

Reproductive Biology and Sexual Maturity of Female Jack Mackerel, *Trachurus declivis* (Jenyns), in Eastern Tasmanian Waters

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Abstract

The reproductive biology of female jack mackerel, *Trachurus declivis*, was determined from fish sampled from November to March, 1987 to 1991, from commercial purse-seine catches and research trawling. Histological, microscopic and macroscopic techniques were used to examine the ovaries of *T. declivis*. Half of the female fish were sexually mature (Stage 3) at 31.5 cm fork length, and all fish were mature by 37.0 cm fork length. Oocyte development and pre-ovulatory atresia were similar to those of other species of the same genus. The size–frequency distribution of oocyte diameter was polymodal, indicating serial spawning. Atresia was present in all oocyte stages studied, with its occurrence increasing with increasing stage of development. Despite sampling during the spawning season, post-ovulatory follicles were not found, possibly owing to rapid reabsorption or to spawning fish not being vulnerable to the sampling gear.

Introduction

Jack mackerel, *Trachurus declivis*, is a pelagic species found in the coastal waters of southern Australia and New Zealand. In Australia, the species is distributed from Shark Bay in Western Australia around to the central New South Wales coast, including waters off Tasmania (Lindholm and Maxwell 1988). *T. declivis* supports a substantial fishery in south-eastern Tasmanian waters, with landings peaking at almost 40 000 t in the 1986–87 season (Williams *et al.* 1987). The fishery is based on large seasonal surface and subsurface schools that appear on the shelf on the eastern coast of Tasmania between November and May (Williams *et al.* 1987). Schools are targeted by purse-seine vessels operating predominantly in inshore waters.

Reproductive biology and oocyte development have been studied in several *Trachurus* species, namely *T. symmetricus* (MacGregor 1976), *T. trachurus* (Macer 1974; Hecht 1990), *T. murphyi* (Kaiser 1973; Andrianov 1985) and *T. japonicus* (Chigirinskiy 1970). These studies found *Trachurus* species to be serial spawners, except that Kaiser (1973) reported a single spawning habit for *T. murphyi*. The presence of atresia has been documented only in *T. trachurus* (Macer 1974).

Through seasonal gonadal staging, *T. declivis* is known to spawn during spring in New South Wales waters (Maxwell 1979) and during summer in the Great Australian Bight (Stevens *et al.* 1984) and off Tasmania (Webb 1976). The results detailed here are part of an ongoing programme investigating the biology of *T. declivis* in eastern Tasmanian waters. In this paper, we present data on oocyte development, size at sexual maturity, and atresia in *T. declivis*. The implications of the reproductive biology of this species for estimates of annual fecundity are discussed.

Materials and Methods

Sampling Regime

Specimens of *Trachurus declivis* were collected from commercial purse-seine vessels and the FRV *Challenger*, which were using demersal trawling gear. Most fish were caught on the eastern coast of Tasmania (Fig. 1), between November and March, 1987 to 1991. A maximum of 20 fish were sampled at random from commercial or research catches for histological purposes. Up to 50 fish from commercial catches were collected, measured, and staged macroscopically for estimates of length at maturity. The fork length (FL) of each fish was measured to the nearest centimetre below. Fish were sexed and their macroscopic gonadal stages determined (Table 1) according to criteria modified from Blackburn and Gartner (1954). One or both ovaries were fixed for a minimum of two weeks in 4% formaldehyde in sea water buffered with 4% β -glycerophosphate.

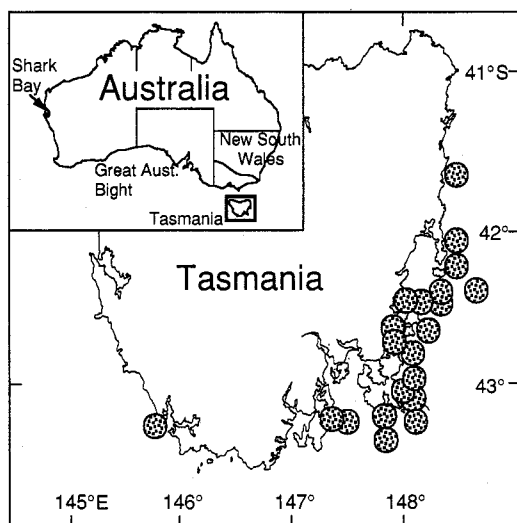


Fig. 1. Study area. Circles show distribution of catches subsampled for analysis.

