Abstract.–The reproduction of blue-eye trevalla, *Hyperoglyphe antarctica*, off Tasmania, southern Australia, is studied in detail through analysis of gonad maturation, spawning location and season, size at maturity, fecundity, and spawning frequency.

Results show that the fecundity of blue-eye trevalla is determinate, and it has a high annual fecundity which increases exponentially with the length of females (to a maximum of about 11 million oocytes). Females are partial spawners and possibly spawn all their oocytes in 3 or 4 large batches, the size of batches increasing with the length of females. Both sexes reach sexual maturity at large sizes, 71.3 and 61.6 cm fork length for females and males, respectively. One major spawning ground was identified off Tasmania where blue-eye trevalla aggregate from October to May. Smaller fish join the aggregation first, at early stages of gonad maturation, whereas larger fish appear to join the aggregation later, just prior to spawning. Spawning takes place at the end of summer–autumn (early March to early May).

Biology and dynamics of the reproduction of blue-eye trevalla, *Hyperoglyphe antarctica* (Centrolophidae), off Tasmania, southern Australia

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Blue-eye trevalla, *Hyperoglyphe antarctica* (Centrolophidae) are widely distributed in the southern oceans, from New Zealand to southern Australia, South Africa, and the southern Indian Ocean (Haedrich, 1967; McDowall, 1982). In Australia, they are found from central New South Wales to southern western Australia (Fig. 1) and on offshore seamounts. The fishery has developed off southeast Australia, particularly off Tasmania (Fig. 1). Fishing is traditionally done with drop-lines on hard sea bottom associated with the continental shelf break, at depths between 300 and 500 m. Commercial landings are relatively small (about 800 metric tons per year), but blue-eye trevalla is an excellent table fish and fresh fish fetch high prices on the domestic market.

In the late 1980's, a conflict arose between traditional line fishermen and trawl fishermen who intended to develop mid-water trawling techniques to target blue-eye trevalla. At that time, there was limited information on the biology and size of the resource, and it was feared that mid-water trawling would increase fishing effort to unsustainable levels. As a result, a research program was implemented in 1991 to study the biology of blue-eye trevalla off Tasmania. Anecdotal information

on the breeding season of this species was available from Jones[1] in South Australia and from Horn and Massey (1989) in New Zealand; no fecundity study had been undertaken. In this paper the reproductive biology (gonad maturation, size at maturity, spawning frequency, and fecundity) and the composition and dynamics of the main spawning aggregation are studied in detail, and a discussion is provided on some of the implications for the fishery.

Materials and methods

Sampling

Blue-eye trevalla were collected on board commercial vessels during drop-line fishing operations, between November 1991 and July 1993. Drop-lines are polypropylene lines that are anchored with a weight to the sea bottom at depths between 300 and 500 m and that are supported vertically by boys. Ten to 15 lines are used during fishing, each carrying about 100 hooks. At least one sample was obtained each

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[1] Jones, G. K. 1988. The biological status of the deepsea trevalla (*Hyperoglyphe antarctica*) offshore line fishery in South Australian waters. Department of Fisheries, South Australia, discussion paper, April 1988, 15 p.

month from most fishing grounds around Tasmania (Fig. 1). A sample represented the total catch made during one fishing trip (of 1–3 day duration) on the same ground. Fish were examined individually as they were hauled on deck, and the entire catch (or the majority of it) was processed during each fishing trip (representing between 50 and 500 fish). Fish were measured (fork length [FL]) to the nearest cm below the true length, sexed, and staged macroscopically by using the maturity stages described in Table 1 (adapted from Hunter and Macewicz, 1985, a and b; Schaefer, 1987; West, 1990). To calculate the gonadosomatic index (GSI), ovaries and testes were collected to be weighed in the laboratory to the nearest 0.1 g. The GSI was calculated as the proportion of gonad weight divided by body weight with the following length-weight relationship: Log (gutted weight) = 3.081 × Log (fork length) –4.385, where weight is in g and length in cm (Baelde, unpubl. data). For later histological examination and measurement of whole oocytes, ovaries at various stages of maturity were preserved in Davidson's solution immediately after the catch. Nearly all mature ovaries (stages 4 to 6, Table 1) were preserved.

