Studies on the age, growth and reproduction of Lophiomus setigerus and Lophius litulon in the East China Sea and the Yellow Sea

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CHAPTER IV REPRODUCTION OF *LOPHIUS LITULON*

Introduction

As described earlier, the anglerfish *Lophius litulon* (Jordan) is distributed throughout Japanese waters, in the Gulf of Po-Hai and the East China and Yellow Seas (Caruso, 1983; Yamada, 1986; Yoneda et al., 1997b). In Japan, this species is consumed as food, and its liver is considered a delicacy. In spite of their commercial importance, there is little biological information on *L. litulon* available to the fishery. To date, there been have only two reports on the reproduction of *L. litulon*. One on the spawning season and size at sexual maturity of *L. litulon* in Sendai Bay (Kosaka, 1966). The other on the spawning season and size at sexual maturity of *L. litulon* in the East China and Yellow Seas (Yamada, 1986).

According to Yamada (1986) and Tokimura (1992), the distribution of *L. litulon* varies seasonally; in summer anglerfish are found mainly in the Yellow Sea while during the winter and spring seasons their range extends into the East China Sea. However, the actual reasons for this seasonal difference in the distribution of *L. litulon* remain unclear. Understanding the significance of the seasonal distribution of a specific fish within its range should provide useful information for managing the fishery of that species.

The purpose of this study is to examine the reproductive characteristics of both sexes of *L. litulon* and to understand the movement of the population within the East China and Yellow Seas. Firstly, I describe the specialized gonadal structures of both sexes, to further understanding of the reproductive biology of this species. Secondly, the annual reproductive cycle, the size and age at sexual maturity of both sexes and batch fecundity are examined. Thirdly, the distribution of sexually immature and mature specimens at

three different times of the year is examined in order to identify the spawning grounds, and to search for possible differences in the migratory patterns between the mature sexes.

Materials and methods

The anglerfish were collected from the commercial trawl fishery and from two trawl surveys conducted by the Seikai National Fisheries Research Institute (SNFRI) and Nagasaki University, during the period from March 1991 to July 1997 in the East China Sea and Yellow Seas (Fig. 34). The landing area and date were recorded for all samples.

The SNFRI trawl survey was conducted in the East China and Yellow Seas, covering waters between 27°-37° N and west of 128° E, and depths between 50 m and 200 m, excluding the officially trawl-prohibited area. The area was divided into five sections using the lines of latitude and longitude. Within each section, 30' × 30' square sampling stations were setup systematically from an independent starting point. A total of 118 trawl stations were established in the area. The survey was carried out by RV Kaiho Maru, a 466 ton stern trawler. At each station, a bottom trawl net (SS-RI, B-type) was towed for 30 minutes at 3 knots to collect groundfish. The Nagasaki University trawl survey was conducted in the East China Sea covering the area between 29°-31° N and 126°-127° E in May 1995. Supplemental specimens caught by the commercial fishery in the coastal waters off Kyushu were purchased at the Fukuoka fish market.

The total length (*TL*) of all specimens was measured to the nearest millimeter. The body weight (*BW*) and visceral weight (*VW*) were determined to the nearest gram, while the gonadal weight (*GW*) and liver weight (*LW*) were measured to the nearest 0.1 g. The gonads to be used for histological observations were preserved in Bouin's solution, while those used to measure the oocytes were preserved in 10% formalin.

The gonads were embedded in paraffin, or methacrylate polymer resin (Technovit, Kulzer). Paraffin sections 5-10 μm thick were stained with Mayer's haematoxylin-eosin (H&E). Methacrylate polymer resin sections 2-3 μm thick were stained with a 1% solution

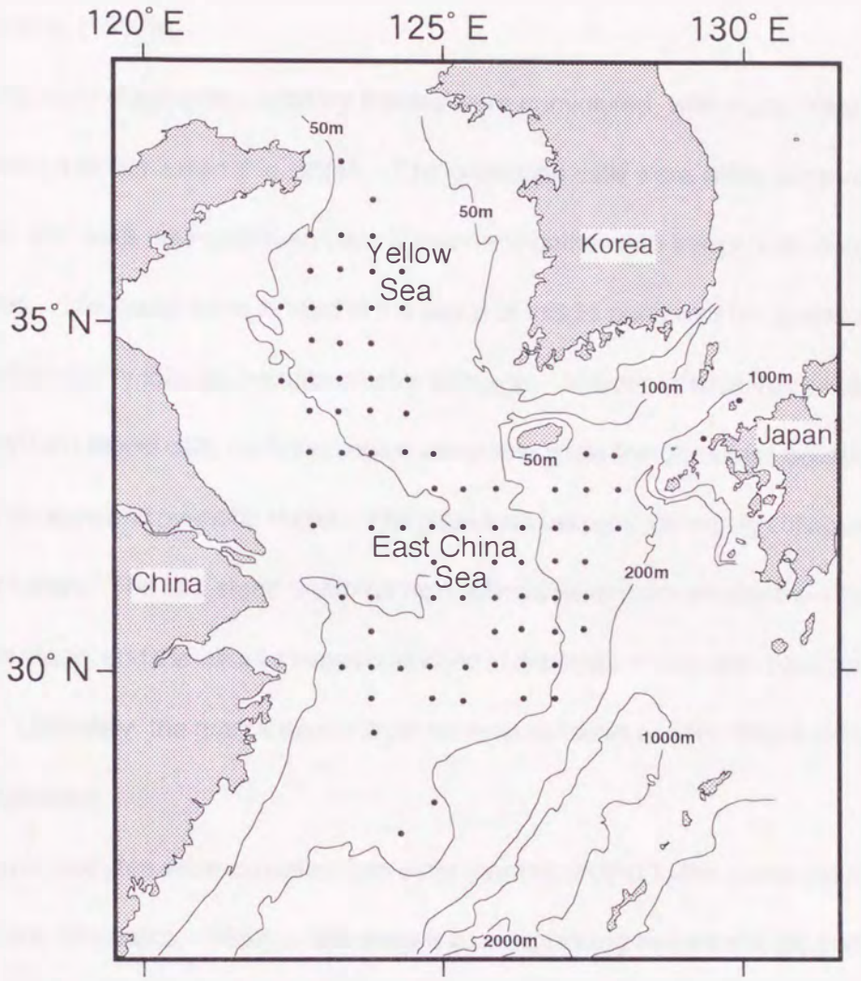


Fig. 34. A map of the East China Sea and the Yellow Sea, showing the location (•) of specimens of *L. litulon*.

of toluidine blue. The developmental stages of the oocytes were categorized according to Yamamoto (1956) and Yoneda et al. (1997a) (Table 11). Histological classification of atretic oocytes and postovulatory follicles followed Hunter and Macewicz (1985) and Yoneda et al. (1997a).

The early-stage postovulatory follicles were convoluted, with many folds, and contained a follicular lumen [Fig. 35(a)]. The granulosa cells were either columnar or cuboidal, and were arranged in an orderly manner together with thecal cells along blood capillaries. The nuclei were located in the basal or middle portion of the granulosa cells. The postovulatory follicles became smaller with age. In older follicles, the single layer of hypertrophied thecal cells contained some vacuoles, while the granulosa cells developed irregular shapes and pycnotic nuclei. The granulosa cell layer ultimately collapsed into the follicular lumen. The late-stage postovulatory follicles were much smaller than those in the previous stage, and the follicular lumen continued to decrease in size until it disappears [Fig. 35(b)]. Ultimately, the granulosa cell layer became indistinct and the thecal cell layer was much regressed.

Atretic oocytes were classified into early (corresponding to the alpha (α) stage (Hunter and Macewicz, 1985)) or late stages (corresponding to the beta (β) and later stages). The early stage was characterized b y the disintegration of the nucleus and yolk globules and by hypertrophy of the follicle layer, and the late stage by the degree of disorganization of the follicular cell layers as well as the presence of many intercellular vacuoles. The final criteria used for characterizing oocytes were the presence or absence of flocculent material and granular pigments in the ovigerous lamella.

Oocyte diameter was measured using a profile projector (20-100 ×) and the range was determined using the means of the largest and smallest oocytes from each

Table 11. Histological characteristics of oocytes at different developmental stages in *L. litulon*

Developmental stage of the oocyte	Oocyte diameter (μm)	Histological characteristics
chromatin nucleus	less than 20	nucleus has a large nucleolus
peri-nucleus	35-160	multiple nucleoli are seen toward the periphery of the nucleus; oil droplets appear around the nucleus and increase in number; follicle cells surrounding the oocyte have formed a narrow layer.
yolk vesicle	180-250	yolk vesicles appear in the peripheral region of the cytoplasm.
primary yolk	300-530	yolk globules appear between the yolk vesicles and increase in number; both granulosa and thecal cell layers are clearly observed.
secondary yolk	480-730	oocytes are larger and yolk globules fill the cytoplasm.
tertiary yolk	750-1000	yolk accumulation progresses rapidly, which results in a marked increase in the size of oocytes.
migratory nucleus	950-1300	yolk globules begin to fuse with one another; oil droplets fuse to form larger ones.
mature	1450-1700	after germinal vesicle breakdown, yolk globules form a single mass and oil droplets coalesce to form larger ones.

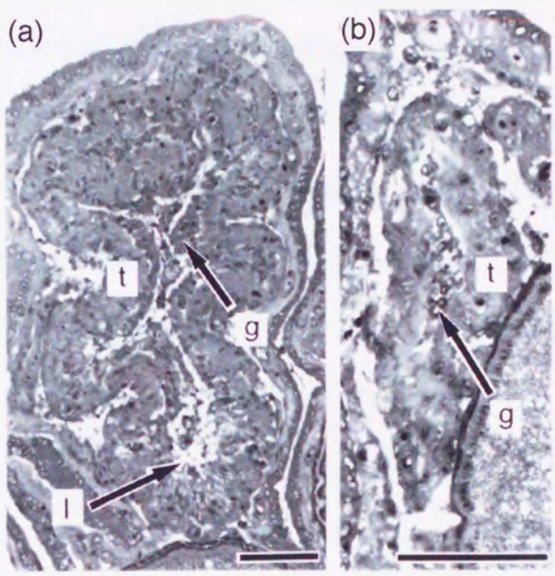


Fig. 35. Photomicrographs of degenerative postovulatory follicles of *L. litulon*. (a) Early-stage postovulatory follicles. (b) Late-stage postovulatory follicles. Bar = 75 μm; l, follicular lumen; g, granulosa cell layer; t, thecal cell layer.

developmental oocyte stage. Each developmental stage was identified by histological observations and its projected appearance. The average oocyte diameter at each developmental oocyte stage was determined from 50 oocyte measurements per stage.

Females with a developing stage ovary (see Results) had yolked oocytes in each ovigerous lamella. In order to examine the composition of yolked oocytes after spawning, 30-50 ovigerous lamellae samples from spawning stage ovaries (those containing postovulatory follicles and yolked oocytes; see Results) were examined, to determine how frequently ovigerous lamellae were found with yolked oocytes.

Between 300 and 550 oocyte samples from each ovarian stage were examined, to determine the size-frequency distribution of oocytes within each ovarian stage. All oocytes ≥ 100 μm in the yolk vesicle stage ovaries were measured while at other ovarian stages only oocytes ≥ 200 μm were measured.

