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Reproduction of cutlassfishes *Trichiurus* spp. from the South China Sea

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ABSTRACT: Cutlassfishes, *Trichiurus* Linnaeus, 1758, are the most important commercial marine fish species of China in terms of weight and they are found in all Chinese waters. However, no study has been conducted on the populations of *Trichiurus* in the South China Sea. The aim of this study was to investigate the reproduction of the populations of *Trichiurus* spp. in the South China Sea. In a 12 mo sampling period between December 1996 and November 1997, 1495 specimens of *T. lepturus* and *T. nanhaiensis* were collected from Hong Kong coastal waters. Spawning period and reproductive cycle were studied by checking the temporal profile of the Relative Gonadal Index/Gonosomatic Index, and by examining ovaries macroscopically and whole oocytes microscopically. All 3 methods provided similar results: the spawning periods of *T. lepturus* and *T. nanhaiensis* were March to June and April to August, respectively. Both species were found to practice group-synchronous spawning and mature females are capable of spawning more than once each spawning season. The mean preanal lengths at sexual maturity of *T. lepturus* and *T. nanhaiensis* females were 255 and 282 mm respectively. The sex ratios of both species were significantly different from 1:1 among different sampling months, and different age and size ranges.

KEY WORDS: Cutlassfish · Reproduction · Spawning season · Size at maturity · Sex ratio

INTRODUCTION

Cutlassfish, *Trichiurus lepturus* Linnaeus, 1758 is caught from all Chinese seas (Jiang et al. 1991) and is the most important commercial marine fish species of China in terms of weight (Luo 1991). Reproduction and recruitment are the major events in the life history of the fish and also are the main determinants of yield (King 1995). Numerous investigations covering most aspects of the reproduction of *T. lepturus* have been carried out in the past few decades (Table 1). However, research has focused on northern (East China Sea, Yellow Sea and Bo Hai) populations, and no study has been conducted on the South China Sea populations.

Trichiurus lepturus only spawns once in the Yellow Sea, from May to July (Chu 1982, cited in Lin 1985), while it has a very long spawning period, from April to October, in the East China Sea (Li 1982, Luo et al. 1982, 1983). The age at sexual maturity (T_m) of the Yellow Sea and the Bo Hai populations was about 3 yr old for females in the 1960s (Lin 1985). For the East China Sea female cutlassfish in 1963–1964, the T_m was about 1 yr old with the size being 240 mm (preanal length), which then decreased in 1979–1980 to about 7 mo old with the size being 200 mm (Luo et al. 1983). Similarly, the biological minimum size of females at first maturity was 238 mm in 1962 (Lin 1982), which decreased to about 170–180 mm in 1979–1980 (Luo et al. 1983).

The situation of cutlassfish populations in the South China Sea is further complicated by the fact that there are 3 species—*Trichiurus lepturus*, *T. nanhaiensis* Wang & Xu in Wang et al. (1992) and *T. brevis* Wang & You in Wang et al. (1992)—instead of 1—*T. lepturus*—as in the northern seas of China (Wang et al. 1992, 1993, 1994). Previous studies have shown that populations in the Bo Hai, the Yellow Sea and the East China Sea have suffered from serious overfishing (Lin 1985, Ye & Rosenberg 1991, Xu et al. 1994). The Bo Hai and the Yellow Sea cutlassfish fisheries have collasped

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Table 1. Summary of reproductive studies of *Trichiurus lepturus*