Histological staging of ovaries

A total of 447 ovaries were examined histologically to check macroscopic staging and to note the presence of atretic oocytes and postovulatory follicles (see description in Table 1; Fig. 2; Fig. 3, A and B). Ovary sections were stained in haematoxylin and eosin and ovaries were staged on the basis of the most advanced type of oocytes present, regardless of their abundance (West, 1990).

Size at maturity

The average size at maturity $(FL_{0.5})$ was the size at which 50% of the fish caught during the breeding season were mature (i.e. stages 4 to 6 for females, and stages 3 and 4 for males). For each sex, the proportion (p) of mature individuals, by 1-cm fork length intervals, was fitted to the logistic function

$$p = e^{(a+bFL)} / \left(1 + e^{(a+bFL)}\right)$$
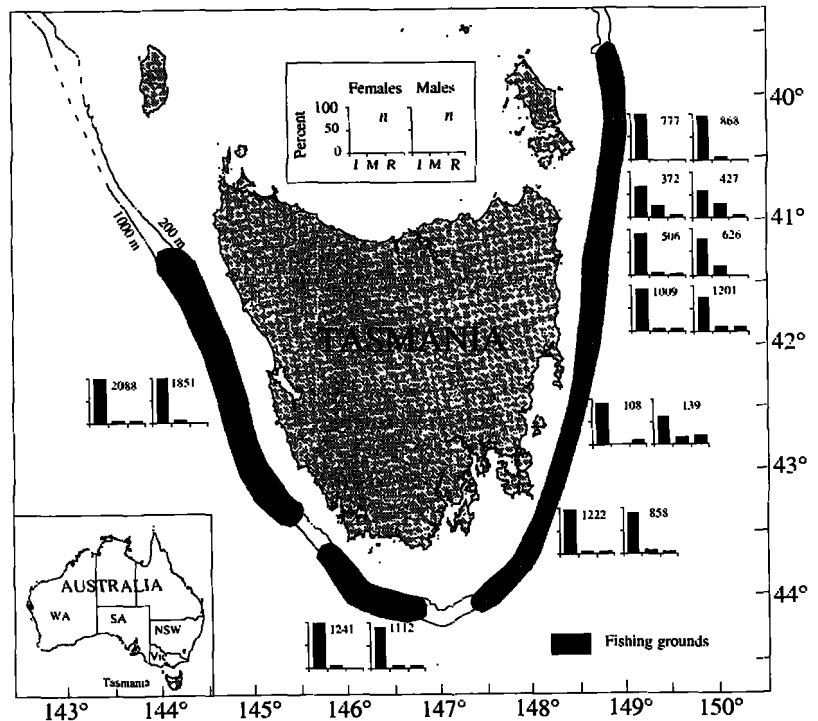

Figure 1

Proportions (as a percentage) by sex of immature (I), mature (M), and resting (R) blue-eye trevalla, *Hyperoglyphe antarctica*, in samples collected from major fishing grounds around Tasmania. I = stages 1 to 3 for females, 1 to 2 for males; M = stages 4 to 6 for females, 3 and 4 for males; and R = stages 7 and 8 for females, stage 5 for males. Depth contours in meters. WA = Western Australia, SA = South Australia, Vic = Victoria, and NSW = New South Wales. Numbers in graphs are the number of fish sampled.

by using generalized linear models (Genstat 5 Reference Manual). The average size at maturity was also estimated for length and maturity data collected off the east coast of Tasmania during the 1950's (Cowper and Downie[2]).

Spawning frequency and fecundity

Hunter et al. (1992) have identified three main factors that can affect fecundity estimates: 1) the rate of atresia in reducing the number of oocytes spawned; 2) the occurrence of previous spawnings (as shown by the presence of postovulatory follicles); and 3) the accurate identification of which oocytes to include in estimating fecundity. These three factors were examined as shown below.

Rate of atresia The proportion of atretic oocytes was determined in ovaries at various stages of maturity

[2] Cowper, T. R., and R. J. Downie. 1995. CSIRO, Division of Fisheries and Oceanography, Cronulla, New South Wales, Australia. Unpubl. data.