The size and age at sexual maturity estimates were based on an examination of males (193-692 mm *TL* and ages 2-11) and females (174-1,013 mm *TL* and ages 2-15) collected in the spawning season (see Results) between February and May. Sexually mature individuals were defined as males with testes in the late spermatogenesis or mature stages and females with ovaries in the mid-developmental (secondary yolk stage of the oocyte) or more advanced stages (see Results). The age of individual fish was determined by counting the annual ring marks on the surface of the vertebral centrum (Yoneda et al., 1997b). To estimate the mean total length (L_{50}) and age at sexual maturity of males and females, the fraction of mature fish in each interval (10 mm length or year of age) was fitted with a logistic function using the Marquardt method (Draper and Smith, 1966).

The gonadosomatic index (*GSI*) and hepatosomatic index (*HSI*) were calculated in the following manner:

$$GSI = (GW / (BW - VW)) \times 100$$

$$HSI = (LW / (BW - VW)) \times 100$$

All the mature specimens ($TL \geq L_{50}$) of each sex were used to determine the monthly changes in *GSI* and *HSI*. The Kruskal-Wallis test (one-way analysis of variance, ANOVA) followed by Dunn's multiple comparison test were used to test for significant differences between the *GSI* and *HSI* values of groups of fish.

Estimation of batch fecundity followed Yoneda et al. (1997a). Batch fecundity was estimated using secondary yolk stage ovaries that contained no postovulatory follicles. Samples were collected from six different parts of the ovary, in the anterior, middle and posterior portion of each ovarian lobe. Ovarian tissue samples (30-120 mg), each containing approximately 100-350 oocytes, were placed on a slide in water and covered with a cover slip. The most advanced oocytes were counted using a profile projector (50-100 ×). Batch fecundity for each female was calculated as the product of the number of secondary yolk stage oocytes per unit weight, times the total ovarian weight for each of the six samples. Linear regression analysis was used to examine the relationship between batch fecundity and the total length of the fish (mm).

In order to determine whether secondary yolk stage oocytes were randomly distributed throughout the ovary, the densities (no. oocytes/ g ovary wt.) of secondary yolk stage oocytes from the six locations within the ovaries of five fish were compared. Samples were taken from the center of the middle lobule of the left and right ovarian lobes. The samples taken from the posterior and anterior parts of the ovary were taken from either the interior or exterior part of the ovary. A two-way ANOVA was performed to test for the

effect of sample location on oocyte density within each ovary.

To examine the seasonal distribution of these fish, the numbers of specimens collected at each sampling station during each of the three study periods (September, November-January and February-May) were compared. The September samples were collected in the 1993 SNFRI trawl survey. Samples for the other two periods came from the trawl surveys conducted by SNFRI between January and February in 1995-1997 and from the commercial trawl fishery in 1991-1997. Additional samples for February-May were collected in the trawl survey conducted by Nagasaki University in May 1995. Sexually mature individuals collected in September and November-January were defined as those larger than the L_{50} (see Results) for that sex. In February-May, sexually mature individuals were defined as males with testes in the mature stage and females with ovaries in the late-developing (tertiary yolk stage of oocyte), mature, spawning, or spent stages (see Results).

Results

Structure of the testis and ovary

The paired testicular lobes were located in the posterior portion of the abdominal cavity and suspended from the mesorchium. The main longitudinal sperm ducts, covered with layers of thick connective tissue, were located beneath the testicular groove (hilus) in each testis. These ducts fused near the posterior end of the testicular lobes to form a common sperm duct that led to the genital pore. The seminal lobules radiated towards and terminated blindly at the testicular periphery of the main sperm duct. Spermatogonia, each with a prominent nucleolus, were distributed randomly along the seminal lobules. Spermatocytes were oval or spherical and had nuclei with abundant, irregularly condensed chromatin. Young spermatids had large round nuclei. With age, the spermatids became rounder with much more cytoplasm and an intercellular cavity, while the nuclei became more condensed. The germinal cysts containing spermatogonia or developing spermatocytes were arranged on the walls of the seminal lobules [Fig. 36(a)]. Spermatids and spermatozoa with oval heads were both found in the lumina of the seminal lobules and sperm ducts [Fig. 36(a) and (b)], while only spermatids were present in the germinal cysts of the testis. The spermatids were quickly released into the lumina of the seminal lobules, where they were transformed into spermatozoa.

The right and left ovarian lobes of *L. litulon* were connected to each other at their posterior ends, forming a single organ. The ovarian wall consisted of a layer of squamous epithelium, a connective tissue layer, a smooth muscle layer and a single layer of ovarian wall epithelium facing the ovarian lumen. Stalk-like ovigerous lamellae protruded from the ovarian wall and were covered by a single cell layer of ovigerous lamella epithelium. So, the ovarian lumen was lined with both ovarian wall epithelium and ovigerous lamella

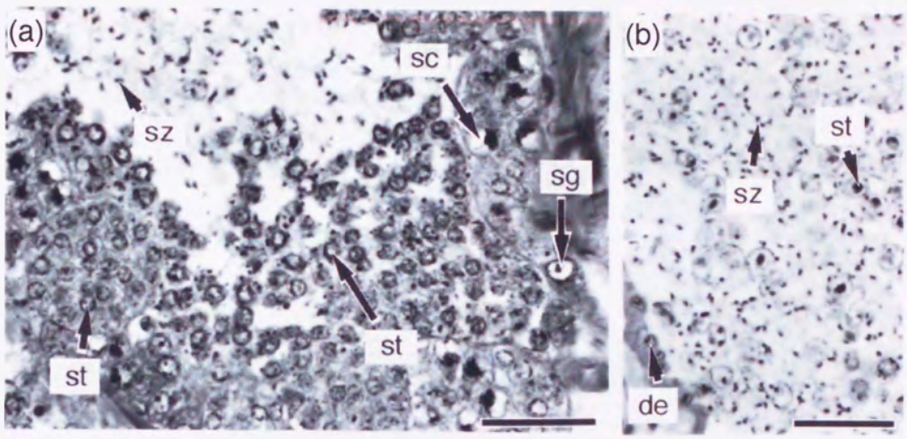


Fig. 36. Photomicrographs of sections of the testis of *L. litulon*. (a) Transverse sections of the seminal lobule during spermatogenesis, showing that spermatids are released into the lumen of the seminal lobule. (b) Transverse section of the main sperm duct during spermatogenesis, showing that both spermatids and spermatozoa are present in the main sperm duct. Bar = 25 μm; sg, spermatogonia; sc, spermatocyte; st, spermatid; sz, spermatozoon; de, main duct epithelium.

ovigerous lamella epithelium. These epithelia underwent morphological changes accompanying the ovarian maturation cycle (Fig. 37). As ovarian development continued in the secondary and tertiary yolk stages, gelatinous material was secreted from both the ovigerous lamella epithelium and ovarian wall epithelium, and filled the ovarian lumen. The ovigerous lamella contained many oocytes at different stages of development. In reproductively active ovaries, one or two of the most advanced oocytes were located in the terminal portion of each ovigerous lamella, while previtellogenic oocytes were found near the base of the ovigerous lamella throughout the year.

Maturity stages of testes and ovaries

The testes can be classified into four stages of maturity based on their histological characteristics (Fig. 38).

Immature stage [Fig. 38(a)]. Germinal cysts containing spermatogonia, spermatocytes and spermatids were observed along the wall of the seminal lobules. Spermatids and spermatozoa were not present in the lumina of the seminal lobules and the small main duct. All specimens with testes at this stage were ≤ 306 mm *TL*.

Early spermatogenesis stage [Fig. 38(b)]. The testes were larger than in the previous stage. Germ cells at all stages of spermatogenesis were present. Spermatids and a few spermatozoa were observed in the lumina of the seminal lobules and main sperm duct.

Late spermatogenesis stage [Fig. 38(c)]. Active spermatogenesis occurred in the testes. Spermatids and spermatozoa were more abundant in the lumina of the seminal lobules and main sperm duct than in the previous stage.

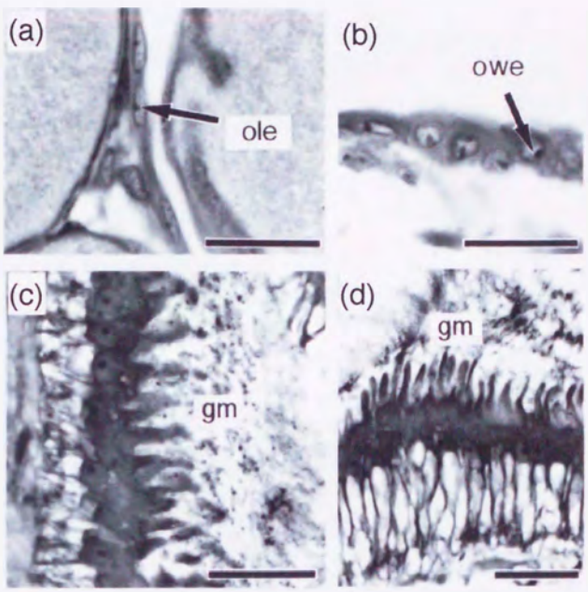


Fig. 37. Photomicrographs of the ovigerous lamella epithelium and ovarian wall epithelium at various stages of ovarian maturation in *L. litulon*. (a) Ovigerous lamella epithelium (ole) at the previtellogenic stage. (b) Ovarian wall epithelium (owe) at the previtellogenic stage. (a) and (b) show the epithelial cells of both the ovigerous lamella and ovarian wall are squamous or cuboidal in shape and contain a small nucleus. (c) Ovigerous lamella epithelium at the tertiary yolk stage. (d) Ovarian wall epithelium at the tertiary yolk stage. (c) and (d) show that gelatinous material is actively secreted from the apical surfaces of the epithelia of both the ovigerous lamellae and ovarian wall. Bar = 25 μm; gm, gelatinous material.

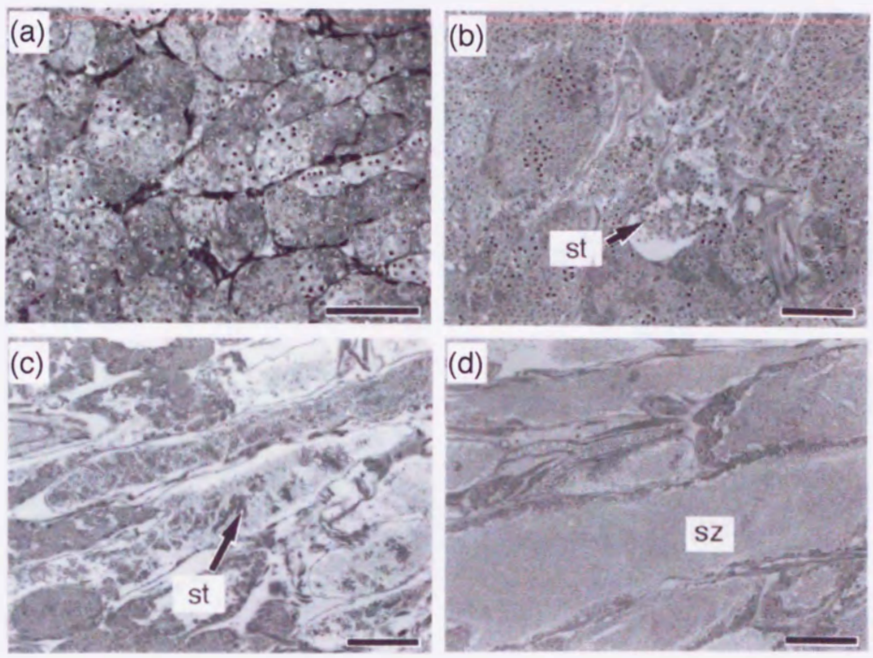


Fig. 38. Photomicrographs of testes in the four different stages of maturity in *L. litulon.* (a) Immature stage. (b) Early spermatogenesis stage. (c) Late spermatogenesis stage. (d) Mature stage. Bar = 100 μm; st, spermatid; sz, spermatozoon.

