

Abstract.—We investigated the spawning dynamics of southern bluefin tuna, *Thunnus maccoyii*, using ovaries obtained from fish caught on the spawning ground in the northeast Indian Ocean and their main feeding grounds in the Southern Ocean, between October 1992 and June 1995. Only sexually mature southern bluefin tuna were taken on the spawning ground and were caught in every month except July, although relative abundance was low from May to August. Peaks in abundance occurred during October and February. Individuals do not spawn over the whole season, and there is a turnover of fish on the spawning ground. The presence of oocytes in all stages of development and the absence of a hiatus in the oocyte size-frequency distributions between unyolked and early yolked oocytes indicate that southern bluefin tuna have asynchronous oocyte development and indeterminate annual fecundity. The presence of either migratory nucleus or hydrated oocytes and postovulatory follicles in the ovaries of many females indicates that southern bluefin tuna are capable of multiple spawning. On the basis of the proportion of females with postovulatory follicles, it appears that females spawn on average every 1.1 days. The average spawning batch fecundity, estimated from counts of hydrated oocytes, was 6.0 million oocytes or 57 oocytes per gram of body weight.

Reproductive dynamics of southern bluefin tuna, *Thunnus maccoyii*

Jessica H. Farley

Tim L.O. Davis

CSIRO Division of Marine Research

GPO Box 1538, Hobart, Tasmania 7001, Australia

E-mail address (for Jessica Farley): Jessica.Farley@marine.csiro.au

Southern bluefin tuna, *Thunnus maccoyii*, are large, migratory pelagic fish with a circumglobal distribution between 30°S and 50°S. Stocks are considered to be overexploited, and parental stocks, in particular, are considered depleted (Caton et al., 1990; Anonymous¹). Of all the tunas, bluefin tunas (*T. maccoyii* and *T. thunnus*) are the best adapted to cold water (Carey, 1973) and thus are able to occupy the rich feeding grounds of the temperate oceans. However, like other tunas, the early life history of southern bluefin tuna is restricted to warm waters, and the only known spawning area is in the tropical east Indian Ocean where surface water temperatures exceed 24°C during the spawning period (Yukinawa and Miyabe, 1984; Yukinawa, 1987) (Fig. 1). Juveniles leave the spawning grounds within a few months of hatching and move south along the continental shelf of Western Australia. This movement is probably assisted by the Leeuwin Current (Shingu, 1967; Maxwell and Cresswell, 1981). Juveniles first appear in the warm waters of the Great Australian Bight as one-years-olds in summer and then disperse along the West Wind Drift in winter.

Ichthyoplankton surveys have been used to define southern bluefin tuna spawning grounds and season of spawning. Southern bluefin tuna larvae have been caught within latitudes 7° and 20°S and

longitudes 102° and 124°E from September to March (Ueyanagi, 1969; Yonemori and Morita, 1978; Yukinawa and Miyabe, 1984; Nishikawa et al., 1985; Yukinawa and Koido, 1985; Yukinawa, 1987; Davis et al., 1990). However, the northerly limit of spawning is not clear because there has been little sampling effort in Indonesian territorial waters. Apart from a general understanding of the location and timing of spawning and the associated migration patterns, little detailed information is available on the reproductive dynamics of southern bluefin tuna. To understand spawning seasonality, spawning frequency, and batch fecundity with greater accuracy, we analyzed ovarian samples from fish captured on spawning grounds in the northeast Indian Ocean and feeding grounds in the Southern Ocean (in waters off Tasmania, New Zealand, and South Africa)

Materials and methods

Southern bluefin tuna ovaries were obtained from two sources: Indonesian-based longlining vessels fishing on the northern part of the spawning

¹ Anonymous. 1994a. Report of the thirteenth meeting of Australian, Japanese and New Zealand scientists on southern bluefin tuna. Report to management, 20–29 April 1994, Ministry of Agriculture and Fisheries, Wellington, New Zealand, 13 p.

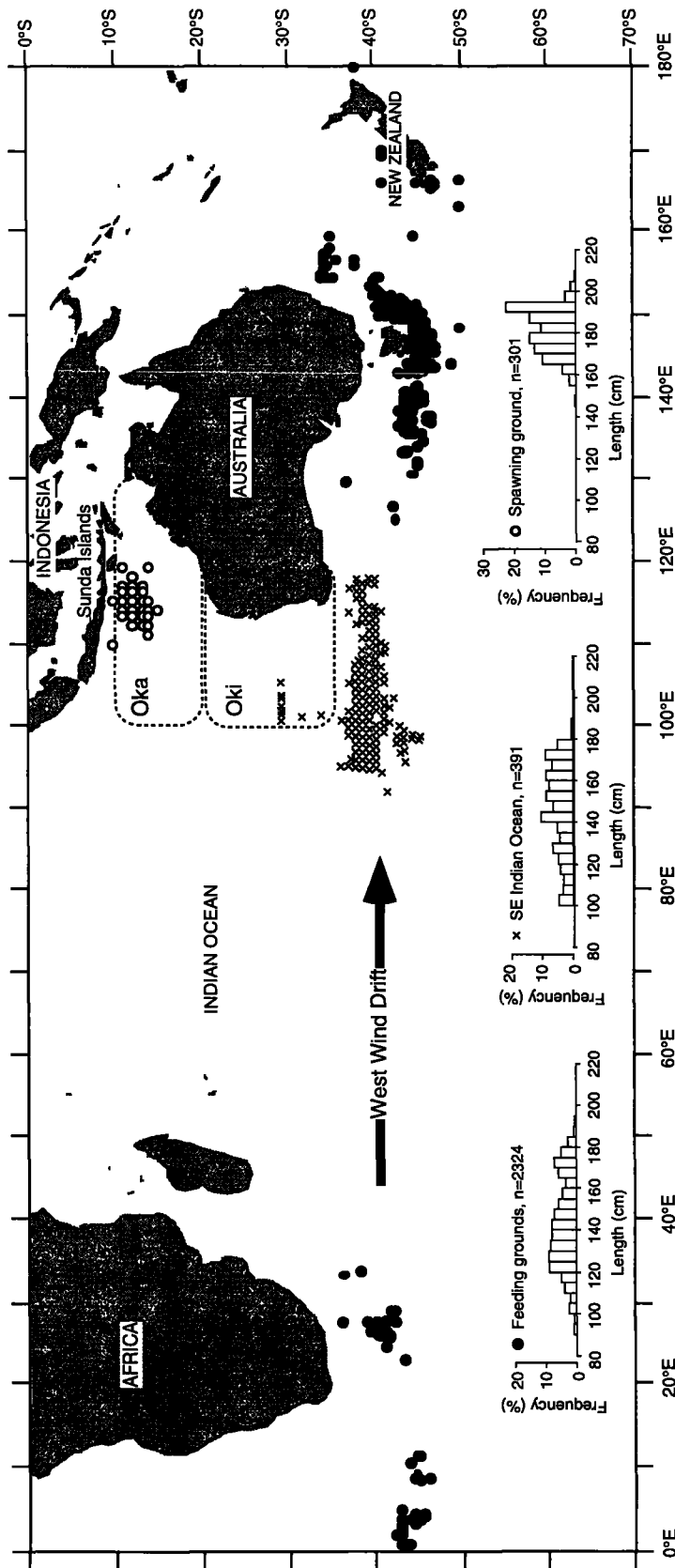


Figure 1

Locations where southern bluefin tuna ovaries were collected. Length-frequency distributions are shown for tuna sampled on the spawning grounds (○) in the northeast Indian Ocean; in the SE Indian Ocean (x) through which the spawning grounds are accessed; and on the feeding grounds along the West Wind Drift (●) in waters off Tasmania, New Zealand, and South Africa. The "Oka" and "Oki" fishing grounds referred to by previous researchers (Kikawa, 1964a, 1964 b; Shingu, 1970) are shown.

ground in the northeast Indian Ocean; and Japanese longline vessels operating in the Southern Ocean (on feeding grounds off Tasmania, New Zealand, and South Africa and on staging grounds in the southeast Indian Ocean) (Fig 1).