Table 1

Female and male blue-eye trevalla, *Hyperoglyphe antarctica,* maturity stages based on macroscopic and histological examination. Adapted from Hunter and Macewicz (1985, a and b); Schaefer (1987); West (1990); Hunter et al. (1992); Davis and West (1993).

| Females			
Stage	Macroscopic description	Histological description	Oocyte development
1 Immature	Small thread-like ovaries, pink and translucent;	Chromatin nucleolar stage: very small oocytes, nucleus surrounded by a thin layer of dark-blue-stained cytoplasm;	
2 Early developing	Oocytes not visible, ovaries pink and translucent; *First-time developing females:* ovaries up to 10 cm long, 1 cm across, ovary wall thin and transparent; *Redeveloping females:* ovaries up to 20 cm long, 5 cm across, flaccid, ovary wall thick, whitish, and opaque;	Perinucleolar stage: oocyte size increases slightly as dark-blue-stained cytoplasm thickens, nucleoli appear at the periphery of nucleus;	Cytoplasm homogeneous, brownish and transparent, comparatively large dark nucleus;
3 Developing	Small oocytes becoming visible, still translucent, ovaries occupy less than 20% of body cavity;	Cortical alveoli stage: appearance of cortical alveoli in pale-blue-stained cytoplasm, pink-stained zona radiata distinguishable, oil vesicles appearing, lampbrush chromosomes often visible in the nucleus;	Oocytes more or less spherical, cytoplasm thickened, darker, granular, but still translucent, nucleus still visible;
4 Late developing (yolked)	Small opaque oocytes clearly visible, marked increase in ovary size (20% to 100% of body cavity) and change from pink to yellow-orange color, ovary wall thin and transparent;	Yolk stage: marked increase in oocyte size, cytoplasm filled with pink-stained yolk granules, cortical alveoli and oil vesicles increase in size and number; degenerating postovulatory follicles visible if spawning has started;	Oocytes dark, completely opaque, size increasing with development, nucleus occluded; degenerating postovulatory follicles visible if spawning has started;
5 Ripe	Ovary size as in previous stage, large transparent (hydrating) oocytes visible among smaller opaque oocytes;	Nuclear migration stage: migration of nucleus to periphery of oocyte, fusion of yolk granules into yolk plates; fusion of oil vesicles into the oil droplet; degenerating postovulatory follicles visible if spawning has started;	Occurrence of partly translucent oocytes (hydrating), yolk plates visible;degenerating postovulatory follicles visible if spawning has started;
6 Running-ripe	Ovary size as in previous stage, hydrated oocytes larger, easily expressed from ovaries;	Hydration stage: further increase in size of oocytes, all yolk granules fused into a few plates;	Occurrence of very large, almost totally translucent oocytes, oil droplet visible;
7 Spent	Ovaries flaccid, occupy about 20% of body cavity, greyish ovary wall thickened and wrinkled, some residual oocytes visible within translucent material;	Postovulatory follicles clearly visible, no yolked oocytes left except for a few undergoing atresia; structure of ovaries generally loose, hydrated oocytes may be present in lumen;	Postovulatory follicles visible, remaining yolked oocytes at early stage of atresia;

continued

Table 1 (continued)

Females (continued)

Stage	Macroscopic description	Histological description	Ooycte development
8 Resting	Aspect of ovaries as in previous stage, not accurately distinguishable.	Oocytes at stages 2 and 3 predominate, no trace of postovulatory follicles left, advanced atresia of remaining yolked oocytes, hydrated oocytes sometimes still present in lumen.	Very small oocytes (stages 2 and 3) predominate, advanced atresia of remaining yolked oocytes.

Males

Stage	Macroscopic description
1 Immature	Testes very small, flat, and threadlike;
2 Early developing	Testes increase in size, rounder in shape;
3 Developing	Size of testes increases further, lobed in formation and marked groove in the middle of each testis visible, creamy or white milt sometimes present;
4 Late developing to running-ripe	Testes very large and multilobed, white or pinkish, sometimes bloodshot, free-flowing milt;
5 Spent and resting	Testes much smaller, very bloodshot, milt sometimes present, become thinner, brownish and rubbery as they regress to resting stage.

by using samples preserved in Davidson's solution. Only early stages of atresia (stages alpha and beta as described by Hunter and Macewicz, 1985b) were considered (Fig. 3, B, C, and D); oocytes at later stages of atresia are too difficult to identify with commonly used histological techniques.