Mature stage [Fig. 38(d)]. Large quantities of spermatozoa and a few spermatids were present in the lumina of the seminal lobules and main sperm duct. Spermatogenesis and spermatogonial division also occurred in the seminal lobules, though few, if any, germinal cysts containing spermatogonia or spermatocytes were found around the main sperm duct.

The ovaries can be divided into six stages of maturity based on the development of the most advanced oocytes and their histological characteristics (Fig. 39).

Immature stage [Fig. 39(a)]. Only previtellogenic oocytes were present and the epithelia of both the ovigerous lamellae and ovarian wall were thin.

Developing stage [Fig. 39(b)]. Most advanced oocytes had reached the primary to tertiary yolk stages. This stage can be subdivided into early and late stages. The early stage was defined by the presence of primary or secondary yolk stage oocytes and the late stage by the presence of secondary or tertiary yolk stage oocytes with gelatinous material.

Mature stage [Fig. 39(c)]. The most advanced oocytes were in the migratory nucleus or mature stages. The ovulated oocytes were found in the gelatinous material forming within the ovarian lumen just before spawning.

Spawning stage [Fig. 39(d)]. Vitellogenic oocytes (in the primary or secondary yolk stages of the oocyte) and postovulatory follicles were present. Degenerating residual mature oocytes were frequently observed. The frequency of ovigerous lamellae with yolked oocytes presented clearly differentiates two ovarian stages (Fig. 40). At this stage, less than 40 % of the ovigerous lamellae had yolked oocytes in females with primary yolk stage oocytes, while more than 75 % of the ovigerous lamellae had yolked oocytes in females with secondary yolk stage oocytes, regardless of the degenerative stage of the

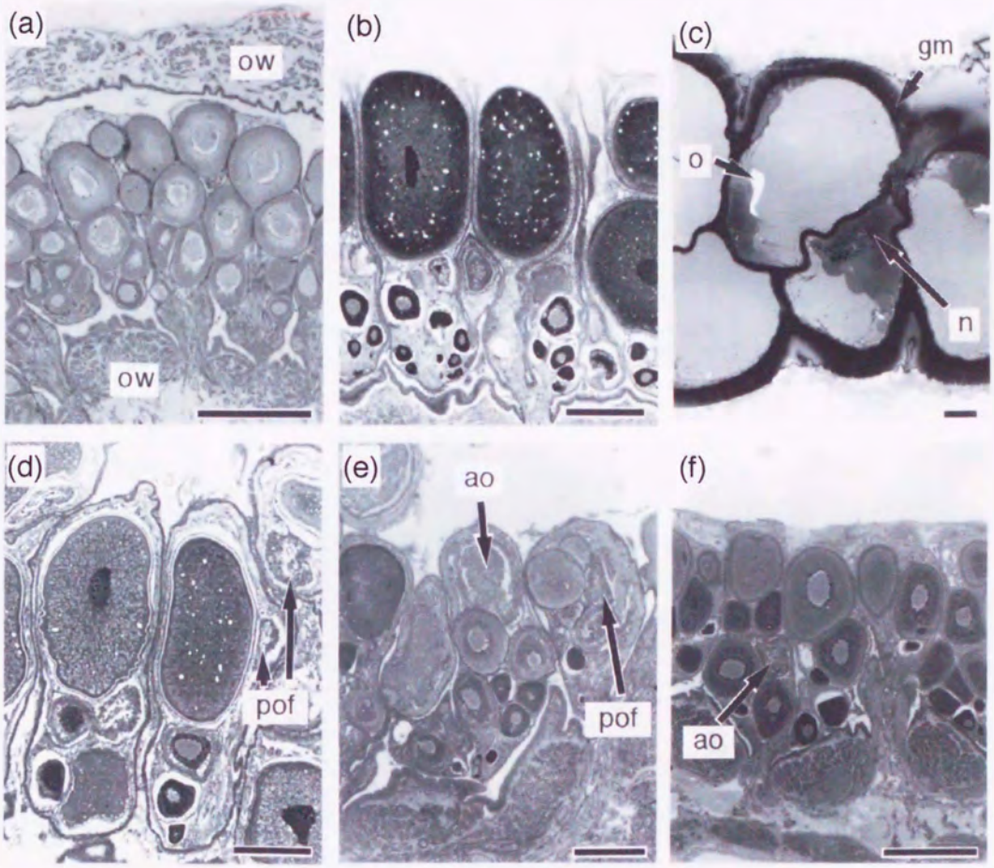


Fig. 39. Photomicrographs of ovaries at the six different stages of maturity in *L. litulon*. (a) Immature stage. (b) Developing stage. (c) Mature stage. (d) Spawning stage. (e) Spent stage. (f) Resting stage. Bar = 250 μm; ow, ovarian wall; gm, gelatinous material; n, nucleus; o, oil droplet ; pof, postovulatory follicle; ao, atretic oocyte.

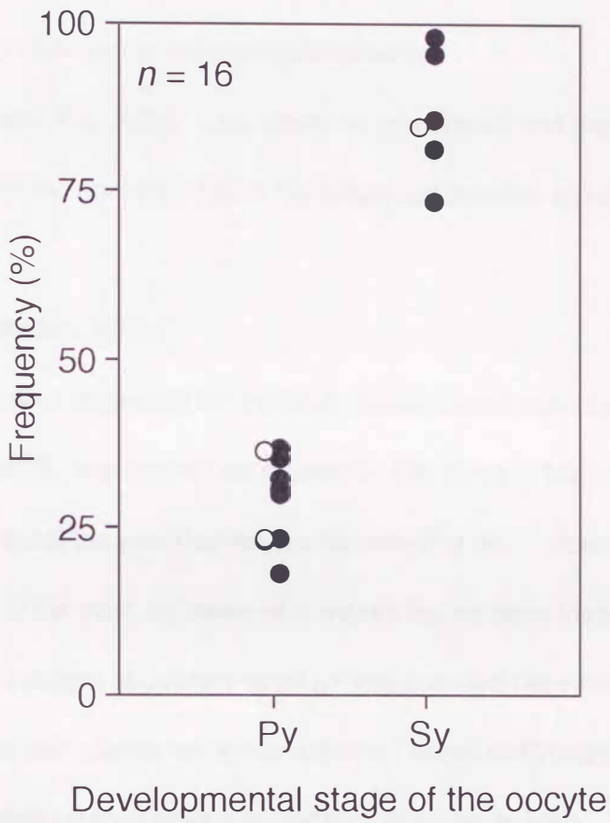


Fig. 40. The percentage of ovigerous lamellae with yolked oocytes in the spawning stage ovaries of *L. litulon*. Open circles represent ovaries containing early-stage postovulatory follicles and closed circles represent those with late-stage postovulatory follicles. The spawning stage ovaries are subdivided into two stages according to the developmental stage of the most advanced oocytes. *n*, number of fish examined; Py, primary yolk stage; Sy, secondary yolk stage.

postovulatory follicles. Some yolked oocytes in the process of becoming atretic were found in specimens with primary yolk oocytes.

Spent stage [Fig. 39(e)]. Vitellogenic oocytes were degenerating (early atretic stage) and late postovulatory follicles were observed.

Resting stage [Fig. 39(f)]. Late atretic stage oocytes and previtellogenic oocytes were present, and the epithelia of both the ovigerous lamellae and ovarian wall were thin.

Annual reproductive cycle

Only specimens at or exceeding the minimum size at sexual maturity (males = 325 mm *TL*, females = 546 mm *TL*; see below) were used for this study. Mature males were found over a longer period of the year than mature females (Fig. 41). Spermatogenesis occurred throughout most of the year, so males with mature testes were frequently collected. In females, the early stages of ovarian development occurred between November and February, and the later stages were reached from December through April. Females in the mature and spawning stages were collected from February to May. This is considered the spawning season. Between May and November, most females had immature, spent, or resting ovaries.

Size and age at sexual maturity

There were clear differences between males and females in the size and age at sexual maturity (Fig. 42). The minimum size and age at sexual maturity were 325 mm *TL*, age 4, for males and 546 mm *TL*, age 5, for females. The mean values for sexually mature males and females were 356 mm *TL*, age 5.4 and at 567 mm *TL*, age 6.2, respectively. All males ≥ 390 mm *TL* and age 7, and all females ≥ 630 mm *TL* and age 8, were mature.

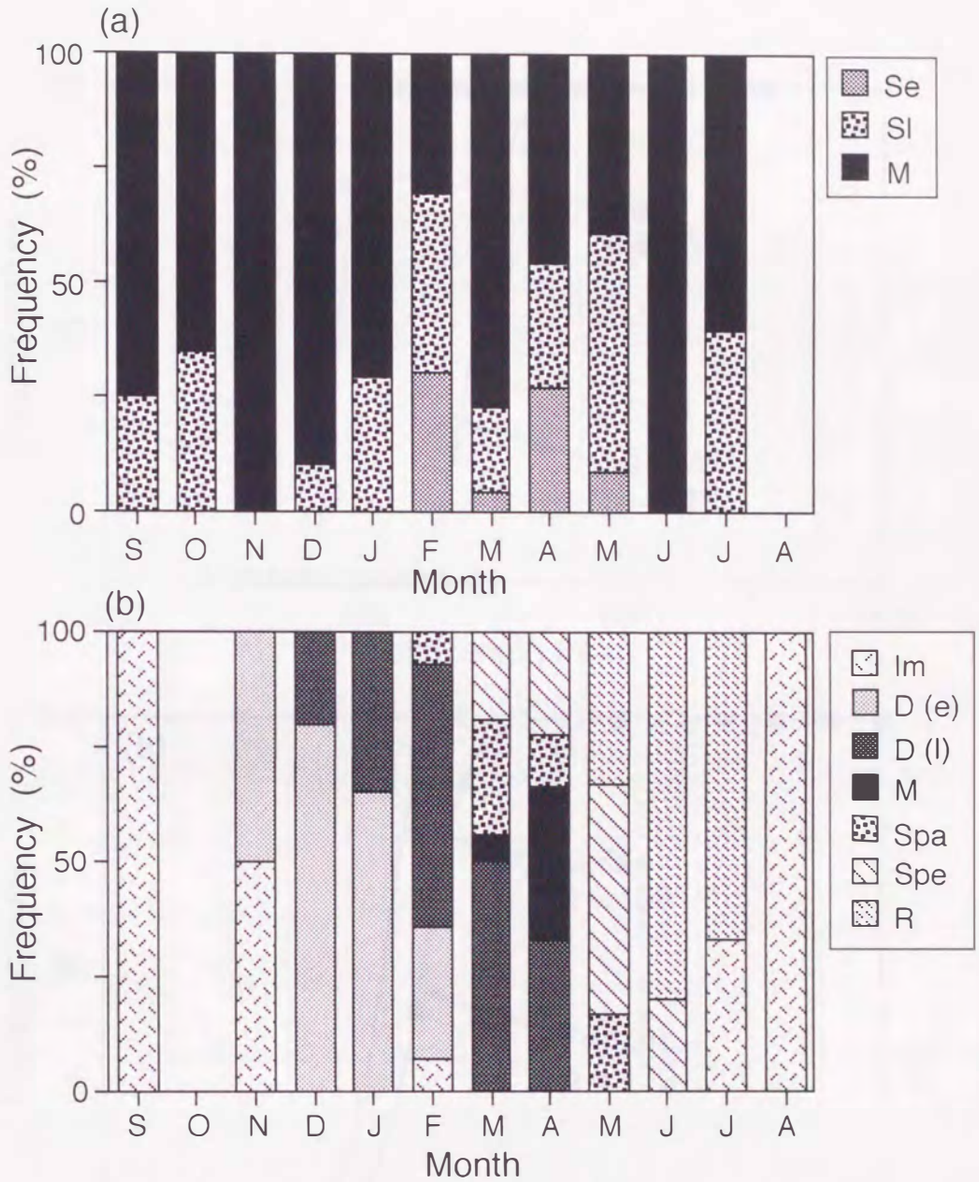


Fig. 41. Monthly changes in the frequency of occurrence of the various maturity stages of the gonads of male (a; $n = 187$) and female (b; $n = 70$) *L. litulon* in the East China and Yellow Seas. Only specimens larger than the minimum total length (*TL*) at sexual maturity for males (*TL* = 325 mm) and females (*TL* = 546 mm) were used in this study. Se, early spermatogenesis stage; Sl, late spermatogenesis stage; M, mature stage; Im, immature stage; D (e), early-developing stage; D (l), late-developing stage; Spa, spawning stage; Spe, spent stage; R, resting stage.