The ovaries of 475 females were collected from the complete size range of southern bluefin tuna caught on the spawning ground. Ovaries were removed at sea, labelled, stored on ice, and matched with the corresponding tuna carcass at Benoa in the Sunda Islands. Dressed weight (where fish was gilled, gutted, its fins removed, and its tail stock left intact) was measured to the nearest kg, and fork lengths of most fish to the nearest cm. A subsample was removed from 200 ovaries and fixed in 10% buffered formalin. The ovaries were frozen and flown by airfreight, along with the subsample, to Australia. In addition, up to 30% of all longline catches landed at Benoa were monitored and the individual weights and lengths of southern bluefin tuna were recorded.

Ovaries from the Southern Ocean were collected at sea from the fishing grounds around Tasmania, New Zealand, South Africa, and the southeast Indian Ocean. The areas around Tasmania, New Zealand, and South Africa are considered to be feeding grounds for immature and adult southern bluefin tuna, whereas the southeast Indian Ocean is the area where pre- and postspawning fish are caught during the spawning season. In total, ovaries were collected from 2,340 females from the feeding grounds in the Southern Ocean and from 393 females from the southeast Indian Ocean. Ovaries were frozen immediately after collection. Fork lengths were measured to the nearest cm.

In the laboratory, a core subsample was taken from each ovary while frozen. Subsamples were fixed in 10% buffered formalin, embedded in paraffin, and standard sections were prepared for histological examination (cut to 6 μm and stained with Harris's haematoxylin and eosin). All ovaries collected on the spawning grounds and 53 of the ovaries collected from the Southern Ocean were processed in this way.

Ovaries were thawed, trimmed of fat, blotted dry, and weighed to the nearest g. The mean diameter (random axis to the nearest μm) of five oocytes from the most advanced group of oocytes (MAGO) was determined for each ovary with a video coordinate digitizer connected to an Ikegami video camera mounted on a stereomicroscope at 50 \times magnification. Gonad index was calculated as

$$GI = W/L^3 \times 10^4,$$

where W = gonad weight in g; and

L = length to caudal fork in cm (Kikawa, 1964a; Shingu, 1970).

All ovaries were examined for residual hydrated oocytes as evidence of spawning activity.

Histological classification and spawning frequency

Because many of the ovaries were frozen before a subsample could be removed, it was necessary to assess whether histological sections prepared from frozen ovarian material could be used to determine gonad stage and spawning activity. A comparison was made between histological sections prepared from 200 ovaries which were subsampled both before and after freezing. Although considerable cell destruction was observed in the histological sections from frozen tissue, oocytes, atretic oocytes, and postovulatory follicles were still distinguishable and could be classified.

Histological sections were classified with criteria similar to those developed for northern anchovy, *Engraulis mordax* (Hunter and Goldberg, 1980; Hunter and Macewicz, 1980, 1985a, 1985b), skipjack tuna, *Katsuwonus pelamis* (Hunter et al., 1986) and yellowfin tuna, *Thunnus albacares* (Schaefer, 1996). Each ovary was staged by the most advanced group of oocytes present into one of five classes: unyolked, early yolked, advanced yolked (Fig. 2A), migratory nucleus (Fig. 2B), or hydrated (Fig. 2C). In order to determine the relation between atresia (resorption of oocytes) and spawning, ovaries were also classified by the level of α and β stage of atresia in advanced yolked oocytes. During the α stage of atresia, yolk resorption takes place (Fig. 2D). During the

β stage of atresia, the remaining granulosa and thecal cells are reorganized and resorbed leaving a compact structure containing several intercellular vacuoles.

Ovaries were classified into one of the following five atretic states:

- 0 no α atresia present, but advanced yolked oocytes are;
- 1 <10% of advanced yolked oocytes are in the α stage of atresia;
- 2 10–50% of advanced yolked oocytes are in the α stage of atresia;
- 3 >50% of advanced yolked oocytes are in the α stage of atresia;
- 4 100% of advanced yolked oocytes are in the α stage of atresia, or no advanced yolked oocytes are present but oocytes in the β stage of atresia are present.

Spawning frequency was determined by the postovulatory follicle method of Hunter and Macewicz (1985a). This method uses the incidence of females with postovulatory follicles less than 24 hours old to define the fraction of the population spawning. Because the time of capture was not available, we could not assign ages to postovulatory follicles based on the estimated time of death relative to the estimated time of spawning. Postovulatory follicles were, therefore, aged according to their state of degeneration with criteria developed for skipjack tuna, yellowfin tuna, and bigeye tuna, *Thunnus obesus* (Hunter et al., 1986; McPherson, 1988; Nikaido et al., 1991; Schaefer, 1996), all of which spawn in water temperatures above 24°C and resorb their postovulatory follicles within 24 hours of spawning. We assumed that southern bluefin tuna resorb postovulatory follicles at the same rate as other tropical spawning tuna because water temperature appears to be the dominant factor governing resorption rates (Fitzhugh and Hettler, 1995). We recorded postovulatory follicles in histological sections according to methods of Hunter and Macewicz (1985a), Hunter et al. (1986) and Schaefer (1996). Postovulatory follicles were classified as either 0 (absent), 1 (new) (Fig. 2E), 2 (less than 12 hours old), 3 (12 to 24 hours old), or 4 (indistinguishable owing to tissue decay). The incidence of females with postovulatory follicles of any age was used to determine spawning frequency.

Females were classified into one of four spawning states depending on the oocytes, atretic state, and postovulatory follicle class present.

- 1 Immature: Ovaries contain no advanced yolked oocytes or advanced yolked oocytes in the α stage of atresia. No residual hydrated oocytes present.

2 Spawning: Ovary contains advanced yolked oocytes and evidence of spawning activity (migratory nucleus or hydrated oocytes or postovulatory follicles). Less than 100% of advanced yolked oo-

cytes are in the α stage of atresia. If >50% of advanced yolked oocytes are atretic, early yolked oocytes are considered nonatretic.