Country	Study area	Study period	Study items	Methods	Source
China	Yellow Sea and Bo Hai	1958-64	Egg and larva development	Artificial fertilization and plankton net collection	Sha et al. (1981)
China	East China Sea, Yellow Sea and Bo Hai	1952-57	Spawning ground and spawning season, age at sexual maturity, oocyte diameter and maturation stage	Gonosomatic index, survey	Misu (1964)
China	East China Sea	1963-64	Fecundity		Qiu & Jiang (1965)
China	East China Sea	1976	Fecundity		Li (1983)
China	East China Sea	1976-79	Fecundity		Li (1986)
China	East China Sea	1977-79	Maturation stage and spawning season, oocyte diameter	Gonosomatic index, macroscopic and microscopic examination	Li (1982)
China	East China Sea (north)	1977-80	Spawning season	Gonosomatic index and first otolith annular radius	Luo et al. (1982)
China	East China Sea	1979-80	Maturation stage and spawning season, oocyte diameter, size at sexual maturity	Macroscopic and microscopic examination	Luo et al. (1983)
China	East China Sea	1960-80	Prematuration		Lin (1982)
China	East China Sea	1980-81	Maturation stage and spawning season	Microscopic examination	Gong et al. (1984)
China	East China Sea	1976-79	Fecundity		Li (1988)
Japan	Suruga Bay	1965	Spawning season and maturation stage	Gonosomatic index, ova diameter	Kosaka et al. (1967)
Japan	Kii Channel	1972-74	Spawning season	Gonosomatic index	Sakamoto (1976)
Japan	Kumano-Nada	1978-79	Sex ratio, spawning season, fecundity, size at sexual maturity	Gonosomatic index and oocyte diameter	Suzuki & Kimura (1980)
Japan	Wakasa Bay	1981-83	Sex ratio and spawning season	Gonosomatic index	Munekiyo & Kuwahara (1984a)
Japan	Wakasa Bay	1982	Size at sexual maturity and fecundity		Munekiyo & Kuwahara (1988)
Japan	Tsushima waters	1967-87	Spawning season	Gonosomatic index	Hanabuchi (1989)
Japan	Ariake Sound	1961	Spawning season, egg and larva development	Macroscopic examination, artificial fertilization	Tsukahara (1961)
Korea	South-western waters	1965-70	Spawning season and area, age at sexual maturity	Eggs and larvae survey, gonosomatic index, egg diameter	Park & Hwang (1978)

and could only be harvested as bycatch (Lin 1985). However, the situation of the populations in the South China Sea remains unclear.

To evaluate the validity of the Gonosomatic Index (GSI) is crucial and, in fact, a prerequisite in employing this method to study reproduction (DeVlaming et al. 1982). However, this has not been addressed in previous studies (Misu 1964, Kosaka et al. 1967, Sakamoto 1976, Park & Hwang 1978, Suzuki & Kimura 1980, Li 1982, Luo et al. 1982, Munekiyo & Kuwahara 1984a, Hanabuchi 1989). In this study, gonad indices are validated and are utilised to estimate spawning periods.

In order to reveal the vital biological parameters of the South China Sea cutlassfishes and to prevent and/or mitigate the possible over-exploitation, a thorough study in the South China Sea is necessary. The objective of this study is to describe the reproductive cycle and to estimate the spawning period, the age and length at sexual maturity, and the sex ratios of cutlassfishes *Trichiurus* spp. from the South China Sea. Hopefully, the findings of this study will contribute to the development of an ecologically sustainable cutlassfish fishery as well as stimulating relevant studies of the natural resources in the South China Sea.

MATERIALS AND METHODS

In the 12 mo (December 1996 to November 1997) sampling period, 960 *Trichiurus lepturus* and 535 *T. nanhaiensis* were collected from commercial catches within Hong Kong coastal waters (about 12 nautical miles). Fishing methods included longlining, purse seining and bottom trawling. The freshly caught specimens were chilled onboard with crushed ice and transported to the laboratory. Specimens were identi-

fied using the diagnostic key of Wang et al. (1992, 1993); if frontal bone can be split laterally it is *T. lepturus*, otherwise it is *T. nanhaiensis*. Preanal lengths (from the tip of the lower jaw with the mouth closed to the middle of the anus; PL) were measured to the nearest mm. Bodies (gutted and ungutted) and ovaries were blotted dry and weighed to the nearest 0.01 g.

Reproductive cycle and spawning period. Three different examination methods were employed: (1) ovary examination, (2) whole oocyte examination, and (3) gonad indices (gonosomatic index and relative gonadal index).

(1) Ovaries were macroscopically staged using a scale modified from Li (1982), Luo et al. (1983) and Ni & Templeman (1985) (Table 2). Stage of ovarian maturity was assessed according to color, size and shape. The accuracy of the macroscopic staging of ovarian maturity was validated by comparing it with the findings from whole oocyte examination. The monthly profile of ovarian maturity was used to estimate the spawning period (Luo et al. 1983).

(2) Fresh, unfixed oocytes were examined microscopically shortly after dissection. Oocytes that had already undergone post-mortem autolysis were not used in the analysis. Oocytes were examined under a compound microscope at 40 to 100× and staged using the scale adapted from Li (1982), Luo et al. (1983), and Gong et al. (1984) (Table 2). The maturity stage of each ovary was classified according to the oocyte stage found in more than 50% of the ovarian area (adapted from Gong et al. 1984).

Preliminary analysis indicated that ovaries were at the same maturity stage throughout the length of the ovary. Subsequently, only oocytes from the central section of each ovary were retrieved and investigated. Monthly profiles of the stages of oocyte maturity were used to estimate the spawning period (Luo et al. 1983). Since Stage 3B oocytes were fully mature, they were grouped with Stage 4 oocytes as 'mature and spawning' whereas Stage 5 (spent) and Stage 6 (atresia) were grouped as 'spent'.