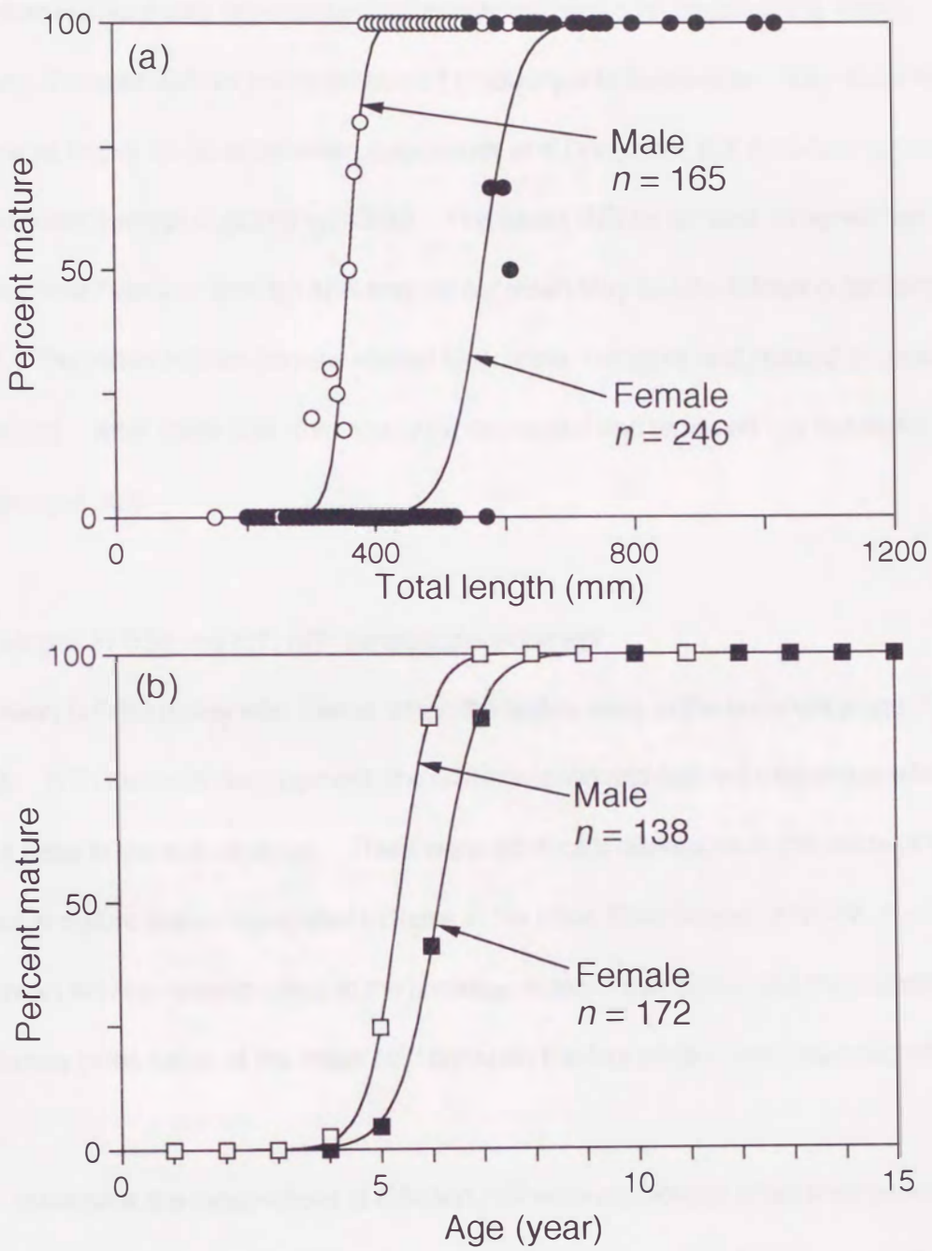


Fig. 42. The percent of mature fish, for fish in different size (10 mm length intervals) (a) and age (years) (b) classes fitted with a logistic function for male (open circles) and female (solid circles) *L. litulon* collected from February through May. *n*, number of fish examined.

Monthly changes in GSI and HSI

The mean *GSI* for males increased in September and peaked in January [Fig. 43(a)]. After January, the mean *GSI* for males decreased gradually until September. The mean *HSI* for males was highly variable between September and December, but remained constant from January through August [Fig. 43(b)]. The mean *GSI* for females remained high and variable from February through April and low between May and the following January [Fig. 43(c)]. The mean *HSI* for females started to increase in August and peaked in December [Fig. 43(d)]. After December, the mean *HSI* decreased and remained low between January and July.

Changes in GSI and HSI with gonadal development

The mean *GSI* for males was lowest when the testes were in the immature stage [Fig. 44(a)]. With testicular development, the *GSI* increased and reached a maximum when the testes were in the mature stage. There were significant differences in the value of these indices in mature testes, compared to those in the other three stages (ANOVA, $P < 0.05$). The mean *HSI* for males peaked in the immature stage of the testes, but the statistical differences in the value of the mean *HSI* between the four stages were insignificant ($P > 0.05$).

In females, the mean values of *GSI* and *HSI* were also lowest when the ovaries were in the immature stage [Fig. 44(b)]. The mean *GSI* for females gradually increased until ovaries reached the early developing stage and then increased markedly and peaked during the mature ovarian stage. The mean *GSI* was significantly higher at the mature stage than at all other ovarian stages (ANOVA, $P < 0.001$). The mean *HSI* for females increased rapidly and reached a maximum when ovaries were in the early developing

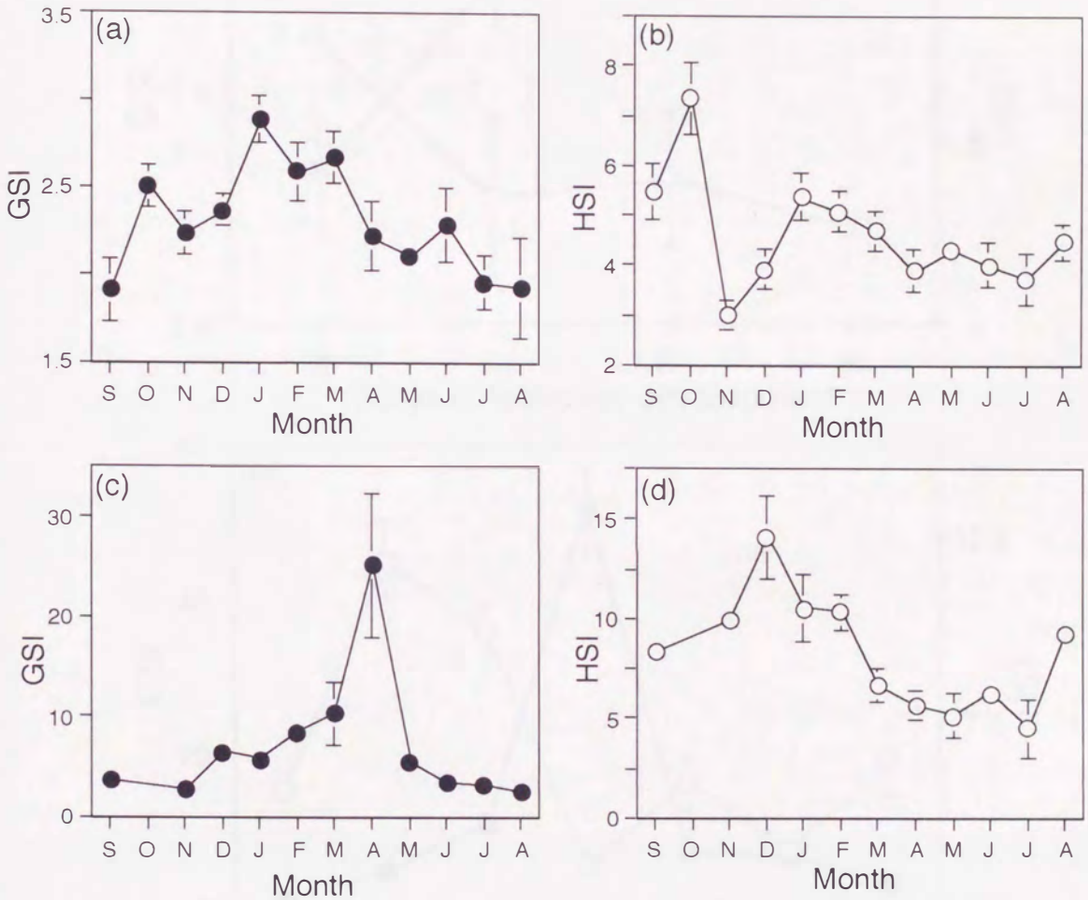


Fig. 43. Monthly changes in the mean gonadosomatic index (*GSI*, solid circles) and hepatosomatic index (*HSI*, open circles) for mature male (a, b; $n = 306$) and female (c, d; $n = 67$) *L. litulon* in the East China and Yellow Seas. Only specimens larger than the mean total length at sexual maturity for males (L_{50} = 356 mm) and females (L_{50} = 567 mm) were used in this study. Vertical lines indicate standard error.