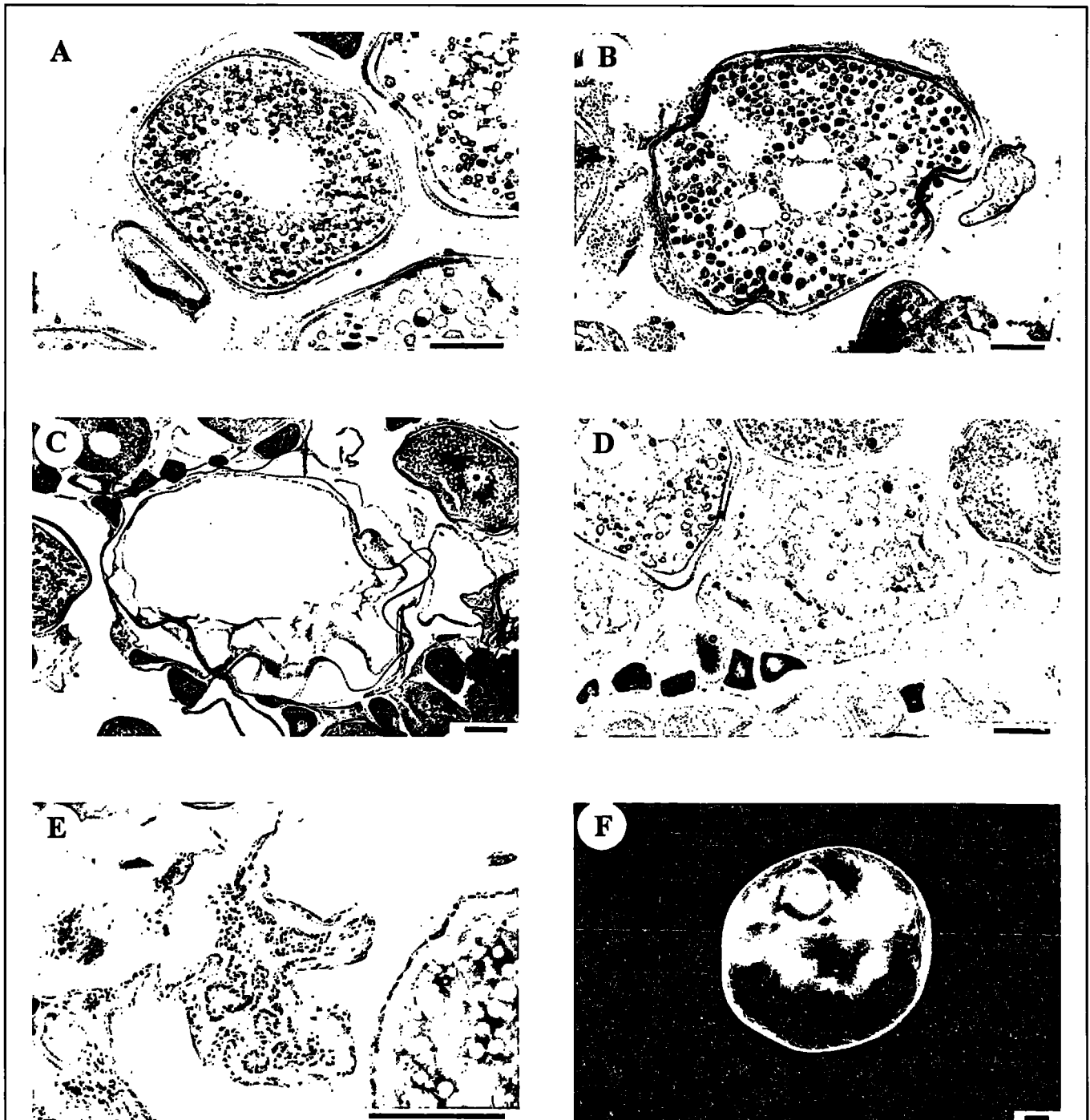


Figure 2

Photomicrographs of southern bluefin tuna, *Thunnus maccoyii*, ovarian tissue collected from the spawning ground (northeast Indian Ocean) between October 1992 and June 1995. (A-E) Transverse sections stained with Harris's haematoxylin and eosin. (A) advanced yolked-stage oocyte; (B) migratory-nucleus-stage oocyte; (C) oocyte in the early stages of hydration with some yolk plates still visible; (D) fully yolked oocyte in a stage of α atresia; (E) new postovulatory follicle; (F) hydrated-stage whole oocyte. Bar = 0.1 mm.

- 3 Nonspawning (mature): Ovary contains advanced yolked oocytes but no evidence of spawning activity (migratory nucleus or hydrated oocytes or postovulatory follicles). Less than 100% of advanced yolked oocytes are in the α stage of atresia. If >50% of advanced yolked oocytes are atretic, early yolked oocytes are considered nonatretic.
- 4 Postspawning: Ovaries contain either: 1) >50% of both early and advanced yolked oocytes in the α stage of atresia; 2) 100% of advanced yolked oocytes in the α stage of atresia; or 3) no yolked oocytes are present but oocytes in the β stage of atresia are, and residual hydrated oocytes may or may not be present.

Fecundity

To find out if the annual fecundity of southern bluefin tuna could be determined before spawning began, we measured the distribution of oocyte sizes within ovaries of four females at various stages of maturity. Ovarian subsamples containing at least 1,000 oocytes were removed from each ovary, teased apart, and each oocyte (greater than 100 μm in diameter) was measured in a random orientation to the nearest μm under a stereomicroscope.

We estimated batch fecundity (the number of hydrated oocytes released per spawning) by the gravimetric method (Hunter et al., 1985) for 21 females with unovulated hydrated oocytes (Fig. 2F). A split-plot analysis of variance (ANOVA) was used to determine the appropriate locations to subsample the ovary. The data were structured with 6 fish examined as blocks, ovarian lobe (left or right) as main plots and twelve subsamples as subplot effects. Six subsamples were taken from each ovarian lobe in the anterior, middle, and posterior regions of both lateral sides (Table 1). A significant difference between ovarian lobes was found in the number of hydrated oocytes per gram of total ovary weight and in the lobe \times lateral side interaction. Consequently, a subsample of less than 1 g was taken from both sides of each ovarian lobe. Each subsample, consisting of a core from the periphery to the lumen, was weighed to the nearest 0.01 mg and fixed in 10% buffered formalin. Each subsample was teased apart and

washed through two sieves, similar to those of Lowerre-Barbieri and Barbieri (1993) to separate out the hydrated oocytes, which were counted under a stereomicroscope. The number of hydrated oocytes per gram of ovary was raised to the weight of both ovaries to give an estimate of batch fecundity for each of the four subsamples.

Results

Ovary maturation

Ovaries obtained from fish on the spawning ground (northeast Indian Ocean), the staging ground (southeast Indian Ocean), and the feeding grounds (Southern Ocean) show clear differences in development based on ovary weight (Fig. 3). Females less than 140 cm showed no or minor ovary development; therefore it appears that they would not spawn in the coming season. The majority of ovaries collected from the feeding grounds weighed less than 1 kg and had a gonad index (GI) of <3.2, whereas ovaries from the southeast Indian Ocean weighed up to 2.8 kg and had GI values up to 4.9. Some of the ovaries of females caught between August and December on the feeding grounds showed signs of maturity, because their MAGO's were in advanced yolked stage with diameters greater than 400 μm . Females from the spawning ground had larger ovaries, weighing up to 7.4 kg. All ovaries from fish collected on the spawning ground had a MAGO diameter greater than 400 μm , except three ovaries with MAGO's between

Table 1
Split-plot ANOVA of the effect of location of tissue sample from southern bluefin tuna, *Thunnus maccoyii*, ovaries on the number of hydrated oocytes per gram of ovary.

