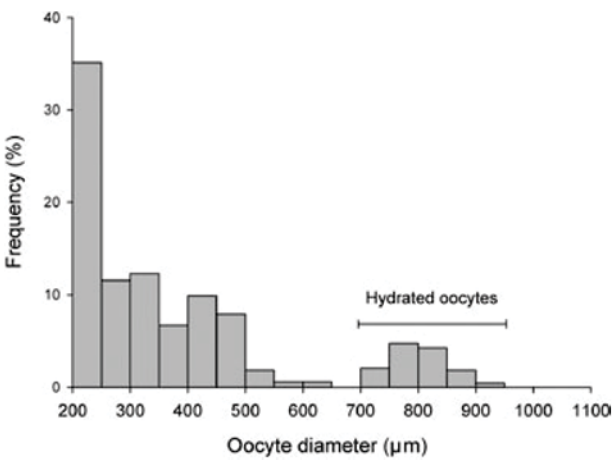


**Fig. 8** Frequency distribution of oocyte diameter in an ovary with hydrated oocytes of Pacific bluefin tuna. Oocytes <0.2 mm were measured, $n = 1668$. Specimen was collected on 6 June 6 1999 with 196 cm fork length, 126 kg eviscerated weight and 8260 g ovary wet weight.

oocytes, and only a few females with the most advanced group of oocytes in early yolk stage were found in mid-May and early June. As indicated in Figure 9, the proportion of females with ovaries defined under the migratory nucleus stage and mature stage was approximately 15–25% of the total mature females included in this study.

## Batch fecundity and spawning frequency

The simple linear relationship between batch fecundity $F$ and fork length $L$ (cm) is illustrated in Figure 10:

$$F = 3.2393 \times 10^5 \times L - 5.2057 \times 10^7 \quad (R^2 = 0.600,\ n = 20) \tag{3}$$

Fractions of spawned females in trimester periods, estimated by histological examination of postovulatory follicles, were relatively high in mid-May

**Table 3** Fraction of females with postovulatory follicles by trimester for bluefin tuna sampled from the waters of south-western North Pacific during 1999 fishing season by Taiwanese small-scaled longline fishery

| Time intervals | Number of females examined A | Females with postovulatory follicles B | Fraction of spawned females C = B/A | spawning frequency (days) D = 1/C |
|---|---|---|---|---|
| Early May | 6 | 2 | 0.33 | 3.0 |
| Mid- May | 12 | 6 | 0.50 | 2.0 |
| Late May | 27 | 6 | 0.22 | 4.5 |
| Early June | 18 | 4 | 0.22 | 4.5 |
| Mid-June | 10 | 4 | 0.40 | 2.5 |

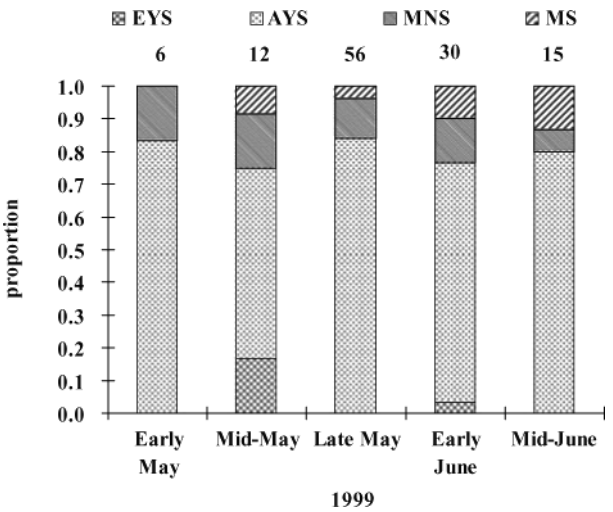


**Fig. 9** Trimester proportion of five developed oocyte stages of bluefin tuna from the south-western North Pacific during the fishing season from May to June, 1999. EYS, early yolk stage; AYS, advanced yolk stage; MNS, migratory nucleus stage; and MS, mature stage. Numbers above bars are sample sizes.