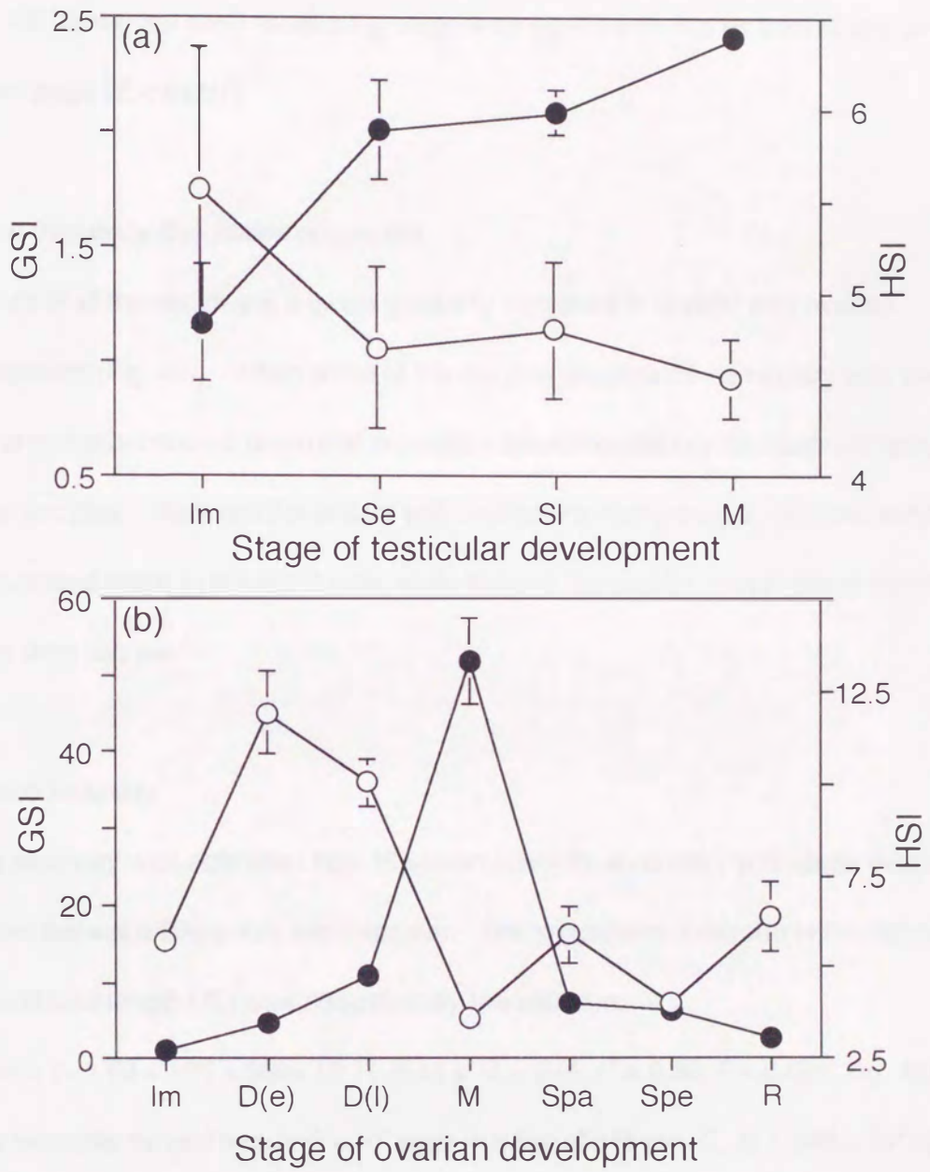


Fig. 44. Mean gonadosomatic index (*GSI*, solid circles) and hepatosomatic index (*HSI*, open circles) at each stage of maturity for male (a) and female (b) *L. litulon*. Vertical bars indicate the standard error. Im, immature stage; Se, early spermatogenesis stage; SI, late spermatogenesis stage; M, mature stage; D (e), early-developing stage; D (l), late-developing stage; Spa, spawning stage; Spe, spent stage; Re, resting stage.

stage and then decreased until it reached a minimum at the mature ovarian stage. The mean *HSI* during the early developing stage was significantly higher than at any other ovarian stage ($P < 0.001$).

Size frequency distribution of oocytes

The size of all the oocytes in a group gradually increased in tandem with ovarian development (Fig. 45). When some of the oocytes reached the secondary yolk stage, they formed an advanced batch that separated almost completely from adjacent groups of smaller oocytes. Between the tertiary yolk and mature ovary stages, only the oocytes in the advanced batch increased in size, while those in the smaller oocyte group remained smaller than 550 μm.

Batch fecundity

Batch fecundity was estimated from 15 specimens with secondary yolk stage ovaries, collected between December and February. The relationship between batch fecundity (*BF*) and total length (*TL*) was described by the equation:

$BF = (-1.64 \times 10^6) + 3688.13\ TL$ ($546 \leq TL \leq 846$; $r^2 = 0.86$; $P < 0.001$; Fig. 46).

Batch fecundity ranged from 310×10^3 eggs in a fish of 578 mm *TL*, to $1{,}540 \times 10^3$ eggs in a 796 mm *TL* fish.

There was no significant effect of the location of oocytes within the ovaries on oocyte density (Table 12). Advanced yolked (secondary yolk stage) oocytes were randomly distributed within the ovary and samples could be taken from any location without bias.

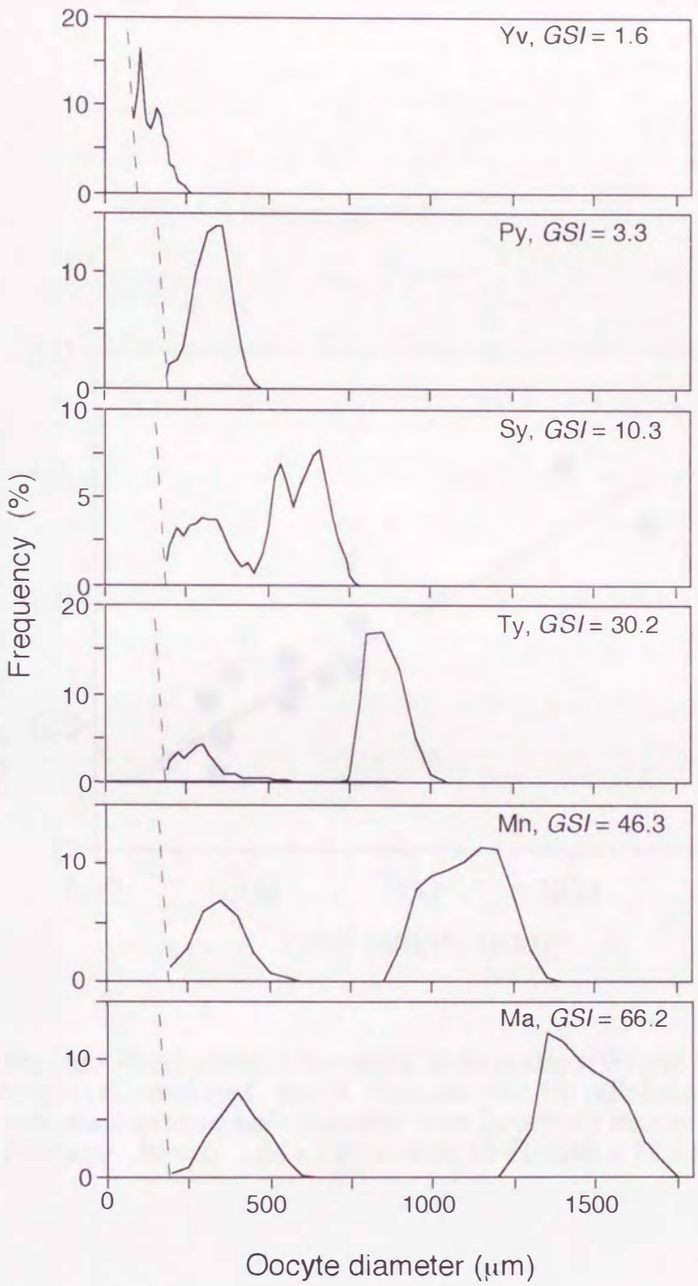


Fig. 45. Size-frequency distribution of oocytes at the different stages of maturation in the ovaries of *L. litulon*. All oocytes ≥ 100 μm diameter were measured in yolk vesicle stage ovaries, while at all other ovarian stages only oocytes ≥ 200 μm were measured. *GSI*, gonadsomatic index; Yv, yolk vesicle stage; Py, primary yolk stage; Sy, secondary yolk stage; Ty, tertiary yolk stage; Mn, migratory nucleus stage; Ma, mature stage.

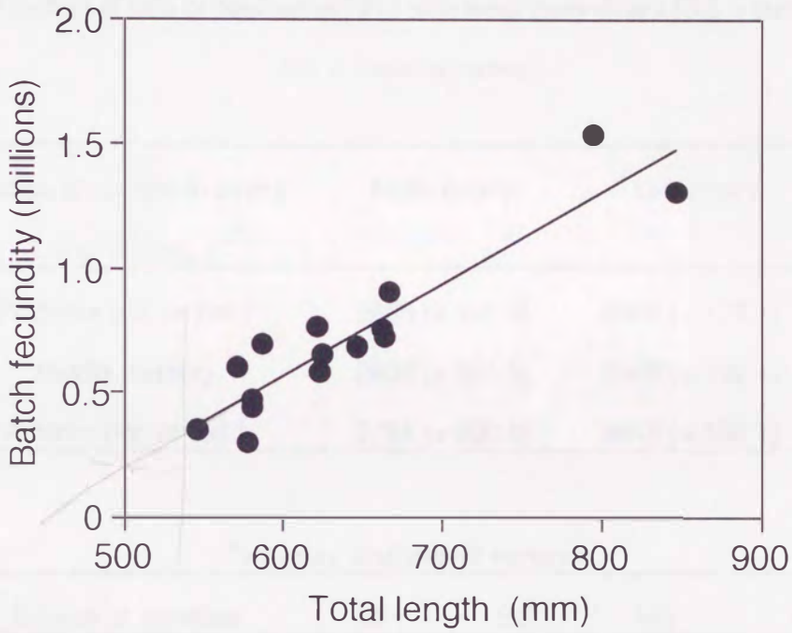


Fig. 46. Relationship between batch fecundity (*BF*) and total length (*TL*, mm) for *L. litulon*. Females ($n = 15$) with secondary yolk stage ovaries were collected from December through February. $BF = (-1.64 \times 10^6) + 3688.13\ TL$ ($546 \leq TL \leq 846$).