Source	df	Sum of squares	Mean square	F-value	P-value
Blocks					
Fish	5	17,201,897	3,440,380	279.721	<0.001
Main plots					
Lobe	1	168,326	168,326	13.686	0.014
Main plot error	5	61,497	12,299	0.764	0.580
Subplot effect					
Lateral side	1	711	711	0.044	0.834
Region	2	34,209	17,104	1.062	0.353
Lateral side \times region	2	82,599	41,300	2.565	0.087
Lobe \times lateral side	1	152,159	152,159	9.450	0.003
Lobe \times region	2	12,944	6,472	0.402	0.671
Lobe \times region \times lateral side	2	58,207	29,103	1.808	0.175
Subplot error	50	805,044	16,101		

153 and 207 μm . These three female had recently finished spawning because their ovaries contained either 100% of advanced yolked oocytes in an α atretic state or residual hydrated oocytes but no healthy advanced yolked oocytes.

Spawning Season

Southern bluefin tuna were caught on the spawning ground during every month, except July. Catch per unit of effort (CPUE), expressed as the number of fish caught per vessel fishing day, showed that abundance was low from May to August (Fig. 4). In the 1993–94 season, abundance peaked in February, and in the following season, abundance peaked in October and February.

Females with high GI values were caught on the spawning ground during all months that ovaries were collected. Gonad index values were variable, however, ranging from 1.3 to 13.1. There were no peaks or trends during this time. These observations suggest that spawning activity is constant throughout the season.

Histological classification

All ovaries examined histologically from the Southern Ocean were classified as immature, nonspawning (mature), or postspawning. Females greater than 140 cm, with advanced yolked oocytes, collected between August and December were probably prespawners preparing to migrate to the spawning ground. Surprisingly, 78% of these prespawning females had α atresia of advanced yolked oocytes. The level of atresia present was related to ovary weight or GI (Fig. 5). The ovaries of all females with GIs < 2 had no or < 10% α atresia (atretic states 0 or 1), whereas 80% of females with GIs > 2 had 10 to 50% α atresia (atretic state 2). This finding suggests that females begin resorbing yolked oocytes as their ovaries mature. Atresia of unyolked or early yolked oocytes was not observed in these females. Postspawning females were found in the Southern Ocean in all months that ovaries were collected, including both the early and late months of the spawning season (September to December). Ovaries, however, were not collected between January and March from the Southern Ocean.

The ovaries of all females sampled on the spawning ground were classified as mature because they contained either advanced yolked oocytes or oocytes in either an α or β stage of atresia. Of the females, 69.2% were classed as spawning, 30.2% as nonspawning, and the remaining 0.6% as postspawning on the basis of oocyte stage, atretic stage, and postovulatory follicle class present. The mean GI

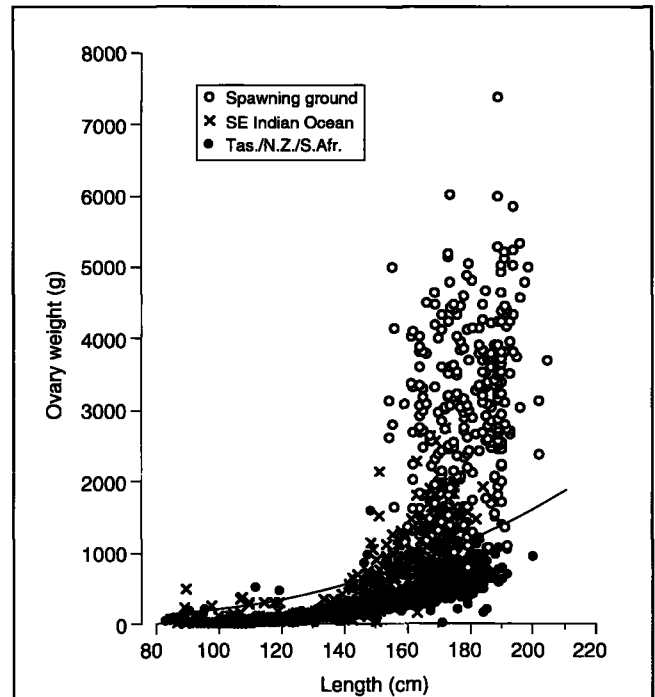
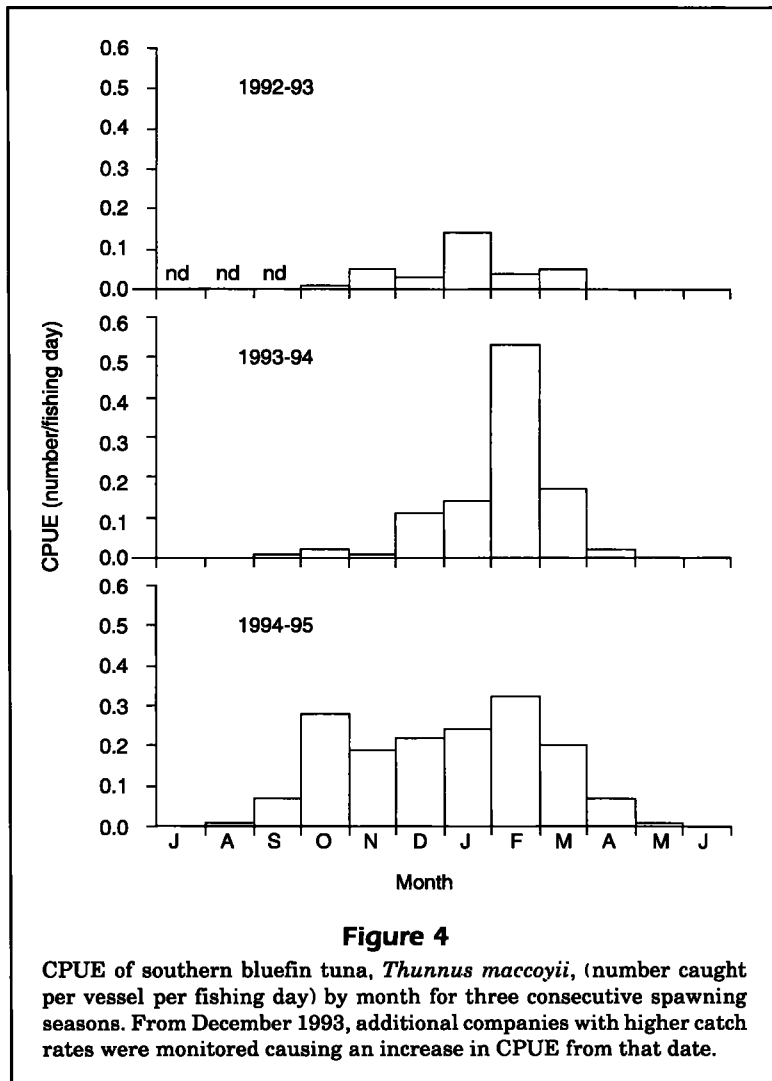


Figure 3

The relation between ovary weight and body length for southern bluefin tuna, *Thunnus maccoyii*, caught on the spawning ground in the northeast Indian Ocean, on the staging grounds in the southeast Indian Ocean, and on feeding grounds off Tasmania, New Zealand, and South Africa. The line represents a gonad index of 2.