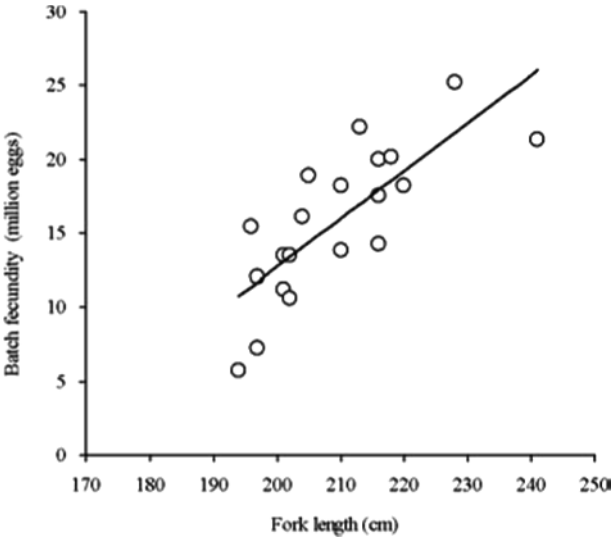


**Fig. 10** Relationship between batch fecundity and fork length for bluefin tuna from the south-western North Pacific, $n = 20$. The line represents the regression of batch fecundity and fork length.

(0.50) and mid-June (0.40), with an overall mean estimate of 0.3 (Table 3). For determining estimates of spawning frequency from the spawning fractions, it was assumed that postovulatory follicles existed approximately 24 h following ovulation, postovulatory follicles could be identified accurately, and that sampling of mature females was random. Consequently, the spawning frequency of Pacific bluefin tuna in the south-western North Pacific Ocean estimated by the postovulatory follicle method ranged from 2.0–4.5 days, with a mean of 3.33 days.

## Spawning season

Areas where ovaries with hydrated oocytes and postovulatory follicles were found simultaneously in the same ovary are illustrated in Figure 11. High

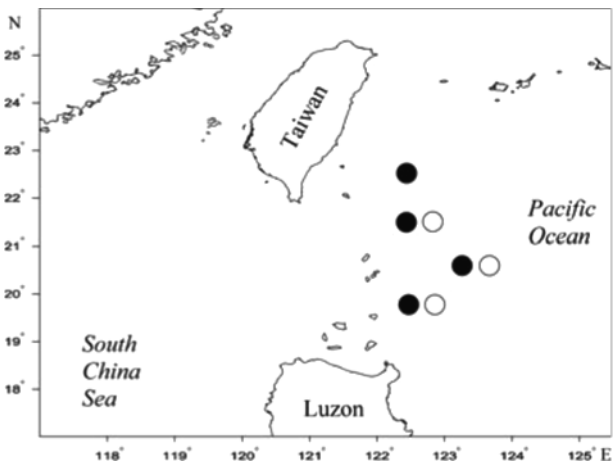


**Fig. 11** Areas where ovaries with hydrated (●) and spent follicles (○) were found during the fishing season.

proportions of ovaries with hydrated oocytes occurred in mid-May and early June, which is consistent with the period of high gonadosomatic indices and the presence of the postovulatory follicles. Accordingly, in the waters of the south-western North Pacific Ocean, the fishing season of Pacific bluefin tuna varies annually and thus, the 1999 season may have started earlier than May and peaked from mid-May to early June. This trend is consistent with that observed in condition factor estimates (Fig. 4).

## DISCUSSION

### Size-frequency and age-frequency distributions

As defined by Rivas,[18] Atlantic bluefin tuna *Thunnus thynnus* individuals are classified as giant members of the population if FL exceed 180 cm. Thus, Pacific bluefin tuna landed at domestic ports in Taiwan would nearly always be considered giant specimens (Fig. 3). Further, even an individual with a FL of 172 cm analyzed in this study had an oocyte diameter of 556 μm and was determined to be mature. Therefore, it is likely that nearly all Pacific bluefin landings from this Taiwanese longline fishery are composed of sexually mature (giant) fish (Fig. 3).

Based on a generally accepted aging method (length-at-age model),[19] the smallest individual measured in 1999 was 165 cm in FL (Fig. 3), which would translate to an approximately 6-year-old fish. This size may not represent the size at first maturity (length that fish is sexually mature); however, it is the smallest length class of fish observed in the landings since 1999. Further, nearly all of the historical catch by the Taiwanese longline fleet is greater than 190 cm (8-year-old fish), with a mode at 208–219 cm (9–10-year-old fish). Hirota *et al.*[8] and Kumai[11] reported that the age of first spawning of reared Pacific bluefin tuna was 5 years. Tanaka[6] reported that smaller Pacific bluefin tuna caught around the Ryukyu Islands and in the Sea of Japan had hydrated oocytes. Joint studies of the minimum maturation size and the proportion of mature females at length classes are necessary among international scientists interested in this tuna population.