Table 12. The effect of ovarian tissue sample location on oocyte density (the number of secondary yolk stage oocytes per unit sample weight (g)) in *L. litulon* expressed as mean (± standard deviation). This was evaluated by taking tissue samples from three positions in both the right and left ovary (*n* = number of fish examined). Analysis of variance indicated the effect of side or position within a side were insignificant (SS = sum of squares; MS = mean squares)

Position of sample in ovary Long. (Cross.)	Right ovary	Left ovary	*n*
Posterior (Int. or Ext.)	2828 (± 142.6)	2955 (± 177.1)	5
Middle (center)	2835 (± 221.5)	2909 (± 199.4)	5
Anterior (Int. or Ext.)	2781 (± 200.6)	2816 (± 168.1)	5

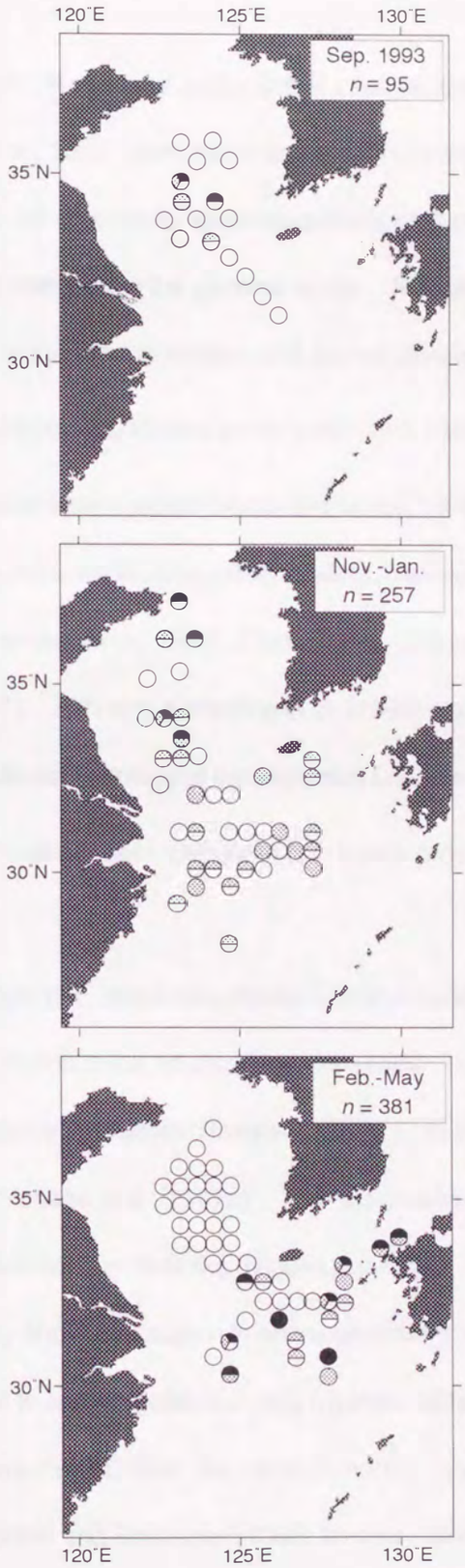
Two-way analysis of variance

Source of variation	df	SS	MS	*F*
Right vs. left ovary	1	23130	23130	0.73
Position within ovary	2	105500	52730	1.66
Interaction	2	48140	24070	0.76
Error	24	764700	31860	

Seasonal distribution

In September, most of the specimens from both sexes were collected in the Yellow Sea (Fig. 47). Between November and January their distribution extended from the Yellow Sea to the East China Sea. At this time, sampling sites showed a clear difference in the distribution of sexually mature males and females. Males were collected mainly in the East China Sea, while females were only collected in the Yellow Sea. During the spawning season, from February throughout May, sexually immature individuals were collected throughout the East China and Yellow Seas, whereas sexually mature individuals were only caught in the East China Sea and the coastal waters off Kyushu, and did not occur in the Yellow Sea.

Fig. 47. Geographical distribution of specimens of *L. litulon* collected in the East China and Yellow Seas at three different times of the year. Specimens are identified as sexually immature individuals (open area), sexually mature males (stippled area) and females (solid area). Sexually mature individuals were defined as fish collected in September and November-January, larger than the mean total length at sexual maturity (male = 356 mm, female = 567 mm) or fish caught in February-May with mature stage testes or ovaries that had matured to a least the late-developing (tertiary yolk stage of oocyte) stage. The type of fish collected at each station is indicated. *n*, number of fish examined.


120°E
125°E
130°E
Sep. 1993
n = 95
35°N
30°N
Nov.-Jan.
n = 257
35°N
30°N
Feb.-May
n = 381
35°N
30°N
120°E
125°E
130°E

Discussion

The testicular structure of *L. litulon* was similar to that of other teleosts with unrestricted spermatogonial (Grier et al., 1980; Grier, 1981) or lobular type testes (Billard et al., 1982; Billard, 1986). Although the process of spermatogenesis conformed to that of other teleosts, it was not completed within the germinal cysts. Rather, spermatids were released into the lumina of the seminal lobules and did not differentiate synchronously. This specialized spermatogenesis, termed 'semi-cystic' type (Mattei et al., 1993), was first discovered in *Lepadogaster lepadogaster* (Mattei and Mattei, 1978) and has subsequently been reported in *Neoceratidae* fishes (Jespersen, 1984), blenniid fishes (Lahnsteiner and Patzner, 1990a, b; Lahnsteiner et al., 1990), *Ophidion* sp. (Mattei et al., 1993) and *L. setigerus* (Yoneda et al.[4]). Although Armstrong et al. (1992) and Afonso-Dias and Hislop (1996) examined the testicular histology of the anglerfish *Lophius americanus* and *Lophius piscatorius*, they did not classify spermatogenesis in these species as the 'semi-cystic' type.

The ovarian structure of *L. litulon* was similar to that reported in other Lophiiformes including: *L. piscatorius* (Fulton, 1898; Afonso-Dias and Hislop, 1996), *Antennarius scaber*, *Histrio histrio*, *Ogcocephalus vespertilio* (Rasquin, 1958), *L. americanus* (Armstrong et al., 1992) and *L. setigerus* (Yoneda et al., 1997a). The two ovarian lobes become confluent at their posterior ends, and contain stalk-like ovigerous lamellae, within which the oocytes are arranged so that they show a gradation in developmental stages. Most female Lophiiformes are thought to spawn gelatinous egg masses, within which individual eggs float in separate chambers (Fulton, 1898; Gill, 1908; Connolly, 1920; Dahlgren, 1928; Berril, 1929; Breder, 1949; Bigelow and Schroeder, 1953; Mosher, 1954; Rasquin, 1958; Ray,

1961; Mito, 1963; Pietsch and Grobecker, 1980; Feinberg, 1984; Armstrong et al., 1992; Afonso-Dias and Hislop, 1996; Yoneda et al., 1997a). In *L. litulon*, gelatinous material was secreted from the epithelium of both the ovigerous lamellae and the ovarian wall. This also occurs in other Lophiiformes fishes (Rasquin, 1958; Armstrong et al., 1992; Yoneda et al., 1997a). Rasquin (1958) compared the structure of the ovary of *H. histrio* with that of the released egg mass, and concluded that the shape of the egg mass was a replica of the internal surface of the ovary. This is expected to be the case in other Lophiiformes fishes. Each stalk-like ovigerous lamella is thought to serve as a 'mold', forming a separate chamber within the gelatinous egg mass. The arrangement of oocytes, with the most advanced oocytes at the margins of the ovigerous lamellae, may facilitate the release of mature oocytes into each chamber.

My examination of the gonadal condition of both sexes indicates that *L. litulon* spawns in the period from February through May. Most females with late-developing, mature or spawning ovaries are found in March and April. This agrees with previous reports. The peak of the spawning season of *L. litulon* occurred between February and March, inshore off Kyushu (Mito, 1963) and in March and April in the East China and Yellow Seas (Yamada, 1986). In Sendai Bay, the spawning season of *L. litulon* occurs between May and July (Kosaka, 1966). These facts indicate that the spawning season of *L. litulon* in Japanese waters occurs progressively later, the more northerly the waters. This also occurs with *L. americanus* (Bigelow and Schroeder, 1953) in American waters and *L. piscatorius* (Afonso-Dias and Hislop, 1996) in northern European waters.

Females with ovaries in the spawning stage had postovulatory follicles and yolked oocytes at the primary- or secondary yolk oocyte stages. Specimens with secondary

yoke stage oocytes were collected mainly in the first half of the spawning period (February-March), and developed yolked oocytes normally, with no signs of oocyte atresia. Specimens in the spawning stage with primary yolk oocytes had relatively recently formed postovulatory follicles, indicating that ovulation and spawning had occurred recently. However, in half of the fish collected during the latter half of the spawning period (April-May), the atretic process had occurred and progressed.

A solitary female *L. litulon*, in an aquarium, released an infertile egg mass on 19 April 1994 and 35 days later extruded another (Kofuji, K., Oarai Aquarium, pers. comm.). This indicates that *L. litulon* has the potential to spawn more than once per year, although the two spawnings observed in the aquarium were not accompanied by normal spawning behavior. Recently, I reported a case of repeated spawning in *L. setigerus,* which has a long spawning period from May to November (Yoneda et al., 1997a). In contrast, *L. americanus* (Feinberg, 1984) and *L. piscatorius* (Afonso-Dias and Hislop, 1996) are believed to spawn once per season. Spawning frequency and batch fecundity are the most important factors for estimating the reproductive ability of a species. Future studies in aquariums and in the field should clarify the spawning frequency for *L. litulon.*

Although Kosaka (1966) and Yamada (1986) have already reported that females reach a larger size at sexual maturity than males, this study is the first to examine the size and age at sexual maturity in detail. Differences in size and age at sexual maturity between the sexes are also found in *L. americanus* (Armstrong et al., 1992, Almeida et al., 1995), *L. piscatorius* (Afonso-Dias and Hislop, 1996) and *L. setigerus* (Yoneda et al.[4]). In these three *Lophius* spp., both sexes of *L. piscatorius* at sexual maturity were larger size than in either *L. americanus* or *L. litulon.* This may result from the different growth rates for these three species; *L. piscatorius* grows the fastest of the three (Tsimenidis and Ondrias,

1980; Armstrong et al., 1992; Afonso-Dias and Hislop, 1996; Yoneda et al., 1997b). In *L. litulon*, both sexes seem to reach sexual maturity later than *L. americanus* (Armstrong et al., 1992; Almeida et al., 1995).

At mean sexual maturity, individuals of both sexes of *L. americanus* inhabiting northern waters were larger than southern fish, and the size of females at sexual maturity seems to have decreased substantially in recent years (Almeida et al., 1995). In *L. litulon*, there also appears to be a size difference at sexual maturity between fish from the East China and Yellow Seas (this study) and those from Sendai Bay (Kosaka, 1966). The respective minimum sizes at sexual maturity for males and females were 340 mm in body length (*BL*) and 600 mm *BL* in Kosaka's report and 325 mm *TL* and 546 mm *TL* in this study. Yamada (1986) reported that female *L. litulon* reached sexual maturity at sizes larger than 500 mm *BL* and that most females ≥ 580 mm *BL* were mature in the East China and Yellow Seas. These values are fairly close to my results.

In this study, there was a significant inverse correlation between the development of the ovary and a reduction in the weight of the liver (*HSI*). This was also the case for *L. setigerus* (Yoneda et al.[4]). The rapidly rising *GSI* from the mid-developing to the mature stage of the ovary is due to the accumulation of a large amount of gelatinous material and the increasing oocyte volume. Conversely, the mean *HSI* of females decreased after the mid-developing ovarian stage and reached a minimum at the late mature ovarian stage. In teleosts, as in most other vertebrates, the precursor protein of yolk (vitellogenin) is synthesized in the liver. The secreted vitellogenin is selectively removed from the bloodstream by developing oocytes (Wallace and Selman, 1981; Nagahama, 1987). This suggests that the rapid accumulation of yolk may be one of the reasons for the

decrease in the weight of the liver and the fall in the *HSI*. The relationship between the gelatinous material and the liver is unknown, but it is likely that the liver plays an important role in its synthesis and secretion. This study also found that the seasonal cycle of the *GSI* in females was inversely related to that of the *HSI*. The average *HSI* of females reaches a maximum in December, because of the high proportion of females with early-developing stage ovaries, whereas the decreasing *HSI* in females from December to May is caused by maturing ovaries and spawning.