(3) Gonosomatic index (GSI = gonad wt/gutted wt × 1000) was used to quantify reproductive condition in *Trichiurus lepturus* (Table 1). However, the validity of GSI has not been evaluated in previous studies. The most important assumption of GSI is that it is independent of body size (DeVlaming et al. 1982). Pinpointing this problem, Erickson et al. (1985) introduced a new index called Relative Gonadal Index: RGI = $\alpha_i = G/W^{\beta_i}$, where G is gonad weight, W is gutted weight or other body measurements (e.g. body length), and α_i, β_i are the parameters of gonadal maturity stage i. α_i and β_i

Table 2. Macroscopic characteristics of ovaries and microscopic characteristics of whole oocytes of cutlassfishes, *Trichiurus* spp.

Stage	Classification	Ovary appearance	Oocyte microscopic appearance
1	Immature	Ovarian wall transparent, no egg can be seen. Ovary thread-like and short	Oocyte transparent and irregular or round shape. The nucleus occupies the bulk of the cell and oocyte is surrounded by a thin follicle layer
2A	Developing I	Ovary color cream to yellow, eggs, if present, hard to seen. Ovary about 50% length of ventral cavity	Oocyte is round; multiple nucleoli appear; lipid bodies appear around the nucleus while yolk vesicles are observed in the peripheral region during the initial stage. In later stage, yolk granules start to develop and are difficult to see
2B	Developing II		Vitellogenic oocyte: yolk vesicles decrease in number while yolk granules increase in size and number, and follicular layers increase in thickness
3A	Maturing I	Ovary yellow to orange color, opaque oocytes visible through epithelium. Ovary about 60–70% length of ventral cavity	Oocytes full of yolk granules which then coalesce to form yolk globules. Yolk globules start to aggregate at the central area and conceal the nucleus
3B	Maturing II		Yolk globules start to fuse together and oocytes become more transparent. Lipid bodies start to fuse to form larger droplets and become fewer. The nucleus migrates to the periphery
4	Spawning (ripe)	Ovary swollen, filled with hydrated oocytes visible through epithelium. Eggs in the oviduct transparent, can be extruded with gentle pressure. Ovary about 80% length of ventral cavity	Lipid bodies fuse with one another and become one large oil droplet. Nuclear envelope breaks down (germinal vesicle breakdown) and oocytes increase in transparency. Hydrated oocytes reach the maximum size and ready to spawn
5	Spent	Ovary translucent with pale violet color. Ovary shrunk and flaccid	Empty follicles (post-ovulatory follicles) are present
6	Atresia		Irregular shape, separation of the different follicular layers, change in appearance of the yolk, and breakdown of the outer membranes

can be estimated by applying least squares regression for the log-transformed model:

$$\ln(G) = \beta_i \ln(W) + \ln(\alpha_i)$$

Based on *t*-test results, β values for most ovarian maturity stages of *Trichiurus lepturus* and *T. nanhaiensis* (based on whole oocyte examination) were significantly different from 1. This indicates that GSI was not independent of body size and therefore was not applicable to the study of reproductive condition. The slopes of the log transformed model were homogenous among maturity stages of *T. lepturus* (ANCOVA, $F_{6,609} = 1.682$, $p > 0.12$). Hence, a pooled slope was estimated ($\beta = 1.470$). The intercepts among different maturity stages of *T. lepturus* proved to be significantly different (ANCOVA, $F_{6,615} = 449.326$, $p < 0.001$). If both slopes and intercepts are homogenous among different maturity stages, it indicates either a constant reproductive condition (gonadal weight or stage of development) or erroneous staging of gonadal development (Erickson et al. 1985). Thus, RGI = $G/W^{1.470} \times 1000$ was used for *T. lepturus* to investigate the monthly variation of ovarian development.

The slopes of the log transformed model differed significantly among maturity stages of *Trichiurus nanhaiensis* (ANCOVA, $F_{5,208} = 7.564$, $p < 0.001$). When preanal length was used to replace the gutted weight in the regression, the results were similar. Hence, RGI was not applicable for the collected specimens of *T. nanhaiensis* and GSI was chosen instead. The use of GSI might be justified by the fact that 75% of the specimens were within a reasonably narrow size range (PL = 330–440 mm) and 98% of the specimens were larger than the mean size at sexual maturity.

For all 3 methods mentioned above, only females equal to or larger than the size at sexual maturity were included in the analyses.