Occurrence of postovulatory follicles The presence of postovulatory follicles in ovaries was used to identify females that had begun to spawn. In addition, examination of morphological changes in postovulatory follicles after ovulation (as described by Hunter and Macewicz, 1985b; Schaefer, 1987; Macewicz and Hunter, 1993) provided information on spawning frequency. Postovulatory follicles were classified into two types according to the degree of resorption visible in histological sections. Type-1 postovulatory follicles (Fig. 3A) were more recent, presenting an involuted zona radiata with numerous folds and an open cavity, as well as granulosa cells aligned within the zona radiata; type-2 postovulatory follicles were small, had fewer involutions, and showed a much more reduced follicular cavity; at that stage the zona radiata has thickened markedly and the granulosa cells are disorganized. When present in ovaries, 50 postovulatory follicles were randomly measured (along the perimeter) with NIH image analysis software.

Staging and measurement of whole oocytes Staging and measurement of whole oocytes was used to assess whether the fecundity of blue-eye trevalla is determinate or indeterminate, that is, whether yolk formation is completed before spawning starts or continues after (Hunter et al., 1985). This information is needed to know whether the annual fecundity of blue-eye trevalla can be estimated from a standing stock of yolked oocytes (i.e. vitellogenic) present in ovaries. Subsamples of ovaries preserved in Davidson's solution were mixed in small jars with water and 3-mm glass beads and shaken manually to dissociate the oocytes. All ovaries used had been previously staged histologically, and histological sections were used to stage corresponding whole oocytes under a microscope (see description in Table 1 and Fig 3, C and D, adapted from West, 1990; Hunter et al., 1992; Davis and West, 1993). Fifty oocytes were measured (along the maximum diameter) for 135 females at various stages of maturity. Figure 3D also shows whole, preserved postovulatory follicles of type 1 (type 2 were too small to be properly dissected and photographed).