In many fish, batch fecundity is estimated using migratory nuclei or hydrated oocytes, which can be easily distinguished from the less advanced oocytes: e.g. *Engraulis mordax* (Hunter and Goldberg, 1980; Hunter et al., 1985), *Thunnus albacares* (Schaefer, 1996) and *Rhomboplites aurorubens* (Cuellar et al., 1996). I found that during and after the tertiary yolk stage, a large amount of gelatinous material was rapidly secreted and accumulated in the ovarian lumen. Hence, counts of advanced oocytes from a small portion of the ovary, when extrapolated to the total weight of the gelatinous material, may significantly overestimate batch fecundity. These findings are repeated in *L. setigerus* (Yoneda et al., 1997a). However, the oocyte size-frequency profiles indicate that when the most advanced oocytes reached the secondary yolk stage, they formed a batch that was almost completely separated from the adjacent group of smaller oocytes. These *L. litulon* ovarian characteristics imply that estimates of batch fecundity should only be made using oocytes that have attained the secondary yolk stage.

This study demonstrated a relationship between batch fecundity and total length in *L. litulon* for the first time. The batch fecundity of *L. setigerus* (Yoneda et al., 1997a) has been estimated using the same method as this study. At the L_{50} (the mean size at sexual maturity), 303 mm *TL* in *L. setigerus* and 567 mm *TL* in *L. litulon*, the estimated batch

fecundities are 413 × 10^3 and 451 × 10^3, respectively. The mature female *L. americanus* (Armstrong et al., 1992) is almost the same size as the mature female *L. litulon*. The estimated batch fecundity of *L. americanus* is lower than that of *L. litulon*. For a 700 mm *TL* fish, their equation predicts 743 × 10^3 oocytes while my predicts 942 × 10^3; for an 800 mm *TL* fish the respective values are 1,192 × 10^3 and 1,311 × 10^3 oocytes.

In my study of the seasonal distribution of *L. litulon* I found immature and mature specimens in the East China and Yellow Seas as previously reported (Yamada, 1986; Tokimura, 1992). Tokimura (1992) suggested that *L. litulon* migrates seasonally in response to cyclical changes in the water temperature. *L. litulon* are mainly caught in waters with temperatures ranging from 6 to 13 °C (Yamada, 1986; Tokimura, 1992). In summer, water cooler than 13°C is found only near the bottom of the Yellow Sea, whereas in the winter and spring the water of the East China Sea is affected by the Continental Coastal Cold Water and is also cooler than 13°C (Kondo, 1985; Tokimura, 1992). These oceanographic conditions in the East China and Yellow Seas likely cause the horizontal migration of *L. litulon* throughout the year. A seasonal movement of *L. litulon* has also been reported in Sendai Bay (Kosaka, 1966; Omori, 1979). *L. litulon* is most abundant in shallow waters between February and June. From August through October, they disperse toward deeper waters. The seasonal movement in Sendai Bay is observed mainly in immature fish and is felt to be associated with their feeding activities (Kosaka, 1966). In *L. americanus*, a seasonal migration has been observed along the northeastern coast of the United States (Jean, 1965; Almeida et al., 1995). This phenomenon is also thought to occur in response to changes in oceanographic conditions.

This study provides the first evidence for a spawning ground of *L. litulon* in the East China and Yellow Seas. During the February through May spawning season, mature

males and females with ovaries in a condition that suggests they are either about to spawn, or have just spawned, are found in the East China Sea and the coastal waters off Kyushu. In contrast, immature individuals were distributed throughout the East China and Yellow Seas during the same period. This indicates that the spawning grounds of *L. litulon* cover a large area, from the East China Sea to the inshore waters off Kyushu. Furthermore, this study reveals the migratory pattern of both sexes of *L. litulon* to the spawning grounds in the period before the spawning season. In November through January, most mature males are found in the East China Sea, while all females ≥ 546 mm *TL* (the minimum size at sexual maturity) with immature or early-developing stage ovaries are found in the Yellow Sea. In February, with the onset of the spawning season, females collected in the northern East China Sea had secondary or tertiary yolk stage ovaries with gelatinous material. While those collected in the Yellow Sea had immature or primary yolk stage ovaries. These findings indicate that mature males migrate to the spawning grounds several months before the spawning season, while the ovaries of females develop and mature as they migrate to the spawning grounds, just before spawning season. Different migratory patterns before spawning in the two sexes have also been reported in the plaice *Pleuronectes platessa* in the Dover Strait (Arnold and Metcalfe, 1995). In this study, I identified the spawning ground and migratory pattern of *L. litulon* in broad terms. However, it is not clear whether there are more restricted spawning grounds and more specific migratory behavior in this species. Further research is needed to answer these questions.

EPILOGUE

This study revealed the growth rate, lifespan, gonadal morphology, spawning season, size and age at sexual maturity and batch fecundity of *L. setigerus* and *L. litulon*. In addition, distinct migratory patterns for both sexes were demonstrated in *L. litulon* and the spawning grounds were identified.

In this study, several common biological characteristics shared by these two anglerfish were identified. First, females grow faster and live longer than males. This was reflected in different sizes and ages at sexual maturity in the two sexes. Second, the 'semi-cystic' spermatogenesis and ovarian development accompanied by the secretion of a gelatinous material are reproductive specializations in these two anglerfish. In females, there is a significant inverse relationship between ovarian development and the weight of the liver. This suggests that the liver is an important energy reserve for the reproductive activities of females.

I also found several distinct biological characteristics that separate these two species of anglerfish. Adult *L. setigerus* were smaller than adult *L. litulon* and had a narrower range of sizes. This was reflected in a very different capacity for batch fecundity between the two anglerfish. Furthermore, *L. setigerus* spawned repeatedly during a long spawning season that ran from May through November. On the other hand, the spawning period of *L. litulon* was restricted to February through May. Adult females seemed to spawn once, although they appear to have the potential to spawn more than once per spawning period.

The East China and Yellow Seas are international waters, fished by the Japanese, Chinese, and Korean trawl fisheries. The scientists of all three countries agree that demersal fish resources have been decreasing because of the intense fishing of these

nations, and that steps to remedy this situation should be taken as soon as possible. The neighboring nations must cooperate to establish guidelines for the conservation and proper management of *L. setigerus* and *L. litulon*, because their populations in these waters straddle national boundaries. Unfortunately, no official landings of these two anglerfish are reported, since the catch of anglerfish is far lower than that of other commercially important fish in Japan and other nations. Trawl fishermen and RV officers and crews have told me that the large anglerfish, especially *L. litulon*, are becoming scarce. This is likely the result of commercial fishing pressure, which tends to select larger individuals. If over-fishing and destructive fishing practices are allowed to continue, the stock will be drastically depleted in the future. This study is intended to provide additional information to assess the condition of these species and to design a management strategy for their fisheries.

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SUMMARY

Two anglerfish, *Lophiomus setigerus* and *Lophius litulon*, are occasional targets of the trawl fishery during the winter months in Japanese waters and the East China Sea and Yellow Sea, because of their high market value. In spite of their commercial importance, little is known about the biology of these two anglerfish. In this study, I describe the age, growth and reproduction of *L. setigerus* and *L. litulon* collected in the East China and Yellow Seas.

Chapter I: The age and growth of *L. setigerus* were examined using vertebral centra from specimens collected in the East China Sea between March 1991 and February 1996. Monthly changes in the frequency of appearance of a translucent band on the outer margin of the centrum and marginal increments indicated that the rings form once a year, primarily from November through December. Male specimens revealed 1-8 rings, while females had 1-11 rings. Using the back-calculated total lengths, the growth of anglerfish was expressed as:

$TL_t = 377.6\ (1 - e^{-0.193\,(t + 0.290)})$ ($t \leq 8$) for males and

$TL_t = 616.4\ (1 - e^{-0.109\,(t + 0.120)})$ ($t \leq 11$) for females.

These results suggest that females grow faster and live longer than males.

Chapter II: The gonadal structure, annual reproductive cycle, sexual maturity and batch fecundity of *L. setigerus* were examined using specimens collected in the East China Sea between March 1991 and February 1996. It was found that spermatids were released from the germinal cysts into the lumina of the seminal lobules, and that both spermatids and spermatozoa were found in the lumina of the seminal lobules and sperm ducts. The right

and left lobes of the ovary were connected at their posterior ends. Stalk-like ovigerous lamellae protruded from the ovarian wall and contained many oocytes at different stages of development. During the reproductive season, gelatinous material was secreted from the epithelia of both the ovigerous lamellae and the ovarian wall, and the morphology of the epithelia changed with the ovarian maturation cycle. Spermatogenesis and vitellogenesis occurred throughout most of the year. The testes of males were full of spermatozoa throughout the year. Migratory nucleus stage and mature stage oocytes were found in the ovaries between May and November, when females with postovulatory follicles and developing vitellogenic oocytes were also collected. In addition, from May through November, females with mature oocytes were found at the time of the new and full moons and final maturation of the ovary occurred with the approach of the full moon. These results suggest that there is an extended spawning season from May to November during which females spawn repeatedly, and that females have a weak semilunar spawning periodicity. Males and females reached sexual maturity at a mean total length and age of 178 mm, 3.3 years, and 303 mm, 6.1 years, respectively. Clear seasonal cycles of the gonadosomatic index (*GSI*) and hepatosomatic index (*HSI*) were found in females. The mean *GSI* in females increased rapidly with ovarian development, while the mean *HSI* decreased from the middle of vitellogenesis until final maturation of the ovaries. The mean values of *GSI* and *HSI* in males increased with testicular development. When the most advanced oocytes attained the secondary yolk stage, they form a batch that was separate from the adjacent groups of smaller oocytes. Batch fecundity (*BF*) in 20 females with secondary yolk stage ovaries was related to total length (*TL*, mm) by the equation:

$$BF = 556.2 \times TL^{1.157} \quad (300 \leq TL \leq 396).$$

Chapter III: The age and growth of *L. litulon* were examined using vertebral centra from specimens collected in the East China and Yellow Seas between January 1991 and April 1996. Monthly changes in the frequency of appearance of a translucent band on the outer margin of the centrum and marginal increments indicated that the rings form once a year, predominately in April. Back-calculated total lengths for each sex were calculated by the regression method using a standardized ring radius. The initial growth trend based on young fish (≤ 250 mm in total length) collected monthly was comparable to the mean back-calculated total lengths calculated from the first and second rings of vertebral centra for males and females. Using the back-calculated total lengths, the growth of anglerfish was expressed as:

$TL_t = 1130\ (1 - e^{-0.080\,(t + 0.401)})$ ($t \leq 8$) for males and

$TL_t = 1547\ (1 - e^{-0.064\,(t + 0.345)})$ ($t \leq 13$) for females.

These results suggest that females grow faster and live longer than males.

Chapter IV: The annual reproductive cycle, sexual maturity, batch fecundity, and seasonal distribution of *L. litulon* were examined from specimens collected in the East China and Yellow Seas during the period between March 1991 and July 1997. It was found that spermatids were released from the germinal cysts into the lumina of the seminal lobules, and that both spermatids and spermatozoa were found in the lumina of the seminal lobules and sperm ducts. Stalk-like ovigerous lamellae containing many oocytes at different stages of development protruded from the ovarian wall. During the reproductive season, gelatinous material is secreted from the epithelia of both the ovigerous lamellae and the ovarian wall. The testes of males were full of spermatozoa throughout most of the year. The spawning

season occurred from February to May. Males and females reached sexual maturity at a mean total length and age of 356 mm, 5.4 years, and at 567 mm, 6.2 years, respectively. Seasonal cycles of the gonadosomatic index (*GSI*) and hepatosomatic index (*HSI*) were found in females. The mean *GSI* of females increased rapidly with ovarian development while the mean *HSI* decreased from the middle of vitellogenesis to final maturation of the ovaries. When the most advanced oocytes reached the secondary yolk stage, they formed a batch that was distinct from the adjacent group of smaller oocytes. The relationship between batch fecundity (*BF*) and total length (*TL*, mm) in 15 females with secondary yolk stage ovaries was given by the expression:

$$BF = (-1.64 \times 10^6) + 3688.13\ TL \quad (546 \leq TL \leq 846).$$

In September, most of specimens from either sex were collected in the Yellow Sea. Between November and January their range extended from the Yellow Sea to the East China Sea. During the spawning season, which runs from February throughout May, sexually immature individuals were collected throughout the East China and Yellow Seas, whereas sexually mature individuals were caught in the East China Sea and the coastal waters off Kyushu. This suggests that the spawning grounds of *L. litulon* occupy the waters from the East China Sea to inshore Kyushu.