Size at sexual maturity. The size at sexual maturity (L_m) is defined as the length at which 50% of the fish are sexually mature (Ni & Sandeman 1984) and it can be derived by fitting a logistic curve to the proportion of sexually mature individuals by length: $P = 1/\{1 + e^{[-r(L - L_m)]}\}$ (King 1995). The equation was transformed to:

$$\ln[(1 - P)/P] = rL_m - rL,$$

where P is the proportion of sexually mature individuals (Stage 3A or above were considered as mature), r is the slope of the curve, L is the preanal length in mm and L_m is the mean preanal length at sexual maturity, which corresponds to $P = 0.5$. Coefficients were estimated by plotting $\ln[(1 - P)/P]$ against L; then L_m = intercept/slope (r). Females were grouped in 10 mm groups for estimating size at sexual maturity. For *Trichiurus lepturus*, only specimens caught during the reproductively active season (February to July) were included. However, due to scarcity of specimens of *T. nanhaiensis* (n = 249), the data from the entire year was used.

Sex and species ratio. A chi-square test was employed to study the temporal variation of sex ratio and sex ratio among different age and size ranges. For the temporal variation investigation, only specimens equal to or larger than the size at sexual maturity were included since juveniles were not collected in all months. For the analysis of sex ratio among different size ranges, specimens were grouped in 50 mm groups (Hanabuchi 1989). The ratio between the 2 species was also investigated.

RESULTS

Reproductive cycle and spawning period

Ovaries of both species at the same maturity stage are similar in appearance and size. Ovaries are paired and elongate in shape and attached to the body cavity by the dorsal mesentery. Left and right lobes are of equal length and are fused together but are separated laterally by a membrane. The monthly variation in macroscopic ovarian stage is illustrated in Fig. 1. *Trichiurus lepturus* spawned almost all year round and peaked from March to June while *T. nanhaiensis*

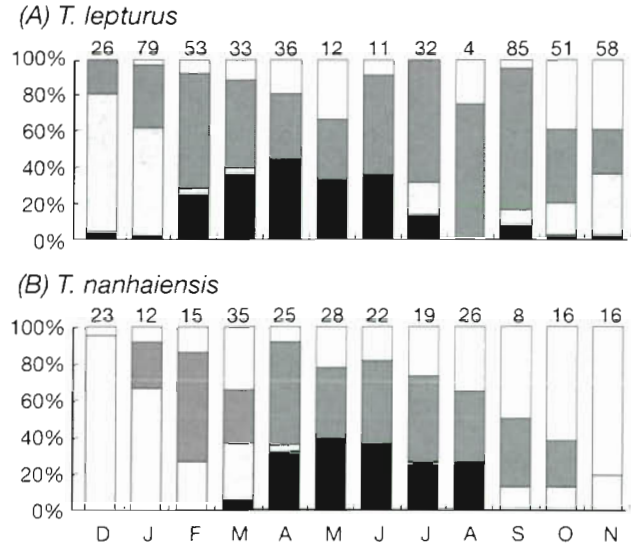

Fig. 1. Monthly variation in macroscopic ovarian stage of cutlassfishes *Trichiurus* spp. The *x*-axes are months of collection, *y*-axes are percentage of ovaries at different maturity stages, numbers on the top are sample sizes. Maturity stages: black, Stage 4 (ready to spawn); light grey, Stage 1–2 (previtellogenic and early vitellogenic); dark grey, Stage 3 (advanced vitellogenic); white, Stage 5 (spent). Maturity stages follow Table 2

spawned from March to August and peaked from April to August. Agreement between macroscopic gonad staging and whole oocyte staging was 84.3% for *T. lepturus* and 85.0% for *T. nanhaiensis*. Most of the discrepancy came from staging of spent gonads.

Whole oocytes were examined microscopically and the characteristics of each maturity stage are listed below:

Stage 1: Oocytes are transparent and pear- or round-shaped. The nucleus occupies most of the cell and a thin follicle layer surrounds the oocyte. During this stage both the chromatin nuclear and early perinucleolar stages occur. No Stage 1 oocytes were found in *Trichiurus nanhaiensis* during the collection period.

Stage 2A (Fig. 2A): Oocytes are round and have multiple nucleoli. The most obvious feature is perinucleolar nuclei. Both lipid bodies and the yolk vesicles (cortical alveoli) are difficult to identify. During this stage both the late perinucleolar stage and the yolk vesicle stage occur.

Stage 2B (Fig. 2B): Yolk granules are found in peripheral regions and appear as small opaque spheres when examined under a light microscope. This marks the beginning of vitellogenesis. Follicular layers composed of theca cell layer, granulosa cell layer and zona radiata increase in thickness. Nuclei are no longer observed because the yolk granules conceal them.