($\pm 95\%$ CI) of spawning and nonspawning females was similar at 5.4 (0.37) and 5.6 (0.29) but GI was not calculated for postspawning females because the sample size was too small ($n=3$). Spawning and nonspawning females were found on the spawning ground throughout the spawning season. All postspawning females were collected in October. The majority of females identified as spawning (86.1%) had ovaries containing no or less than 10% α atresia. The remaining 13.9% of females identified as spawning contained more than 10% α atresia. Nearly 90% of nonspawning females, however, contained 10–50% of advanced yolked oocytes in an α atretic state. We have used this criterion of < 10% α atresia to group fish we considered to be at the height of spawning, which we refer to as “prime spawning condition.”

There did not appear to be any seasonal trends in the proportions of each atretic state throughout the spawning season (Fig. 6), suggesting that spawning in southern bluefin tuna is not synchronized. This is confirmed by an absence of an increase in the incidence of postspawning females at the end of the spawning season.



Spawning frequency

The ovaries of 68.7% of females had evidence of recent or imminent spawning activity. The absence of a peak in the percentage of females spawning during the season (Fig. 7) suggests that spawning intensity was constant. The ovaries of 120 females gave evidence of two spawning events, that is, they contained maturing oocytes (either migratory nucleus or hydrated) and postovulatory follicles. The majority of ovaries contained progressively more developed oocytes with progressively older postovulatory follicles. If postovulatory follicles are resorbed within 24 hours of spawning, then southern bluefin tuna are capable of spawning daily.

The fraction of females that spawned per day, measured by the fraction of females with postovulatory follicles, was 0.62 (Table 2). This gave a weighted mean spawning interval of about 1.6 days. If we examine only

those females in "prime spawning condition" (<10% α atresia), then the spawning fraction was 0.90 giving a weighted mean interval of 1.1 days. This value suggests that once females start spawning, they spawn daily.

Batch fecundity

The ovaries of nonspawning females collected from the southeast Indian Ocean contained a large number of unyolked oocytes less than 150 μm in diameter (Fig. 8). This number was reduced as females matured during the season and began spawning. Oocytes of all stages were present in the ovary of spawning females; therefore it appears that southern bluefin tuna have an asynchronous pattern of oocyte development. Unlike species with determinate annual fecundity, a gap in the oocyte size-frequency distribution did not appear between unyolked (<200 μm diameter) and early yolked (200 to 400 μm diameter) oocytes (Fig. 8). This finding indicates that advanced yolked oocytes are continually maturing during the spawning season, from the pool of unyolked oocytes, and are spawned. The ovaries of 86% of females identified as spawning contained no or <10% α atresia, indicating that the majority of advanced yolked oocytes that are matured are spawned. Residual hydrated oocytes were found in the ovaries of only 5.6% of females collected from the spawning ground, which suggests that all hydrated oocytes are released at each spawning.

The mean relative batch fecundity and 95% CI's estimated for 20 females of known weight was 56.5 (± 16.1) oocytes per gram of body weight. The relation between length (cm) and batch fecundity (BF) was best described by the equation

$$BF = (4.78242 \times 10^{-17}) \times L^{7.530}$$

($F=23.9$, $df=1,18$, $P<0.001$) (Fig. 9).

However, the relation was highly variable with only 57% of the variance explained by the regression.

Discussion

Spawning ground and season

All female southern bluefin tuna sampled on the spawning ground were mature, and the smallest was

147 cm long. Davis² showed that the mean length at which 50% of southern bluefin tuna were mature was around 152 cm based on oocyte diameters >400 μm, and 162 cm based on GI's >2. Warashina and Hisada (1970) considered that southern bluefin tuna caught on the "Oka" grounds (Fig. 1) in the 1960's reached maturity at 130 cm, although reanalysis of these data

² Davis, T. L. O. 1995. Size at first maturity of southern bluefin tuna. Council for the conservation of southern bluefin tuna scientific meeting; 10-19 July 1995, Shimizu, Japan. Far Seas Fisheries Res. Lab., Shimizu, Japan, Rep. CCSBT/95/9, 9 p.

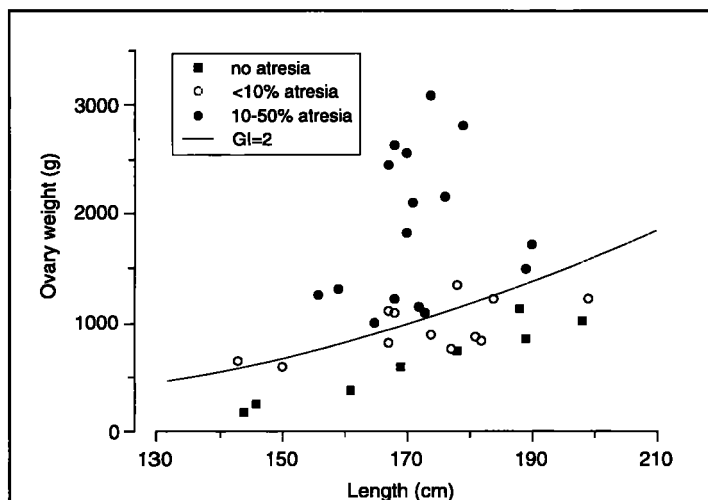


Figure 5

Levels of atresia by length of southern bluefin tuna, *Thunnus maccoyii*, caught off the spawning ground in the northeast Indian Ocean.

showed that this was the smallest size at which they matured and that 50% maturity was not reached until 146 cm (Anonymous³). Size at maturity appears to have increased progressively since then, being 154 cm in the period 1985-89. The increase in length at maturity can be attributed, in part, to an increase in the growth rate of southern bluefin tuna between the 1960's and 1980's reported by Hearn,⁴ because maturity appears to be determined by age rather than length.

The abundance of southern bluefin tuna on the spawning ground was not constant throughout the spawning season. Catch-per-unit-of-effort data indicated that a peak in catches occurred in October for the 1993-94 season and in October and February for the 1994-95 season. Japanese CPUE data also indicate there were two peaks in abundance on the spawning ground in the early years of the fishery; the first in September and October and the second in February and March (Davis and Farley⁵). The reason for two peaks is unknown but could be linked to the widespread distribution of southern bluefin tuna along the feeding grounds of the West Wind Drift. It is possible that the cues for migration to the spawning grounds take place at different times depending on where the fish are prior to spawning. Fish may reach spawning condition earlier in some areas than in others. Also the time needed to migrate to the spawning grounds would differ between areas.

Spawning duration

This study extends the known duration of the spawning season of southern bluefin tuna. Females were caught on the spawning ground in

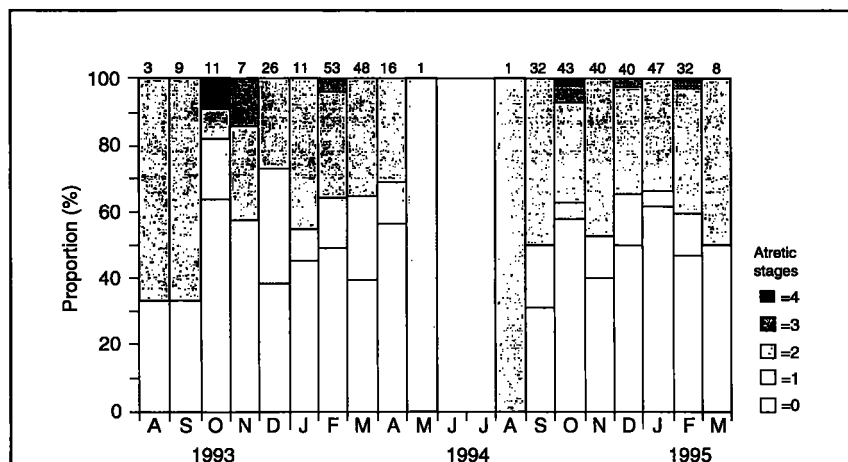


Figure 6

The proportion of each atretic stage by month recorded in southern bluefin tuna, *Thunnus maccoyii*, caught on the spawning ground.