Length at Maturity

Length at first sexual maturity ($LD_{0.50}$) was defined as the fork length at which 50% of females collected over the spawning season were mature. Ovaries were considered mature if their most advanced oocytes were yolked or ripe (the equivalent of Stage 3 or greater). We examined 1259 ovaries from fish subsampled from commercial catches during the known spawning season, December to March (Jordan, unpublished data). Confidence limits (CL) for proportions were calculated for the data (Zar 1984, p. 378), then fitted with a logistic curve in GENSTAT, using a 'logit link function'. $LD_{0.50}$, $LD_{0.25}$ and $LD_{0.75}$ values were calculated with 99% confidence limits.

Histology

Sections of ovary 5 mm thick were placed in plastic cassettes and soaked in 70% ethanol plus 10% glycerol for a minimum of three days before being processed. A Tissue-Tek vacuum infiltration processor was used in a process based on ethanol, toluene and Paraplast-Plus (Drury and Wallington 1973). The sections of material were blocked in paraffin wax, cut at thicknesses of 6 μ m, and stained in Harris' haematoxylin and eosin.

In many studies, no significant differences in oocyte frequency distribution have been found between right and left ovaries (Laroche and Richardson 1980; DeMartini and Fountain 1981; West 1990). However, average oocyte size may vary along the length of the ovary (West 1990). To test for differences in oocyte size within the ovary, five to ten sections from each of three ovaries were used for comparison. No significant difference in average oocyte size was found between transverse sections in the ovaries (analyses of variance: Ovary 1, $F=2.64$, d.f.=(4, 35), $P>0.05$; Ovary 2, $F=3.29$, d.f.=(7, 71), $P>0.05$; Ovary 3, $F=2.858$, d.f.=(7, 72), $P>0.05$). Therefore, random transverse sections were taken for all gonads used histologically and microscopically.

Table 1. Microscopic, macroscopic and histological staging criteria used for *Trachurus declivis*

Stage	Category	Microscopic histology ^A	Macroscopic ovary ^B	Microscopic oocyte ^C
1	Virgin	<i>Chromatin nucleolar</i> : Clear, spherical nucleus surrounded by a thin layer of cytoplasm. No nucleolus visible.	Small strap with rounded edge, less than $\frac{3}{4}$ of body cavity. Pink, firm texture.	<i>Unyolked</i> : Spherical transparent bodies.
2	Maturing virgin	<i>Perinucleolar</i> : Thick, homogeneous cytoplasm around a light nucleus containing few to many peripheral nucleoli. Yolk vesicle may be apparent.	Virgin—at least $\frac{3}{4}$ of body length, pink and glassy. Recovering—as long as body cavity, bloodshot and flabby at posterior.	<i>Unyolked</i> : Spherical transparent bodies.
3	Developing	<i>Yolk vesicle formation</i> : Yolk vesicles apparent in cytoplasm, increasing in size and number with development. Zona radiata thickens, stains pink with haematoxylin and eosin.	Almost length of body cavity, opaque and becoming yellow. Ova not discernible.	<i>Partially yolked</i> : some granular nuclear material visible, becoming darker with increased size but not opaque.
4	Late developing	<i>Yolk granular stage</i> : Evenly distributed and uniform appearance of yolk vesicles, oil vesicles and eosinophilic yolk granules in cytoplasm. Peripheral nucleolus around a distinct nuclear membrane. Aggregation of oil vesicles in late stage.	Full length of body cavity, opaque and yellowish pink. Ova discrete.	<i>Yolked</i> : Opaque bodies. Yolk surrounded by a translucent vitelline border.
5	Ripe	<i>Nuclear migration and yolk fusion</i> : Coalescence of yolk granules to form uniform 'plates'. Migration of nucleus to periphery of cytoplasm, visible nuclear material, and dissolution of nuclear membrane.	Full length of body cavity and swollen, occupying all available space. Ovary and ova becoming transparent.	<i>Nuclear migration</i> : Parts of oocyte become translucent as yolk coalesces. <i>Ripe</i> : Large translucent bodies.
6	Running ripe	<i>(Pre-)Ovulation</i> : Hydration of cell, uniform pink-staining yolk. String-like appearance of thecal cells.	Eggs express with slight pressure. Ovary pinkish, clear and granular.	
7	Spent	<i>Spent</i> : Occurrence of recent post-ovulatory follicles.	Slack and bloodshot. Few residual oocytes present.	