Stage 3A (Fig. 2C): As more yolk granules are incorporated, they coalesce to form yolk globules. Yolk globules then aggregate and occupy the entire central area of the oocytes. Follicular layers further increase in thickness.

Stage 3B (Fig. 2D): Centripetal yolk globules start to fuse together and oocytes become more transparent. Lipid bodies begin to fuse to form larger droplets and resulting in few numbers.

Stage 4 (Fig. 2E): Lipid bodies fuse with one another to form one large oil droplet. Oocytes become transparent and nuclei disappear (germinal vesicles breakdown). Hydrated oocytes reach maximum size and are ready to be spawned.

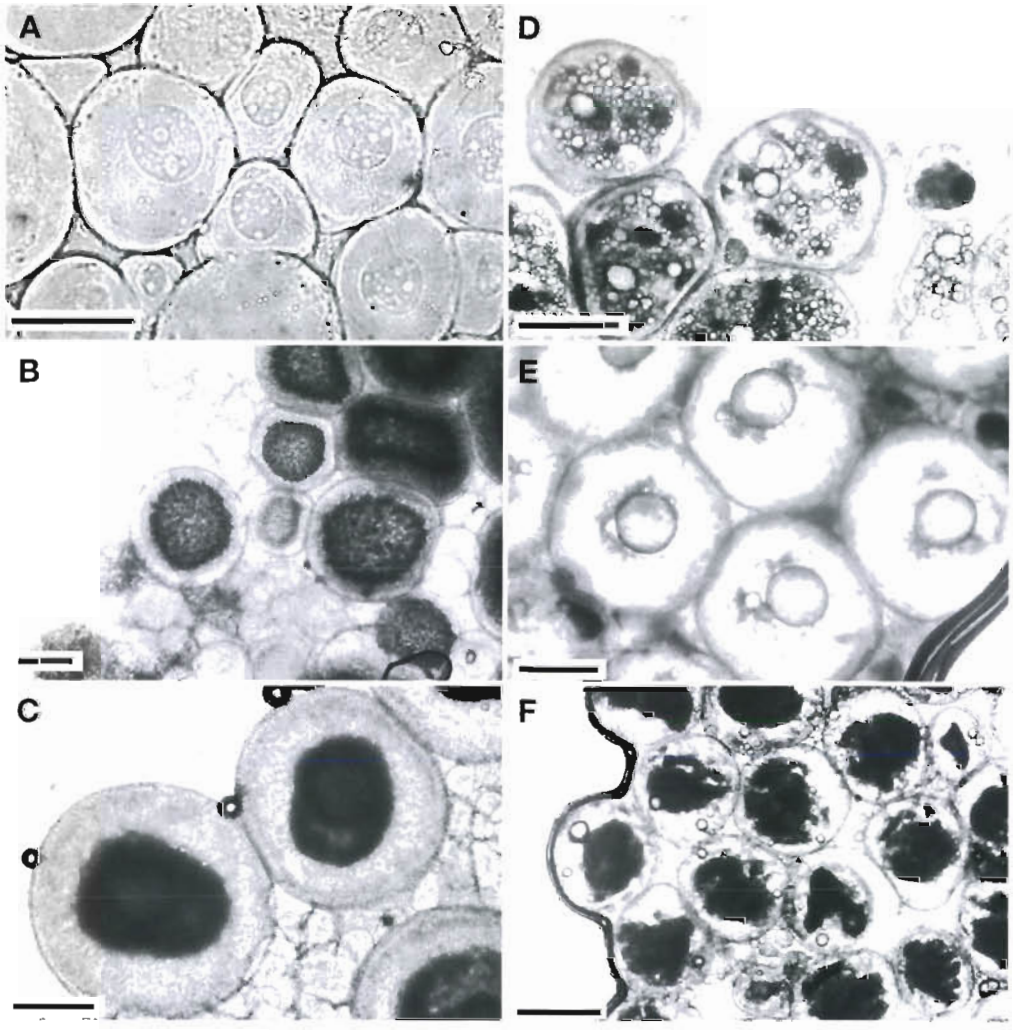

Fig. 2. Whole oocytes of cutlassfishes *Trichiurus* spp. at different stages of maturity. (A) Previtellogenic stage. Scale bar = 100 µm (200×). (B) Early vitellogenic stage. Scale bar = 200 µm (30×). (C) Late vitellogenic stage. Scale bar = 200 µm (40×). (D) Mature. Scale bar = 500 µm (20×). (E) Ripe. Scale bar = 500 µm (30×). (F) Atresia. Scale bar = 500 µm (30×). Maturity stages follow Table 2

Stage 5: Empty follicles occurring after spawning are difficult to identify by whole oocyte examination because of the rapid degeneration of post-ovulatory follicles. During early months of spawning, April to June, spent ovaries staged by ovary macroscopic examination contained oocytes at less advanced maturity stages. In this case, the ovaries were staged according to those normal oocytes. However, approaching the end of the spawning period, spent ovaries consisted mainly of atresic oocytes.