³ Anonymous. 1994b. Report of the southern bluefin tuna trilateral workshop, 17 January-4 February 1994, CSIRO, Hobart, Australia, 172 p.

⁴ Hearn, W. S. 1994. Models for estimating SBT age at length during the transition period. 13th SBT trilateral scientific meeting; 19-29 April 1994, Wellington, New Zealand. Ministry of Agriculture and Fisheries, Wellington, New Zealand, Rep. SBFWS/94913, 16 p.

⁵ Davis, T. L. O., and J. H. Farley. 1995. Catch monitoring of fresh tuna caught by the Bali-based Indonesian/Taiwanese longline fishery. Council for the conservation of southern bluefin tuna scientific meeting; 10-19 July 1995, Shimizu, Japan. Far Seas Fisheries Res. Lab., Shimizu, Japan, Rep. CCSBT/95/2, 18 p.

Table 2

Spawning fraction and spawning interval of southern bluefin tuna, *Thunnus maccoyii*, by month for all females and females in prime spawning condition collected from the spawning ground between October 1992 and March 1995. POF = postovulatory follicles. *n* = no. of fish in sample.

		All females				Females in prime spawning condition (<10% atresia)				
		<i>n</i>	<i>n</i> with POF's	Spawning fraction	Spawning interval (days)	<i>n</i>	<i>n</i> with POF's	Spawning fraction	Spawning interval (days)	
1992	Oct	3	1	0.3	3.0	1	1	1.0	1.0	
	Nov	1	1	1.0	1.0	1	1	1.0	1.0	
	Dec	1	1	1.0	1.0	1	1	1.0	1.0	
1993	Jan	9	8	0.9	1.1	7	7	1.0	1.0	
	Feb	3	1	0.3	3.0	2	1	0.5	2.0	
	Mar	4	4	1.0	1.0	4	4	1.0	1.0	
	Apr	2	0	0.0						
	Aug	3	3	1.0	1.0	1	1	1.0	1.0	
	Sep	9	4	0.4	2.3	3	3	1.0	1.0	
	Oct	11	8	0.7	1.4	9	8	0.9	1.1	
	Nov	7	4	0.6	1.8	4	4	1.0	1.0	
	Dec	26	20	0.9	1.1	19	19	1.0	1.0	
1994	Jan	11	6	0.5	1.8	6	6	1.0	1.0	
	Feb	53	36	0.7	1.5	34	31	0.9	1.1	
	Mar	48	31	0.6	1.5	31	28	0.9	1.1	
	Apr	16	13	0.8	1.2	11	11	1.0	1.0	
	May	1	0	1	0					
	Aug	1	1	1.0	1.0					
	Sep	32	12	0.4	2.7	16	11	0.7	1.5	
	Oct	43	26	0.6	1.7	26	22	0.8	1.2	
	Nov	40	22	0.6	1.8	21	19	0.9	1.1	
	Dec	40	23	0.6	1.7	26	22	0.8	1.2	
	1995	Jan	47	30	0.6	1.6	31	28	0.9	1.1
	Feb	32	20	0.6	1.6	19	19	1.0	1.0	
Mar	8	3	0.4	2.7	4	3	0.8	1.3		
Unknown		16	11	0.7	1.5	8	8	1.0	1.0	
Total		467	289	0.62	1.62	287	259	0.90	1.11	

all months except July, although the main spawning season appeared to be from September to April when CPUE was highest. Previously, the spawning period was reported to be limited to the months of September to March (Mimura, 1958; Kikawa, 1964a). Our study included fish from areas north of that traditionally fished by Japanese vessels, which may explain the extended spawning season. An increase in the length of the spawning season towards equatorial waters has been suggested for many species including black skipjack, *Euthynnus lineatus* (Schaefer, 1987), yellowfin tuna, *Thunnus albacares* (McPherson, 1991), blue marlin, *Makaira nigricans* (Hopper, 1990), and other multiple spawning fish (Qasim, 1955).

The actual duration of spawning in individual southern bluefin tuna could not be de-