^A Adapted from West (1990).^B Adapted from Blackburn and Gartner (1954).^C Adapted from Davis and West (1993).

Histological oocyte developmental stages were assigned (Table 1) based on terminology defined by Yamamoto (1956) and staging criteria from West (1990). Only oocytes that were sectioned through the nucleus were included in oocyte diameter measurements.

Wallace *et al.* (1987) and West (1990), in reviewing oocyte development in teleosts, found that classification of the most advanced oocyte type presents an accurate indication of gonadal stage. This procedure was used for histological gonad staging.

Atretic oocytes were identified by the presence of cuboidal hypertrophic granulosa cells (Hunter and Macewicz 1985a) rather than columnar follicle cells in a convoluted structure characteristic of atretic post-ovulatory follicles (Hunter and Goldberg 1980). Gonads were classified according to the presence or absence of atretic oocytes, and the proportions of ovaries at Maturity Stages 2, 3 and 4 that had atretic oocytes were calculated. Atresia in ovaries at Stages 1, 5 and 6 was not analysed owing to the small numbers of gonads collected.

Size-Frequency Distributions

Size-frequency distributions of oocytes from ovaries in Stages 2 to 5 were obtained by teasing apart an ovarian lamella and examining the oocytes in water under a stereomicroscope, using transmitted light and bright-field illumination. The ovarian lamella was removed from a 1-cm-thick transverse section of the gonad. Oocyte diameter was measured as the maximum diameter of the oocyte in a random orientation. Whole oocytes were classified (Table 1) according to Davis and West (1993).

Results

Length at Maturity

Ovaries were considered mature if macroscopic examination showed that the oocytes had entered vitellogenesis (Stage 3). A logistic curve fitted to a plot of percentage of mature females against length (Fig. 2) gave an $LD_{0.50}$ value of 31.5 cm FL (31.0–32.0 cm, 99% CL). $LD_{0.25}$ and $LD_{0.75}$ values were calculated as 29.6 cm FL (29.1–29.9 cm, 99% CL) and 33.4 cm FL (33.0–34.0 cm, 99% CL), respectively. All females larger than 37.0 cm FL were mature, with the smallest fish in vitellogenesis being 23.4 cm FL.

Histological Ovarian Development

Oocytes less than 35 μ m in diameter constitute the reservoir of oocytes that are present year-round in active, as well as non-active, ovaries. The following descriptions refer to the oocyte stage rather than the gonadal stage, as shown in Table 1.

Histological development of oocytes in *Trachurus declivis* is described in Fig. 3. No chromatin nucleolar cells were noted in a single juvenile fish examined (14 cm FL), whose ovary consisted of ovigerous folds (lamellae) with a well developed blood supply. Only one section showing yolk fusion was noted, and no sections showing migration of the nucleus towards the periphery were observed. Very few running ripe (Stage 6) *T. declivis* specimens

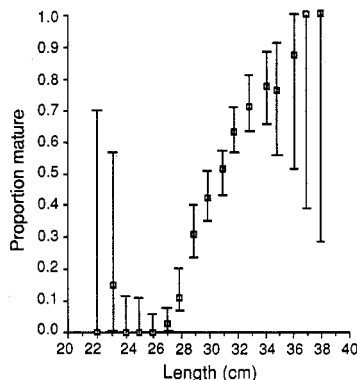


Fig. 2. Proportions of mature females by 1-cm length classes ($\pm 95\%$ confidence limits) as determined from data collected at the height of the spawning season.

have ever been sampled in the fishery, so no histological information is available for this stage. The final stages of oocyte maturation are often difficult to follow in histological material because of the shrinkage and distortion of cells during processing and the loss of oocytes from the ovarian follicle during handling.