Stage 6 (Fig. 2F): Atresia (degeneration) seemed to only affect vitellogenic oocytes, i.e. oocytes at Stage 2B–3B. Atresic oocytes are characterized by separation of different follicular layers (e.g. zona radiata separates from granulosa cell layer), irregular shapes of oocytes, change in yolk appearances, and the breakdown of outer membranes.

In most cases, at least 2 populations of oocytes could be distinguished—a synchronous population of larger oocytes (more advanced in maturity) and a heterogeneous population consisting of oocytes at different and less advanced stages of maturity. This indicates that both species practice group-synchronous spawning (Wallace & Selman 1981). A monthly profile of the oocyte maturity stage is depicted in Fig. 3. Mature and ripe *Trichiurus lepturus* females were found almost all year round and their spawning peaked from March to June. The dip found in August might be due to low sample size (n = 4). Mature and ripe *T. nanhaiensis* females were found from February to October; their peak spawning period lasted from April to August.

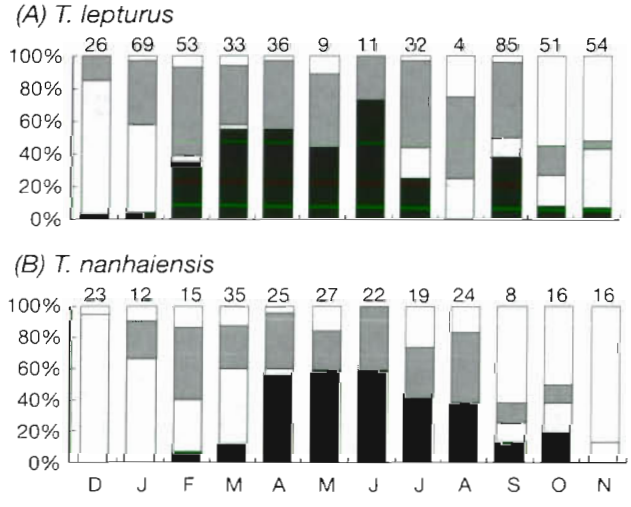

Fig. 3. Monthly profile of the whole oocyte maturity stage of cutlassfishes *Trichiurus* spp. The *x*-axes are months of collection, *y*-axes are percentage of ovaries at different maturity stages, numbers on the top are sample sizes. Maturity stages: black, Stage 3B and 4 (mature and spawning); light grey, Stage 1–2B (previtellogenic and early vitellogenic); dark grey, Stage 3A (advanced vitellogenic); white, Stage 5 and 6 (spent and atresia). Maturity stages follow Table 2

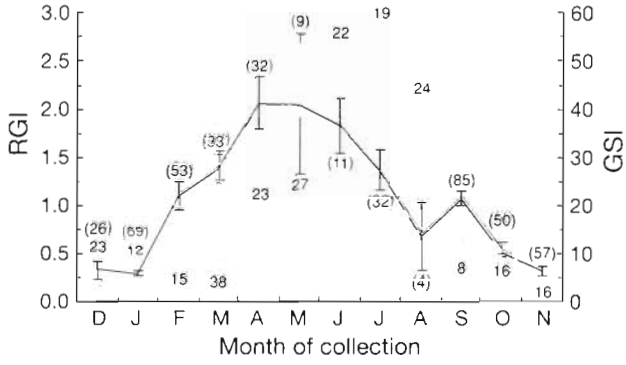

Fig. 4. Monthly variation in the gonad indices of female cutlassfishes *Trichiurus* spp. Black line: relative gonadal index (RGI) ± SE of *T. lepturus*, numbers in parentheses are sample sizes of *T. lepturus*. Grey line: gonosomatic index (GSI) ± SE of *T nanhaiensis*, numbers without parentheses are sample sizes of *T. nanhaiensis*

The monthly variation in the relative gonadal index (RGI) of *Trichiurus lepturus* females and in the gonosomatic index (GSI) of *T. nanhaiensis* females (Fig. 4) indicates that the peak spawning periods of *T. lepturus* and *T. nanhaiensis* were April to June and May to August respectively.