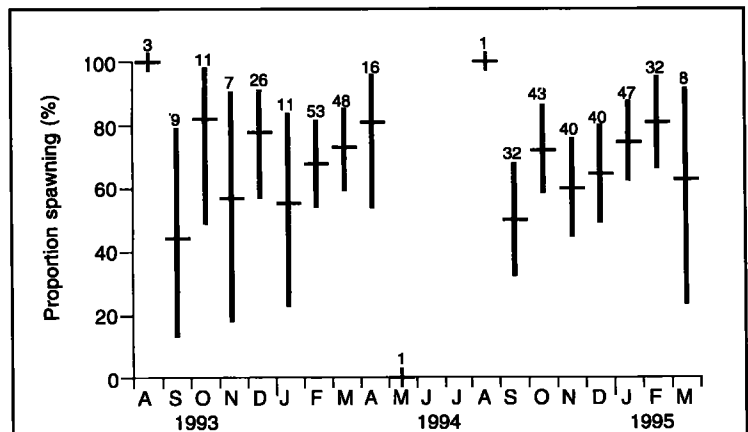


Figure 7

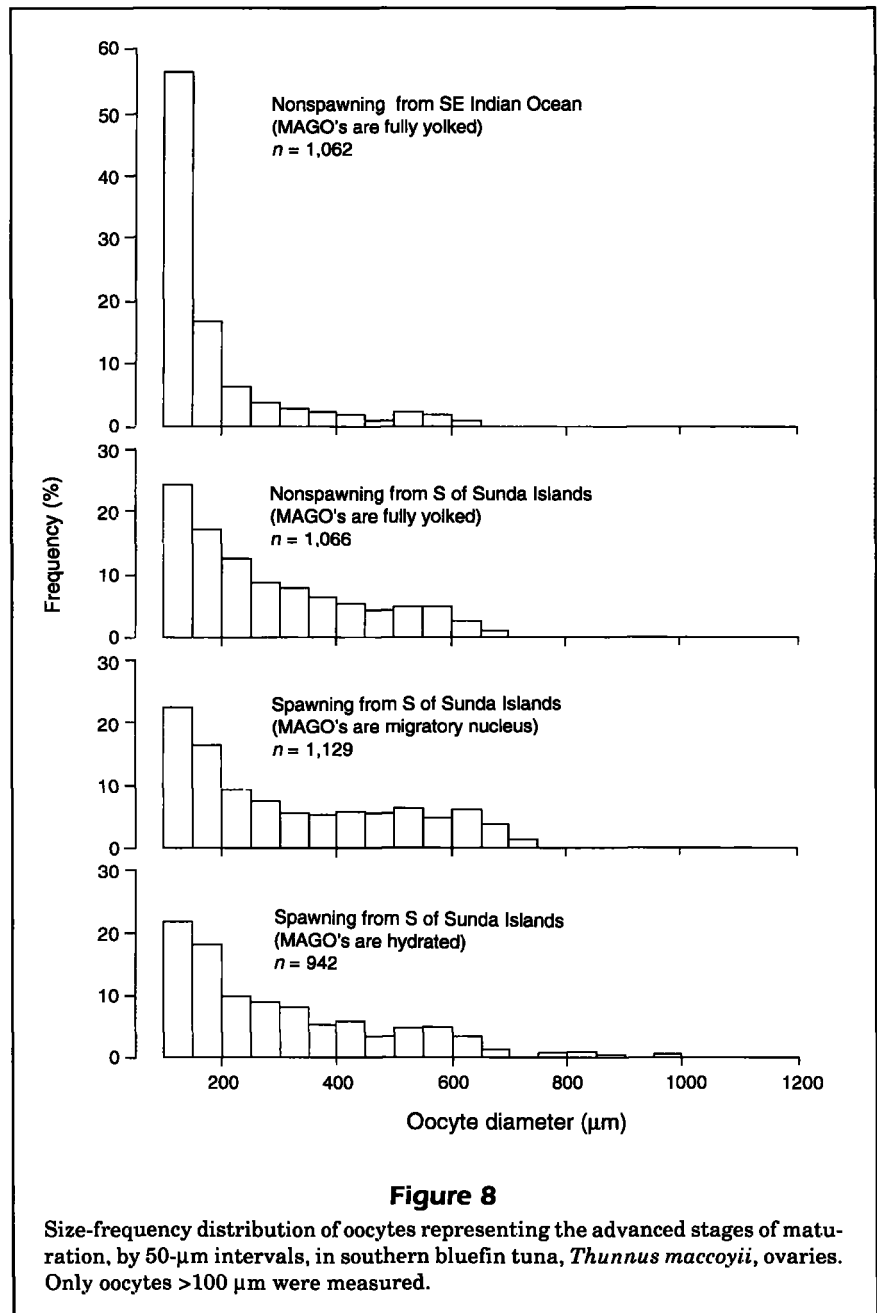
The proportion of southern bluefin tuna, *Thunnus maccoyii*, spawning by month. The vertical bars indicate 95% confidence limits of the mean for samples sizes >5. The numbers indicate sample sizes.

terminated. However, the prevalence of females in different phases of spawning activity (nonspawning, spawning, or postspawning) on the spawning ground should be in direct proportion to the duration of that phase, if females in each phase are equally catchable. The ratio of nonspawners:spawners:postspawners for females caught on the spawning ground was estimated to be 0.30:0.69:0.01 or 0.44:1:0.01 if spawners are set as 1. In other words, spawning females were 2.3 times more prevalent than nonspawning females and 108 times more prevalent than postspawning females on the spawning ground. This finding indicates that the duration of the nonspawning phase is less than half, and the postspawning phase one hundredth, of the duration of the spawning phase.

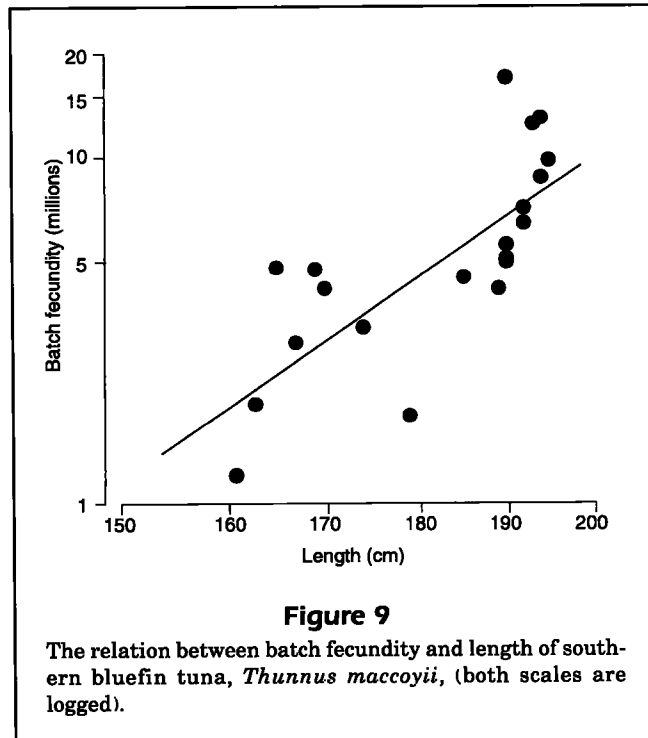
Spawning frequency and fecundity

The potential annual fecundity of southern bluefin tuna is indeterminate (not fixed prior to spawning) because unylked oocytes are continually matured and spawned during the season. Annual fecundity is indeterminate in many tuna species such as black skipjack (Schaefer, 1987), skipjack tuna (Hunter et al., 1986), and yellowfin tuna (Schaefer, 1996). The fecundity of southern bluefin tuna was estimated by Kikawa (1964b) as the number of advanced yolked oocytes in the ovary, and by Thorogood (1986) as the number of oocytes $>300 \mu\text{m}$ in diameter in the ovary. These estimations of fecundity were not potential annual fecundity because southern bluefin tuna are capable of continuously maturing and spawning oocytes from a pool of unylked oocytes ($<300 \mu\text{m}$).

Southern bluefin tuna can spawn many times during a season. The ovaries of 25% of the females collected from the spawning ground contained evidence that they had all recently spawned (postovulatory follicles) and were about to do so again (migratory nucleus or hydrated oocytes). We assume that postovulatory follicles persist in the ovaries of south-



ern bluefin tuna for about 24 hours as has been found in other tropical spawning tunas (Hunter et al., 1986; McPherson, 1988; Nikaido et al., 1991; Schaefer, 1996). The average interval between spawning in southern bluefin tuna, estimated from the proportion of ovaries containing postovulatory follicles, was 1.1 days for females in "prime spawning condition." Similar spawning rates have been reported in other tuna species that spawn in tropical waters: 1.54 and 1.27 days for yellowfin tuna (McPherson, 1991; Schaefer, 1996); 1.1 days for bigeye tuna (Nikaido et al., 1991) and 1.18 days for skipjack tuna (Hunter et



al., 1986). The mean spawning interval of reproductively active yellowfin tuna (those whose ovaries contain advanced yolked oocytes and may or may not contain postovulatory follicles and contain no or less than 50% α atresia) was 1.14 days (Schaefer, 1996). Histological sections indicated that slight variations in the lengths of individual spawning intervals exist in southern bluefin tuna, which may be normal or the result of external stresses such as decreased food availability or the stress of capture (Hunter et al., 1986).

Our estimate of mean relative batch fecundity for southern bluefin tuna (57 oocytes per gram of body weight) is similar to that found in yellowfin tuna (68 oocytes per gram of body weight) (Schaefer, 1996) but less than that for black skipjack tuna (81 to 153 oocytes per gram of body weight) (Schaefer, 1987) and skipjack tuna (40 to 130 oocytes per gram of body weight) (Stéguert and Ramcharrum, 1995). Hunter et al. (1985) reported that the minimum number of females needed for a reliable batch fecundity estimate in northern anchovy was 50. We, however, found only 21 southern bluefin tuna ovaries with unovulated hydrated oocytes from the 475 ovaries collected from the spawning ground. There could be several reasons for this. Oocytes in the hydrated stage may be very short-lived in southern bluefin tuna, which would reduce the chance of sampling females with hydrated ovaries. Spawning may occur during a specific time of the day, and if sampling was not conducted just prior to this, fewer females with hydrated

ovaries would be collected. Spawning in many tuna species is known to occur in the late evening or early morning (Hunter, et al., 1986; Schaefer, 1987; McPherson, 1991; Nikaido et al., 1991; Schaefer, 1996). Because our ovaries were sampled from females caught on Indonesian-based longlining vessels, which generally operate during daylight hours (Ishida et al., 1994), the chances of catching females that were about to spawn would be reduced. Further, if spontaneous spawning occurred while southern bluefin tuna were on the longlines, then fewer females with unovulated hydrated oocytes would be sampled. Spontaneous spawning has been observed in skipjack tuna soon after capture (Kaya et al., 1982).