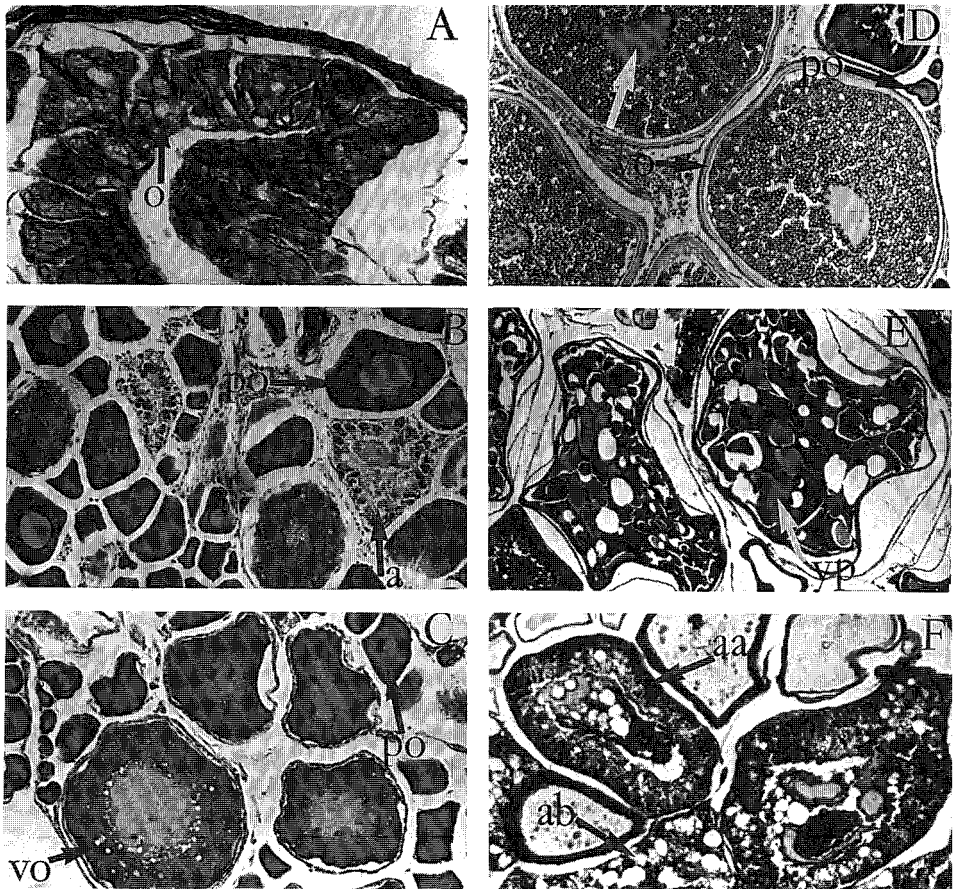


Fig. 3. Photomicrographs showing the development of oocytes stained with haematoxylin and eosin (H&E). (A) Stage 1—Chromatin nucleolus; white spherical chromatin nucleolar bodies (o) are surrounded by small, dense, dark-staining blood vessels. A thin layer of cytoplasm, not apparent in the photograph, surrounds the nucleus. (B) Stage 2—Perinucleolar; the healthy pre-vitellogenic oocyte (po) shows an oval nucleus with few peripheral nucleoli. The cytoplasm stains a dense, uniform dark purple with H&E. Microvilli may give the cytoplasm a granular appearance. Oocyte diameter 35–85 μm . Atresia may also occur in perinucleolar oocytes (a). (C) Stage 3—Yolk vesicle formation; the vitellogenic oocyte (vo) shows an increase in the size and number of peripheral nucleoli in the nucleus. Vesicles appear within the cytoplasm, and the zona radiata broadens to a wide, pink band with H&E. Oocyte diameter ranges from 100 to 130 μm , much larger than the pre-vitellogenic oocyte (po). (D) Stage 4—Yolk granular stage; eosinophilic yolk granules are uniform in size and consistency in the cytoplasm of the yolk granular oocyte (vo). Lampbrush chromosomes (c) are visible as evenly dispersed rods throughout the centre of the nucleus. A pre-vitellogenic oocyte (po) is visible. Oocyte diameter 250–480 μm . (E) Stage 5—Nuclear migration and yolk fusion; the nuclear membrane has dissolved, releasing the nuclear material, and the yolk granules or lipid droplets have coalesced to form yolk plates (yp). The irregular shape of the outer membrane is an artifact of processing. (F) Atresia—a freshly atretic oocyte (aa) has large cuboidal cells around the periphery, whereas an older atretic oocyte (ab) shows little differentiation of the peripheral cells from the phagocytosed interior.