Size at sexual maturity

The results of regressions between $\ln[(1 - P)/P]$ and L are as follows:

Trichiurus lepturus: $\ln[(1 - P)/P] = 0.0227L - 5.785$ ($n = 319$, $R^2 = 0.746$, $p < 0.001$);

T nanhaiensis: $\ln[(1 - P)/P] = 0.0126L - 3.539$ ($n = 249$, $R^2 = 0.427$, $p < 0.05$).

Mean preanal lengths at sexual maturity (L_m) of *T. lepturus* and *T. nanhaiensis* females were 255 mm (8.5 mo old; estimated using von Bertalanffy growth equations derived from a growth study [Kwok 1998]) and 282 mm (12 mo old; estimated using von Bertalanffy growth equations derived from a growth study [Kwok 1998]) respectively (Fig. 5). The minimum preanal length at sexual maturity of *T. lepturus* females was 185 mm while it could not be estimated for *T. nanhaiensis* females due to lack of juveniles.

Sex and species ratio

For both species, a chi-square analysis indicated significant deviation from a 1:1 sex ratio among different months (*Trichiurus lepturus*: $\chi^2_{11} = 263.37$, $n = 595$, $p < 0.001$; *T. nanhaiensis*: $\chi^2_{11} = 21.07$, $n = 525$, $p < 0.05$), different ages (*T. lepturus*: $\chi^2_5 = 247.13$, $n = 832$, $p <$

0.001; *T. nanhaiensis*: $\chi^2_5 = 22.91$, n = 523, $p < 0.05$) and different size ranges (*T. lepturus*: $\chi^2_7 = 308.69$, n = 938, $p < 0.001$; *T. nanhaiensis*: $\chi^2_5 = 41.72$, n = 535, $p < 0.05$). When only the spawning period was considered (spawning period for *T. lepturus* and *T nanhaiensis* was March to June and April to August respectively), the sex ratio of *T. nanhaiensis* did not significantly deviate from the ratio of 1:1 (*T. lepturus*: $\chi^2_3 = 35.72$, n = 131, $p < 0.001$; *T. nanhaiensis*: $\chi^2_4 = 5.9$, n = 237, $p > 0.37$). For *T. nanhaiensis*, classes of larger sizes (PL > 400 mm) and older ages (age ≥5) were comprised mainly of female fish. For *T. lepturus*, however, females outnumbered males for most size and age classes. Furthermore, the 2 species mixed together throughout the whole collection period and the overall ratio was 1.79:1 (*T. lepturus*:*T. nanhaiensis*) which was significantly different from the ratio 1:1 ($\chi^2_1 = 340.86$, n = 1495, $p < 0.001$).

DISCUSSION

Reproductive cycle and spawning period

The accuracy of macroscopic staging of ovaries was found to be reasonably high (about 85%) when compared with the results of whole oocyte examination. Most of the discrepancy came from the staging of spent ovaries. After the first spawning, the spent ovaries contain oocytes at less advanced maturity stages, which will develop and contribute to another spawning. This can only be revealed by whole oocyte examination. Ovary macroscopic examination is less time consuming but it requires some experience and sometimes the staging can be quite subjective and uncertain. Furthermore, macroscopic examination of ovaries does not permit us to address other topics such as detailed descriptions of development stage, atresia, and minimum size at sexual maturity (West 1990).

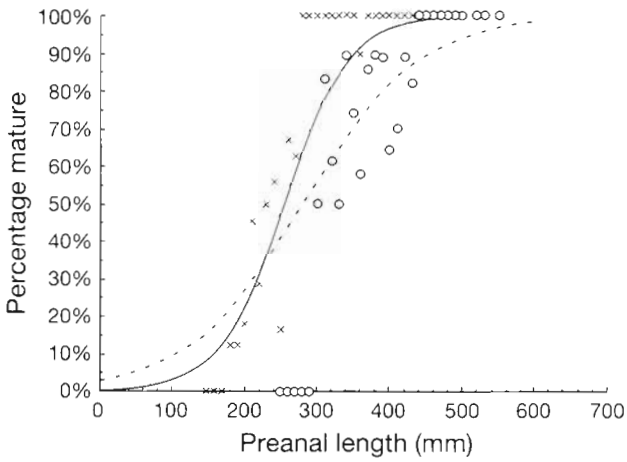

Fig. 5. Proportion mature versus preanal length of female cutlassfishes *Trichiurus* spp. Solid line (regression line) and crosses (raw data): *T. lepturus*. Dotted line (regression line) and circles (raw data): *T. nanhaiensis*