Fecundity estimation Only ovaries that showed no sign of previous spawnings (absence of postovulatory follicles), no sign of major atresia, and in which oocytes were fully yolked (as indicated by their diam-
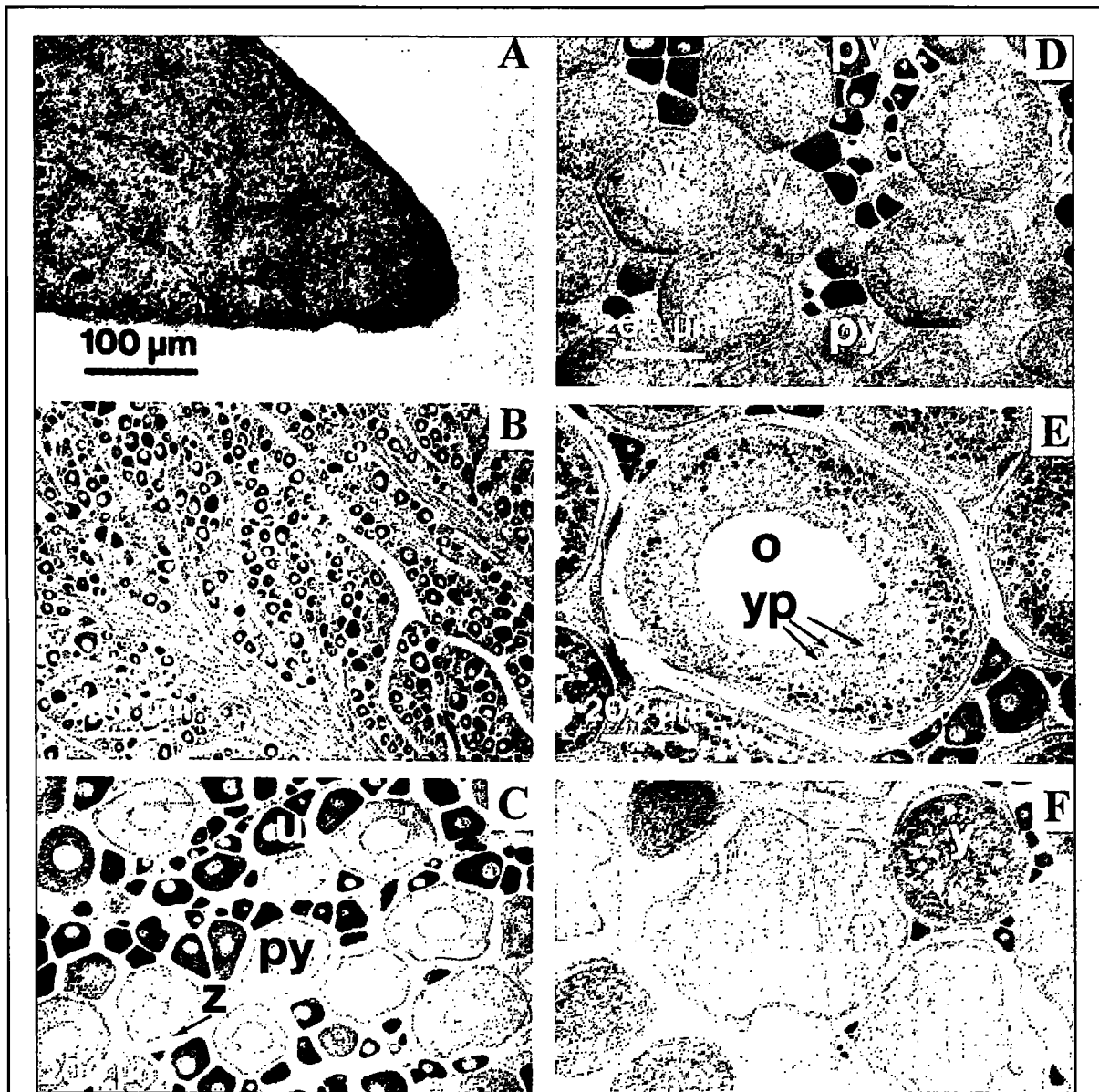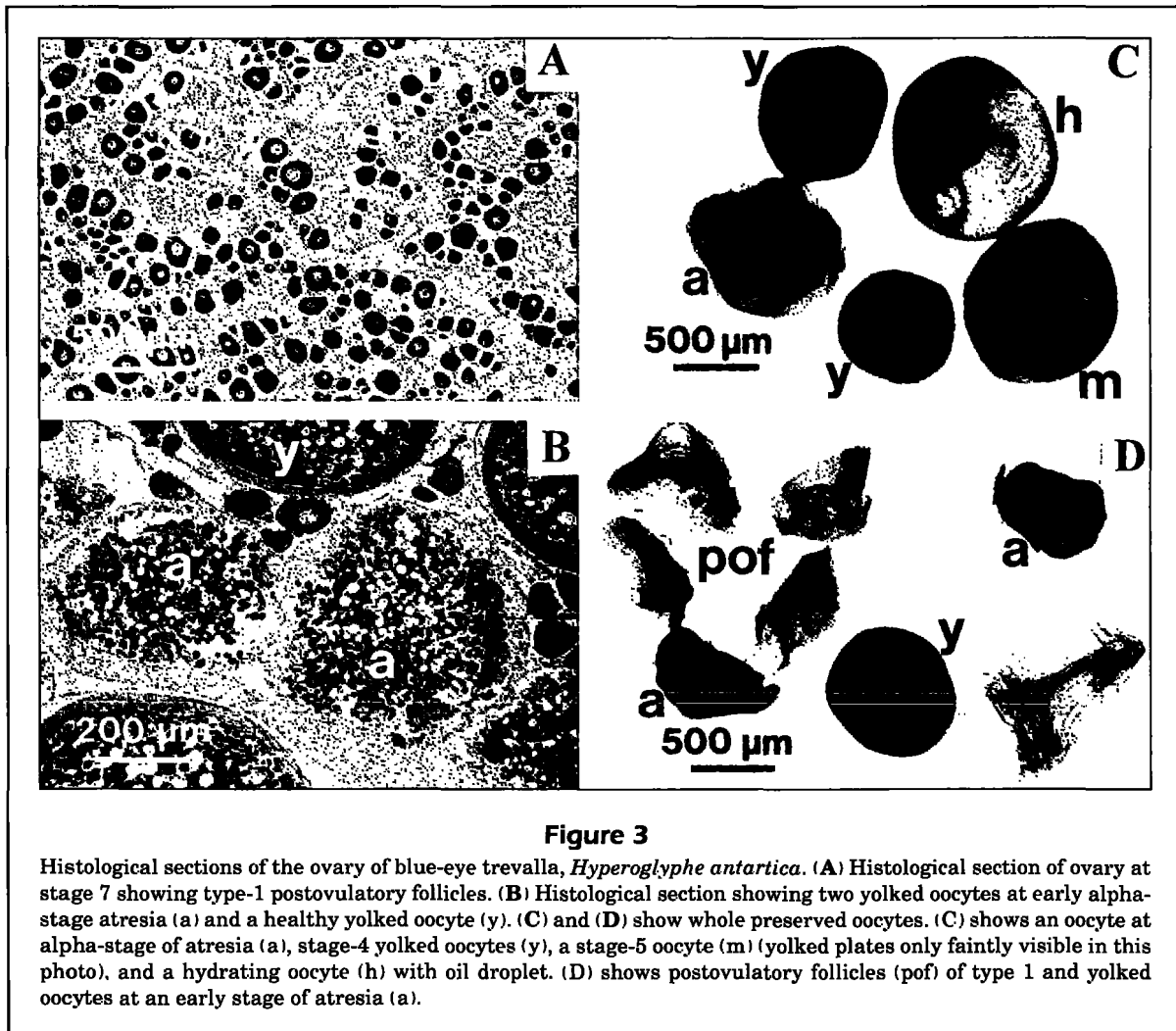
Figure 2