### Sex ratio

The size-combined sex ratio of Pacific bluefin tuna caught in the south-western North Pacific Ocean may not deviate from the expected 1:1 ratio during the period of spawning aggregation, which is generally consistent with previous reports.[7] Therefore, the occurrence of females seems to be not outnumbered during spawning season. Regarding to the dominance of males by size classes, especially for fish larger than 240 cm FL,[20] our results are inconclusive. Maguire and Hurlbut[20] assumed the predominance of males in fish larger than 242 cm for Pacific bluefin tuna, but this was not the case in the present study.

### Batch fecundity and spawning frequency

This study indicated batch fecundity increased with length. Tanaka[6] examined batch fecundity for smaller fish (159–215 cm FL) around Ryukyu Islands and in the Sea of Japan, and found that batch fecundity was also correlated with body size. The aim of our study was to equate the relationship between batch fecundity and FL in the range of 195–240 cm. Moreover, Tanaka's[6] contribution is important to complete the relationship within an entire range of mature sizes.

The condition factor declined during spawning because of reduced feeding activities. In the present study, the spawning season may be inferred from the condition factor of Pacific bluefin tuna as it decreased during the fishing season in the south-western North Pacific Ocean (Fig. 4). Western Atlantic bluefin tuna either cease or decrease feeding activity during the spawning season.[18] Further, fishers experience that ovaries with hydrated oocytes are rarely found in Pacific bluefin tuna. A reason for this phenomenon is that hydrated oocytes may be present in ovaries for a very short period, and/or fish release oocytes due to stress associated with hooking operations by the fishing fleet. If so, postovulatory follicles may be found in caught fish. Therefore, conclusions drawn from estimates of spawning frequency should be interpreted with caution, given potential biases associated with sampling design and methods used in histological examination. The spawning frequency may be shorter than estimated in Table 3 of the present study.

### Spawning season

Based on this study, the spawning season of bluefin tuna in the south-western North Pacific Ocean is likely from late April through mid-June. Periods when a high proportion of females had hydrated oocytes coincided with occurrence of postovulatory follicles in an ovary. The proportion of ovaries with postovulatory follicles did not increase across

the spawning season. It appears plausible that the spawning activity moves in a north direction, as advanced yolk oocytes larger than 467 μm were found in ovaries with postovulatory follicles. McPherson[21] found that the secondary yolk oocytes (advanced yolk stage) of yellowfin tuna *Thunnus albacares* develop to hydrated oocytes within 24 h. Further, the oocytes in the migratory nucleus stage of chub mackerel *Scomber japonicus* suggested spawning occurred within 24 h.[22] Therefore, it was concluded that Pacific bluefin tuna with advanced yolk oocytes may spawn within a short period, and the estimated spawning frequency across batches may span a few days.

The duration of high gonadosomatic index in Pacific bluefin tuna coincided with estimates of spawning season concluded from this study. Moreover, abundant bluefin tuna larvae have been observed in the western North Pacific Ocean during early May and mid-June,[3] as well as in waters off Taiwan during March and August.[23] The spatial and temporal variabilities in egg distribution documented[23] in this study may be due to biases associated with either the sampling design or larvae identification.

Environmental (oceanographic) conditions influence spawning behavior of tuna.[24] The spawning of Pacific bluefin tuna in the Sea of Japan is reported from late June to August,[6] which is later than that reported in this study. Abundant Pacific bluefin tuna larvae occur in May in Taiwanese waters, and the distribution of larvae was correlated with a sea surface temperature of 27°C[6,25] and 34–35 salinity.[25] Yellowfin tuna in the Coral Sea spawn when the sea surface temperature is equal to or greater than 26°C.[22] North Atlantic albacore *T. allege* spawn in a similar range of sea surface temperatures.[24] The sea surface temperatures recorded in this study were between 26 and 29°C during April and June. Thus, the spawning of Pacific bluefin tuna is likely related to critical oceanographic parameters such as sea surface water temperature.[6] It is likely that Pacific bluefin tuna in the south-western North Pacific move in a northward direction during spawning periods, eventually reaching waters around Japan.

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