In comparison with macroscopic ovary observations, the whole oocyte examination was more accurate in staging the development of ovaries. The accuracy is attributed to the characteristics of the oocytes of these species—for example the clarity of the oocyte and its content, fusion of yolk globules and subsequent increased transparency, an ultimate large oil droplet and oocyte expansion induced by hydration. Unlike the histological study, this method failed to identify some stages and features: chromatin nucleolar stage; yolk vesicle (cortical alveoli); structure of follicular layer; nucleus after vitellogenesis, and its subsequent migration and breakdown. Another difficulty associated with the whole oocyte examination method is the identification of empty follicles which indicate recent spawning. Identification of the spent/spawned stage, however, can be assisted by macroscopic examination of the ovary, which provides a more discrete appearance: spent ovaries are pale violet in color, shrunk, and flaccid. During early months of the spawning period, April to June, spent ovaries staged by gonad macroscopic examination contained oocytes at less advanced maturity stages. These oocytes probably would ripen in 1 to 2 mo (Li 1982, Gong et al. 1984) and contribute to a second spawning.

This is the first time that the gonad indices have been validated in studying the reproduction of cutlassfish. In this study, GSI was proven inappropriate, at least for the specimens collected. When validated, nevertheless, gonad indices (RGI and GSI) can be good and objective indicators of seasonal trends for gonad development (West 1990). This was supported by the fact that findings from gonad indices agreed with the ovary examination and whole oocyte examination in this study. In this study, both GSI and RGI were found inapplicable for *Trichiurus nanhaiensis*. In order to compare the gonad indices monthly profile of both species, GSI was chosen for *T. nanhaiensis*. Because the majority of the specimens were within a reasonably narrow size range, the size dependent effect of GSI was reduced. In fact, the result agreed with those from ovary examination and whole oocyte examination.

In the East China Sea, *Trichiurus lepturus* possesses a protracted spawning period (April to October). This is because the East China Sea populations are composed of 2 brood stocks, i.e. spring-summer spawners and autumn spawners (Li 1982), and the former one might spawn twice per year (Li 1982, Gong et al. 1984). However, there is only 1 spawning population per species in this study area (Kwok 1998). Furthermore, spawning season may vary from year to year (El-

Haweet & Ozawa 1996). In the South China Sea, the spawning season is also very long, from February to October (from this study). This agrees with Chen & Liu (1982). The spawning periods derived from the 3 different methods are very similar. Based on whole oocyte examination, both species may spawn twice in the same spawning season. This can explain why cutlassfishes demonstrate a protracted spawning period in the South China Sea. In general, the South China Sea cutlassfishes (in this study) spawn a little earlier than their northern counterparts. This may be due to the fact that the South China Sea has a warmer seawater temperature.

Size at sexual maturity

The decline in the age and size at sexual maturity and the biological minimum size of females at first maturity in the northern seas of China might have been a result of heavy exploitation since size selective fishing would favor early maturity (Smith 1994). However, temporal variation of size and/or age at sexual maturity cannot be evaluated for the South China Sea populations due to the lack of historical data. In this study, the sizes of both species at sexual maturity are larger than those of their northern counterparts. This may be due to light fishing pressure or differences among populations. Nevertheless, the delineation of sexually mature individuals and the estimation method employed may be different, rendering the comparison less accurate. In this study, *Trichiurus lepturus* mature sexually at shorter lengths (PL) and earlier than *T. nanhaiensis*. Both species are capable of spawning in the year after hatching.

Sex and species ratio

In general, the number of female cutlassfish increased with size and age, which was also the case for cutlassfish in the northern seas (Suzuki & Kimura 1980, Hanabuchi 1989). The growth coefficients (k) are significantly different between sexes for both species; *Trichiurus lepturus* males possess lower growth coefficient than females, while the opposite is true for *T. nanhaiensis* (Kwok 1998). Therefore, growth rate cannot explain the skewed sex ratio. The sex ratio deviated from 1:1 for the whole study period. Whether these deviations (sex ratio among different ages, size ranges and months) were related to spatial variation as demonstrated by Munekiyo & Kuwahara (1984b) and/or temporal variation remains a question for further investigation. An understanding of the spatial distribution and abundance (or relative abundance) of both *T. lepturus* and *T. nanhaiensis* are a prerequisite in revealing the species ratio.

Recommendation

The findings of this study provide some vital statistics useful in conducting the stock assessment. However, further investigations are needed to add to our understanding of the reproduction of cutlassfishes *Trichiurus* spp. from the South China Sea. Future research may include (1) the histological examination of male fishes to determine the reproductive cycle, which has not been investigated before even for the northern populations; (2) estimation of the relative fecundity and testing the correlation with the recruitment model; and (3) conducting artificial fertilization and rearing the larvae in captivity to find out whether the 2 species can cross-breed, and studying the early life history and development.

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