Occurrence of Atresia

Pre-ovulatory atretic oocytes in *T. declivis* can be recognized by their irregular cell shape, breakdown of the granulosa, hypertrophy of the cuboidal cells (theca) around the periphery, and degradation of the interior inclusions (Hunter and Macewicz 1985a). This process occurs possibly by phagocytosis (Davis 1977), as seen in Fig. 3F. Gonads with atretic oocytes were noted in all ovarian maturity stages studied, with higher occurrence in the later stages (Table 2). Within the gonad, the percentage of atretic oocytes increased with increasing stage of development. In Stage 2 and 4 gonads atresia occurred predominantly in the most developed oocytes, whereas in the Stage 3 gonad atresia mostly occurred as advanced reabsorption of yolked oocytes. Because the cells were not viable, the gonad has been classified as still being Stage 3. No post-ovulatory follicles were noted in any gonads.

Table 2. Incidence of atresia within and between gonads

Stage	Atretic gonads (%)	Atretic oocytes (%)	Predominant atretic stage	Number of gonads examined
2	58.3	5.17 ± 1.99	2 (100%)	12
3	60.0	9.40 ± 1.74	3 (20%) 4 (80%)	15
4	64.9	10.13 ± 2.16	4 (100%)	37

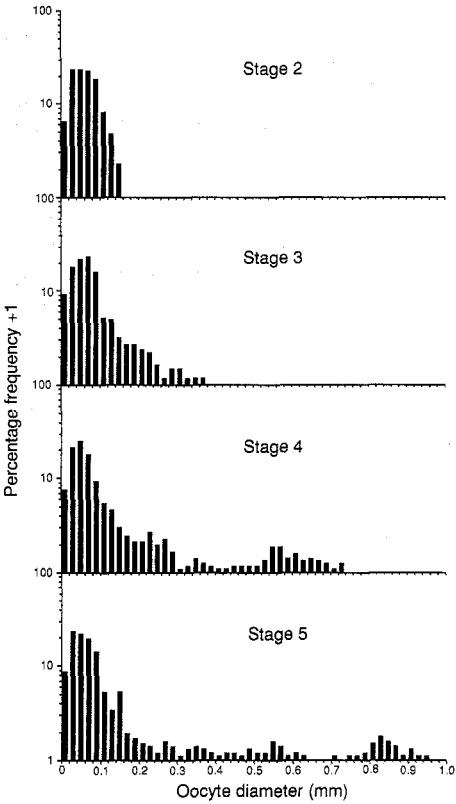


Fig. 4. Oocyte frequency distributions by gonadal stage and 0.02-mm diameter classes, representing the developmental sequence of maturation.

Ovarian Maturation

The size-frequency distribution of oocytes in ovaries shows the developmental sequence of maturation (Fig. 4). Oocyte diameters clearly show polymodal distribution, with peaks corresponding to size ranges shown in the macroscopic stages, with some overlap between stages. Values (mm) for the mean, s.d. and range were as follows: unyolked oocytes 0.08 ± 0.04 ($0.02-0.24$); with a visible yolk 0.24 ± 0.05 ($0.16-0.38$); yolked 0.54 ± 0.12 ($0.28-0.74$); and oocytes with a migratory nucleus 0.87 ± 0.05 ($0.74-0.98$). The presence of all oocyte stages in Stage 5 (ripe) ovaries represents asynchronous oocyte development, indicating that *T. declivis* is a serial spawner. However, it is not possible to predict the number of spawnings from modes in the size-frequency distribution (DeMartini and Fountain 1981) because there may be continuous recruitment of oocytes throughout the season.