In conclusion, this study revealed the growth rate, lifespan, gonadal morphology, spawning season, size and age at sexual maturity and batch fecundity of *L. setigerus* and *L. litulon*. In addition, distinct migratory patterns for both sexes and a spawning ground of *L. litulon* were identified. Neighboring nations need to cooperate to establish guidelines for the conservation and proper management of *L. setigerus* and *L. litulon* populations in the East China and Yellow Seas, because the stocks of these species straddle national

borders. My findings should provide important information to help solve these problems.

要約

東シナ海・黄海産アンコウとキアンコウの年齢、成長および生殖に関する研究

アンコウおよびキアンコウは、日本各地の沿岸水域、東シナ海、黄海において底曳網で漁獲され、特に冬場には高価に取引されている魚種である。これら2種のアンコウ類は重要な漁業資源であるにも拘わらず、その生物学的知見は乏しい。本研究では、東シナ海・黄海産アンコウとキアンコウの年齢、成長および生殖に関する生物学的諸特性を解明した。

第1章： 1991年3月～1996年2月に東シナ海で採集されたアンコウの椎体を用いて年齢査定を行った。椎体縁辺部における透明帯の出現率および縁辺成長率の月別変化から、標示は年1回、ほぼ11～12月に形成されると考えられた。標示は雄で1-8輪、雌で1-11輪まで読みとられた。成長式は、雄：$TL_t = 377.6\,(1 - e^{-0.193(t+0.290)})$ $(t \leq 8)$、雌：$TL_t = 616.4\,(1 - e^{-0.109(t+0.120)})$ $(t \leq 11)$で示された。これらの結果、雌は雄よりも成長が良く、寿命も長いことが明らかとなった。

第2章： 1991年3月～1996年2月に東シナ海で採集されたアンコウの生殖腺の構造、生殖年周期、性成熟およびバッチ産卵数について調べた。精細胞はシストから精小嚢内腔へ放出され、精小嚢内腔および輸精管内には精細胞と精子が認められた。左右の卵巣は後部末端で融合していた。卵巣壁に形成される茎状の卵巣薄板は発達段階の異なる多数の卵を有していた。繁殖期間中、ゼラチン状物質が卵巣薄板および卵巣壁を覆う各上皮細胞から分泌され、これらの上皮細胞は卵巣の成熟周期に伴って形態変化を示した。精子形成および卵黄形成はほぼ周年にわたって行われた。精子を充満させた精巣をもつ雄は周年にわたり認められた。胚胞移動期および成熟期の卵巣をもつ雌は5～11月に採集され、その期間中卵黄卵と排卵痕を有する雌も同様に採集された。さらに、5～11月の間、成熟卵をもつ雌は新月と満月時に出現し、卵巣の最終成熟は満月に近づくにつれて行われた。これらの結果から産卵期間は5～11月の長期間におよび、雌は複数回にわたって産卵し、弱い半月周期の産卵リズムをもつと考えられた。平均成熟全長および年齢はそれぞれ雄178 mm、3.3才、雌303 mm、6.1才であった。雌の*GSI*と*HSI*

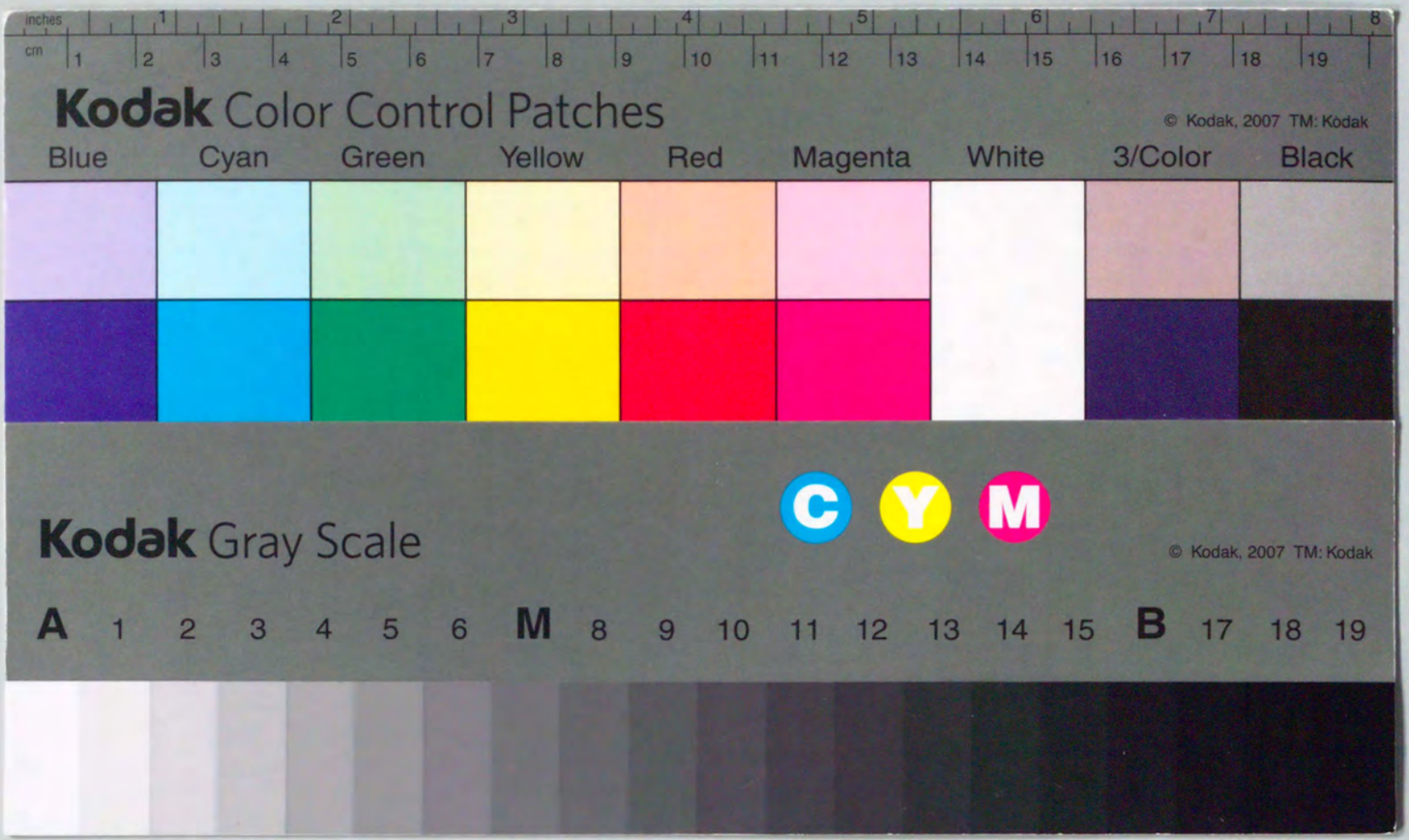
には明確な季節変動が認められた。雌の平均GSIは卵巣の発達に伴い急激に上昇したが、平均*HSI*は卵黄形成中期から最終成熟にかけて減少した。雄の平均*GSI*と*HSI*は精巣の発達に伴い上昇した。最も発達した卵が第2次卵黄球期に達した時、バッチ卵群が形成された。第2次卵黄球期の卵巣をもつ20個体の雌を用いてバッチ産卵数(*BF*)を調べた結果、バッチ産卵数と全長(*TL*, mm)との関係は$BF = 556.2 \times TL^{1.157}$ ($300 \leq TL \leq 396$)で示された。

第3章：　1991年1月～1996年4月に東シナ海、黄海で採集されたキアンコウの椎体を用いて年齢査定を行った。縁辺部における透明帯の出現率および縁辺成長率の月別変化から、標示は年に1回、4月にほぼ形成されると考えられた。若齢魚の月別採集結果から得られた初期の成長傾向は、雌雄の椎体における第1、2標示の平均計算全長と一致した。成長式は、雄：$TL_t = 1130\,(1 - e^{-0.080\,(t + 0.401)})$ ($t \leq 8$)、雌：$TL_t = 1547\,(1 - e^{-0.064\,(t + 0.345)})$ ($t \leq 13$)で示された。これらの結果、雌は雄よりも成長が良く、寿命も長いことが明らかとなった。

第4章：　1991年3月～1997年7月に東シナ海、黄海で採集されたキアンコウの生殖年周期、性成熟、バッチ産卵数および季節的な分布について調べた。精細胞はシストから精小嚢内腔へ放出され、精小嚢内腔および輸精管内には精細胞と精子が認められた。卵巣壁に形成される茎状の卵巣薄板は発達段階の異なる多数の卵を有していた。繁殖期間中、ゼラチン状物質が卵巣薄板および卵巣壁を覆う各上皮細胞から分泌され、これらの上皮細胞は卵巣の成熟周期に伴って形態変化を示した。精子を充満させた精巣をもつ雄はほぼ周年にわたり出現した。産卵期間は2～5月であった。平均成熟全長および年齢はそれぞれ雄356 mm、5.4才、雌567 mm、6.2才であった。雌の*GSI*と*HSI*には明確な季節変動が認められた。雌の平均GSIは卵巣の発達に伴い急激に上昇したが、平均*HSI*は卵黄形成中期から最終成熟にかけて減少した。最も発達した卵が第2次卵黄球期に達した時、バッチ卵群が形成された。第2次卵黄球期の卵巣をもつ15個体の雌を用いてバッチ産卵数(*BF*)を調べた結果、バッチ産卵数と全長(*TL*, mm)との関係は$BF = (-1.64 \times 10^6) + 3688.13\,TL$ ($546 \leq TL \leq 846$)で示された。9月、雌雄ともに大部分の個体は黄海で採集された。11～1月ではその分布域が黄海から東シナ海へと拡大した。

2〜5月の産卵期間では未成熟魚は東シナ海から黄海全域にわたって採集されたが、成熟魚は東シナ海および九州沿岸域で採集された。これらのことからキアンコウの産卵場所は東シナ海から九州沿岸域であることが明らかとなった。

本研究ではアンコウとキアンコウの成長率、寿命、生殖腺の形態、産卵期、性成熟サイズと年齢およびバッチ産卵数を解明した。さらに、キアンコウについては雌雄における移動過程および産卵場所を明らかにした。東シナ海・黄海のアンコウとキアンコウは日本、中国および韓国が共有する漁業資源であるため、これらの近隣諸国がその2種のアンコウ類の資源の保護や適切な管理を行うための指針を協力して確立することが必要である。本研究はそれら課題を解決するための一助となるであろう。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