Batch fecundity in southern bluefin tuna increased with body length. The variation in estimates for females of similar size may be normal because females were collected in different years and at different times in their spawning cycles. Hunter et al. (1985) suggested that the relation between batch fecundity and fish weight should be estimated annually in northern anchovy because batch fecundity can vary by a factor of 2 between years. Batch fecundity is also known to vary significantly during the spawning season in many fish species (Conover, 1985). A decrease in batch fecundity during the spawning season was found in Atlantic mackerel, *Scorpaenopsis scorpaenoides* (Watson et al., 1992), as individuals moved northwards. Batch fecundity can also peak during the middle of the spawning season if conditions are suitable, or it can remain constant if conditions are unpredictable (Conover, 1985).

Spawning strategies

We found that many southern bluefin tuna ovaries, collected both on and off the spawning ground, contained moderate levels of α atresia (10–50% of advanced yolked oocytes). High levels of α atresia are thought to indicate a decline in the spawning rate (Hunter and Macewicz, 1985a) and would normally occur towards the end of an individual's spawning season. Hunter and Macewicz (1980) classified northern anchovy as early postspawning if their ovaries contained less than 50% of advanced yolked oocytes in an α atretic state and postspawning if their ovaries contained more than 50% α atresia. Because we found that ovarian atresia increased with gonad index in the ovaries of prespawning females from the Southern Oceans, it appears that increased α atresia will not always mark the cessation of spawning in southern bluefin tuna. This ovarian atresia found in prespawning females could be a normal hormonal process that occurs during ovary maturation, as suggested by Macer (1974) for horse mackerel (*Trachurus*

trachurus). Atresia can also be caused by starvation as Scott (1962) found in maturing rainbow trout (*Salmo gairdneri*). It is not known if prespawning southern bluefin tuna are resorbing developing oocytes to gain the energy required for migration to the spawning grounds or because the ovary can only accommodate a certain volume of oocytes.

Many ovaries from nonspawning southern bluefin tuna ovaries collected from the spawning ground contained 10–50% atresia of their advanced yolked oocytes. The precise reproductive stage of these females is unclear. The similarity in atretic levels between these females and the prespawning females from the southern oceans, and in their high mean GI values, suggests that these females may have only just arrived on the spawning ground or were in the early stages of their spawning cycle. If this is the case, the relatively large numbers of nonspawning females (30% of females sampled) indicates that southern bluefin tuna may delay the onset of spawning possibly to recover from the energetic costs of migration. Their presence on the spawning ground throughout the spawning season suggests that there is a continual supply of new spawners onto the ground. Alternatively, southern bluefin tuna may not spawn continuously while on the spawning ground, but in pulses. The nonspawning females may be experiencing a lull in spawning activity between spawning episodes. The presence of many nonatretic yolked oocytes in their ovaries suggests that they could recommence spawning in the current season. Lunar spawning cycles have been documented in many tropical spawning fishes (see reviews by Johannes, 1978; Taylor, 1984; Robertson et al., 1990), however, we detected no evidence of a lunar cycle.

Spawning in southern bluefin tuna is not synchronized for the stock as a whole. There are several lines of evidence to support this statement: the presence of prespawning females both on and off the spawning ground throughout the spawning season; the absence of a peak in GI during the spawning season; the constant level of spawning intensity (percentage of females spawning) during the spawning season; the absence of any increase in the incidence of oocyte atresia towards the end of the spawning season; and the presence of postspawning females off the spawning ground both early and late in the spawning season. Thus it appears that there is a turnover of new spawners replacing old spawners on the spawning ground throughout the season. A similar turnover of pre- and postspawning southern bluefin tuna has been reported on the "Oki" fishing ground (Fig. 1) south of the spawning ground (Kikawa, 1964b). Nonsynchronized spawning has been found in other multiple spawning species such as skipjack

tuna (Cayré and Farrugio, 1986), chub mackerel, *Scomber japonicus* (Dickerson et al., 1992), and Atlantic croaker, *Micropogonias undulatus* (Barbieri et al., 1994). Cayré and Farrugio (1986) reported that spawning in skipjack tuna in the Atlantic is synchronized within schools. Individuals in a school can mature rapidly and spawn batches of oocytes simultaneously when conditions become favourable. It is unclear if southern bluefin tuna can do this, or to what extent the long spawning season is the result of individual fish or schools arriving on the spawning ground and maturing at different times. It is also unclear if the spawning period is constant for all individuals. In many species, including jack mackerel, *Trachurus symmetricus*, and chub mackerel, *Scomber japonicus*, older spawners are reported to have a longer spawning period than younger spawners (Knaggs and Parrish, 1973; MacCall et al., 1980).

The low number of postspawning female southern bluefin tuna (3) found on the spawning ground suggests that as soon as individuals have finished spawning they quickly move off the ground. The reasons for this departure are uncertain, but it may be due to decreased food availability through increased competition because many fish are gathering to spawn in a relatively small area, or to an inability to withstand the warmer water temperatures on the spawning ground for extended periods of time. Adult bluefin tuna are unique among the tunas because they live predominantly in cold water (as low as 5°C) and only move into warmer waters to spawn (Olson, 1980). Their ability to maintain their body temperature above ambient water temperature, through the development of an increased lateral blood supply and heat exchangers, has enabled them to occupy higher latitudes than many tuna species can tolerate. This adaptation to cold water, however, may preclude them from extended stays in warm water, resulting in a rapid migration off the spawning ground after spawning.

After spawning, southern bluefin tuna migrate south from the spawning ground into the West Wind Drift (Mimura, 1962) to feed and gain condition over the southern winter months. The minimum time for an individual to travel to the Southern Ocean however, is unknown. The maximum sustained swimming speeds of small yellowfin and skipjack tunas are predicted to be between 2 and 4 body lengths/s (Brill, 1996), and these values are thought to be similar in other active fish species. Southern bluefin tuna are unlikely to travel at their maximum sustained swimming speed in a straight line from the spawning grounds to the southern oceans because they will be feeding on the way south. If a 180-cm fish travelled at between 1 and 2 body lengths/s, from the spawning ground to Tasmania (6,000 km), it would take

between 19 and 39 days. Warashina and Hisada (1970) reported that lean fish with brownish meat have been caught in the Tasman Sea as early in the spawning season as November. These lean fish are believed to be postspawning females who have recently migrated from the spawning ground. The earliest that postspawning females were observed on the spawning ground was in October of both the 1993–94 and 1994–95 spawning seasons. The appearance of these postspawning fish on the spawning ground in October and again around Tasmania in November supports the idea that southern bluefin tuna are capable of travelling that distance in approximately one month. It also supports the idea that individuals spawn for a relatively short time in contrast to the whole season.

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