Histological sections showing ovary maturation stages of blue-eye trevalla, *Hyperoglyphe antarctica*. (A–F) represent stages 1–6 successively. (D) shows an "early stage 4" characterized by the nonuniform size of yolked oocytes. h = hydrating oocyte (irregular shape due to loss of fluid during histological processing); n = nucleus; o = oil droplet; py = partially yolked oocyte; u = unyolked oocyte; y = yolked oocyte; ym = yolk mass (fusion of yolk plates); yp = yolk plate; z = zona radiata.

eter, see below) were used to estimate the annual fecundity of blue-eye trevalla. Before estimating fecundity, a check was made that the oocytes were uniformly distributed within the ovaries. From five fish, the number of oocytes per gram was compared between subsamples taken across the ovaries (near the periphery and near the center) and along the ovaries (within the anterior, median, and posterior regions). ANOVA showed no differences between subsamples across the ovaries (F=0.68, df=1,4, P=0.42), or between subsamples along the ovaries (F=0.74, df=2,8, P=0.49). Oocytes were then routinely dissociated and counted from three weighed subsamples taken randomly within the ovaries.

Batch fecundity was estimated for eight ripe females by estimating the number of hydrated oocytes;

Figure 3

Histological sections of the ovary of blue-eye trevalla, *Hyperoglyphe antartica*. (A) Histological section of ovary at stage 7 showing type-1 postovulatory follicles. (B) Histological section showing two yolked oocytes at early alpha-stage atresia (a) and a healthy yolked oocyte (y). (C) and (D) show whole preserved oocytes. (C) shows an oocyte at alpha-stage of atresia (a), stage-4 yolked oocytes (y), a stage-5 oocyte (m) (yolked plates only faintly visible in this photo), and a hydrating oocyte (h) with oil droplet. (D) shows postovulatory follicles (pof) of type 1 and yolked oocytes at an early stage of atresia (a).

only ovaries in which hydrated oocytes formed a well-defined mode were used. Also, the number of yolked oocytes remaining in partially spent ovaries was determined for 24 females.

Results

Gonad maturation

Ovaries at stages 1 and 2 could not be distinguished accurately by macroscopic examination and were grouped together in the analyses, as were stages 7 and 8. GSI values varied greatly within maturity stages (Table 2) and could not be used alone to assess the development of ovaries. Macroscopic staging of the testes was more difficult than that for the ovaries (Table 1). The main criterion used to assess male maturity development, based on the presence or absence of milt, was not consistent. As already

observed by Horn and Massey (1989) in New Zealand, milt was sometimes present in small, developing testes but absent in large testes.

Histological examination of stage-4 ovaries led to the distinction, within this stage, of ovaries at an early stage of yolk formation. These ovaries were characterized by a great variation in the size of oocytes (Fig. 2D) compared with the uniform size of fully yolked oocytes. They will be referred to as "early stage 4" in the text. Partially spent ovaries (i.e. stage-4 or stage-5 ovaries containing postovulatory follicles and which were not identifiable macroscopically) will be referred to as stages 4* and 5*.

Spawning location and season

Mature fish of both sexes (stages 4–6 for females and stages 3–4 for males) were caught mostly off the northeast coast of Tasmania, at about 41°S (Fig. 1), but a few were occasionally caught in other areas.