Discussion

Length at Maturity

The smallest *Trachurus declivis* specimen that contained yolked oocytes (Stage 3) was 23.4 cm FL. Stevens *et al.* (1984), using a similar (Stage 3) but purely macroscopic criterion, estimated that *T. declivis* from the Great Australian Bight attains sexual maturity at lengths of 16–18 cm FL. The fact that fish from this region are known to be a different stock from those in eastern Tasmanian waters (Lindholm and Maxwell 1988) may also account for some of the difference.

Webb (1976) found that the majority of *T. declivis* specimens larger than 27 cm FL were mature, which is lower than our $LD_{0.50}$ value of 31.5 cm FL. Webb (1976) used a criterion of all fish at macroscopic Stage 2 and above being sexually mature, which may have lowered his mean maturity estimates. Vitellogenesis (Stage 3) is a more accurate and more frequently used indication of sexual maturity (DeMartini and Fountain 1981; Andrianov 1985; Hecht 1990), which suggests that our estimates are a closer estimation of size at sexual maturity.

The $LD_{0.25}$ and $LD_{0.75}$ values (29.6 cm FL and 33.4 cm FL) indicate a broad range of sizes at which sexual maturity occurs. Variation in body size at first sexual maturity is a feature common to serial spawners and to fishes in general (Nikolskii 1969). Although the logistic curve has provided tight 99% confidence limits around the $LD_{0.50}$ value, there is significant residual deviance indicating binomial error. There are two possible upward biases for this error, one being the discontinuity of the data due to restrictions in the sampling regime and the other being the ability of mature fish to rapidly reabsorb the gonad through atresia and hence to appear to be immature.

Sampling bias may have occurred because fish for this analysis were sampled exclusively from the commercial fishery. Williams *et al.* (1987) report that the mean length of *T. declivis* caught by the fishery decreases markedly during the spawning season, postulating that this results from mature fish moving out onto the shelf break to spawn, reducing their vulnerability to the fishery. However, the presence of mature fish in the fishery at this time suggests that there may be some movement of fish between the shelf break and inshore waters during the spawning season. Hecht (1990) suggests that *T. trachurus capensis* also moves to the shelf break to spawn. Andrianov (1985) noted a marked decrease in commercial catches of spawning or ripe *T. murphyi* during the spawning season, suggesting that there is migration of the spawning population away from the fishery at this time.

Estimates of length at maturity for other *Trachurus* species vary considerably. Hecht (1990) estimates an $LD_{0.50}$ value of 32.0 cm total length (TL) for *T. trachurus capensis*, stating that all fish were mature by 36.0 cm TL. Kerstan (1985) estimates the $LD_{0.50}$ value for *T. trachurus* to be 25.4 cm TL; however, he does not state the criteria used to determine maturity. Andrianov (1985) reports that more than 50% of *T. murphyi* females are mature at 39–42 cm FL.

Ovarian Development

Histologically, the process of oocyte development in *T. declivis* ovaries is similar to that of other *Trachurus* species such as *T. murphyi* (Andrianov 1985) and *T. trachurus* (Macer 1974). The presence of oocytes at different growth phases in single histological sections confirms the asynchronous nature of oocyte development.

Peaks in oocyte diameter do not correlate closely with histologically recognizable stages of oocytes but do coincide with visual staging of whole oocytes. Davis (1982) found that histologically sectioned oocytes were, on average, 13% smaller than oocytes preserved in formaldehyde. Macroscopic gonadal staging should be used in conjunction with histology to verify staging techniques.

Atresia

The function of reabsorption of residual oocytes after spawning is to remove unwanted material, but the reason for pre-ovulatory degradation is not well understood (Macer 1974), although it may be related to environmental and dietary factors (Hunter and Macewicz 1985a).

In *T. declivis*, pre-ovulatory atresia was most common in oocytes with advanced yolk formation (Stage 4), but less advanced oocytes were also affected. Other authors have found that atresia is more common in yolked than unyolked oocytes (Hunter and Macewicz 1985a). Our results are similar to those for *T. trachurus* (Macer 1974), which also showed variability between oocyte batches and stages. *T. declivis* showed atresia in oocytes from Stage 2 gonads, which may imply that the gonads are able to be reabsorbed at any developmental stage. However, Macer (1974) found that in *T. trachurus* atresia occurred only in yolked oocytes. In the serial spawner *Engraulis mordax*, the rate of atresia was found to be influenced primarily by food ration, stage of energy reserves, and timing of the reproductive cycle (Hunter and Macewicz 1985a). The fact that atresia occurred predominantly in yolked (Stage 4) oocytes of *T. declivis* gonads may indicate greater sensitivity at this stage to these changing conditions.

To obtain a quantitative assessment of oocyte atresia, it is necessary to sample throughout the spawning season over a range of size classes because rates of atresia are influenced by seasonal, biological and environmental factors (Hunter and Macewicz 1985a). Although it has not been possible to make such an assessment for *T. declivis* from the present incomplete data, it is important to study the implications of atresia. Its effect on fecundity may be underestimated, because the duration of atretic stages is short and small standing stocks of atretic oocytes could be an indication of a high loss rate over the entire spawning season (Hunter and Macewicz 1985a).

Post-ovulatory follicles are rapidly reabsorbed in a number of temperate species, including *Engraulis mordax*, which reabsorbs post-ovulatory follicles to a form that are indistinguishable from atretic follicles within 48 h (Hunter and Goldberg 1980). No structures that could positively be identified as post-ovulatory follicles were noted in *T. declivis*. Several factors could be influencing these results. Firstly, because fish are thought to spawn on the shelf break, as suggested by Williams *et al.* (1987), it is likely that post-ovulatory follicles are reabsorbed by the time the fish are vulnerable to the inshore commercial fleet. Secondly, a relatively small portion of the oocytes is released at any one time, suggesting that unless gonads are sampled frequently the probability of observing post-ovulatory follicles is low (Macer 1974). Research trawling on the shelf break may also undersample the spawning population because jack mackerel are able to avoid trawling gear at normal trawling speeds (3.0 kn) (Jones 1990), the speed used in the present study.

The lack of post-ovulatory follicles appears to be common in other *Trachurus* species. Empty follicles were scarce in both *T. trachurus* (Macer 1974) and *T. murphyi* (Andrianov 1985), resulting from rapid resorption of follicles, low frequency of samples, and reduced availability of spawning fish.

Reproductive Strategy

T. declivis has gonads typical of multiple spawning fish, with asynchronous oocyte development (oocytes in many stages of development) occurring simultaneously in reproductive active ovaries (Wallace and Selman 1981). Ovarian development was similar to that of other serially spawning fish as described by Hunter and Macewicz (1980), Wallace and Selman (1981) and West (1990). Distributions in oocyte diameter similar to that for *T. declivis* have been described for *T. trachurus* (Macer 1974; Hecht 1990), *T. japonicus* (Chigirinskiy 1970) and *T. symmetricus* (MacGregor 1976). Kaiser (1973) reported a single spawning habit for *T. murphyi* in Chilean waters, but more recently Andrianov (1985) found the same species to have a prolonged spawning season on the Peruvian shelf, possibly spawning in batches, but there was no evidence of a polymodal distribution in oocyte diameter.

Neither the spawning frequency nor the number of egg batches spawned each season have been determined for any *Trachurus* species. Estimates of spawning frequency require either the percentage occurrence of post-ovulatory follicles or the incidence of females with hydrated oocytes (Hunter and Macewicz 1985b). Neither of these ovarian stages could be adequately sampled in *T. declivis*, because of the low vulnerability of spawning fish to both trawling and purse seining.

Identifying the oocytes that are potentially capable of release in a current season causes problems in estimating annual fecundity for serially spawning fish. One approach by Macer (1974) has been to estimate the number of yolked (Stage 4) oocytes in each batch. But it is not possible to estimate the number of batches in one season from the number of size-frequency modes of oocytes already present in the gonad because new batches of oocytes are continually being recruited through oogenesis. Also, batch fecundity can vary in different age classes and throughout the season (Parrish *et al.* 1986), and pre-ovulatory atresia could create a substantial difference between potential and actual fecundity (Macer 1974; Hunter and Macewicz 1985a). Hence, to determine annual fecundity in *T. declivis*, estimates of batch fecundity, spawning frequency and rates of atresia are required, all of which have been impossible to obtain given the current problems involved in sampling the spawning population.

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