Table 2

Range and median value of female gonadosomatic index (GSI) by stage of maturity for blue-eye trevalla, *Hyperoglyphe antarctica*. * indicates partially spent ovaries (presence of postovulatory follicles). Standard deviations are in parentheses. n = sample size.
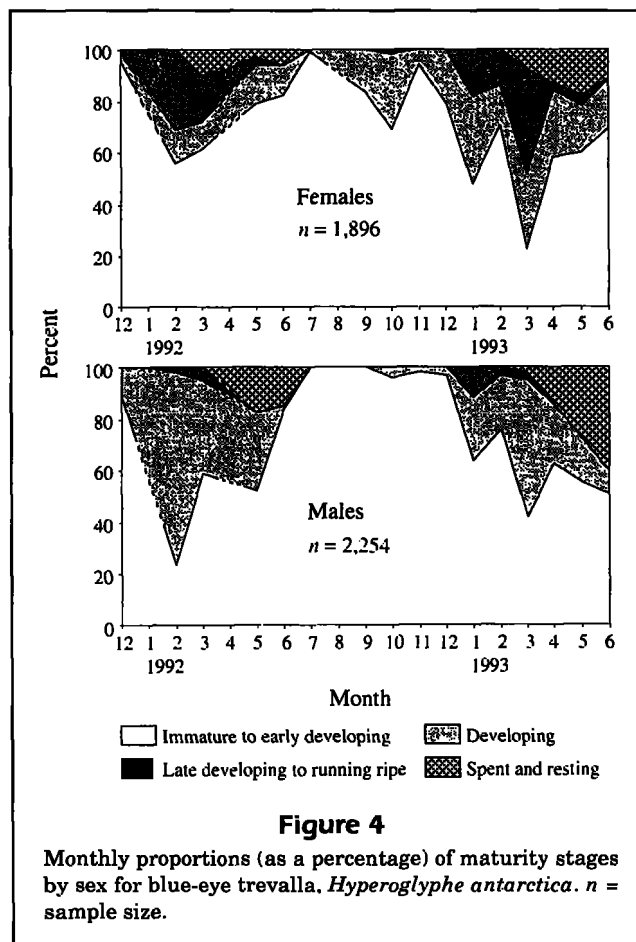
| Stage | Gonadosomatic index | | |
	Range	Mean	n
1+2	0.2–1.1	0.4 (0.2)	58
3	0.3–2.0	0.8 (0.3)	203
Early 4	1.6–12.0	5.2 (2.5)	19
4	3.3–19.5	10.2 (3.1)	92
4*	3.3–15.9	9.5 (3.8)	18
5	8.9–19.4	13.9 (4.7)	5
5*	5.1–14.8	10.0 (3.5)	6
6	20.6	—	1
7	1.6–3.8	2.5 (0.6)	8
8	0.7–2.5	1.5 (0.4)	66
Atretic	0.7–8.1	1.8 (1.6)	21

Table 3

Average size at maturity ($FL_{0.5}$) by sex, and 95% confidence limits for blue-eye trevalla, *Hyperoglyphe antarctica*. Data were fitted to the logistic equation shown in text. Results are shown for data collected during the current study and for data collected in the mid 1950's before the fishery developed (from Cowper and Downie's unpubl. data). CL = confidence limits.

	n	a	b	$FL_{0.5}$	95% CL
Current data					
Females	1803	–29.86	0.419	71.3	70.7–71.9
Males	1613	–21.06	0.342	61.6	61.2–62.1
Cowper and Downie's data					
Females	813	–23.79	0.341	69.8	69.2–70.3
Males	498	–24.05	0.397	60.6	59.6–61.4

Figure 4

Monthly proportions (as a percentage) of maturity stages by sex for blue-eye trevalla, *Hyperoglyphe antarctica*. n = sample size.

Off northeast Tasmania, and over the 20-month sampling period, mature fish were caught in small numbers between October and December; then their abundance increased markedly between January and March (Fig. 4). Stage-4 females caught from October to December 1992 were at early stage of yolk formation (early stage 4) with a low GSI ranging from 1.6 to 2.3. GSI values then increased to a mean of 5.6 (with a standard deviation [SD] of ±2.3) in January, 8.0 (±2.9) in February, and 9.4 (±2.7) in March, 1993. In both 1992 and 1993, ripe (stage-5) and partially spent (stage-4* and stage-5*) females were caught from early March to early May; females in postspawning condition (stages 7 and 8) were caught from mid-March, their maxi-
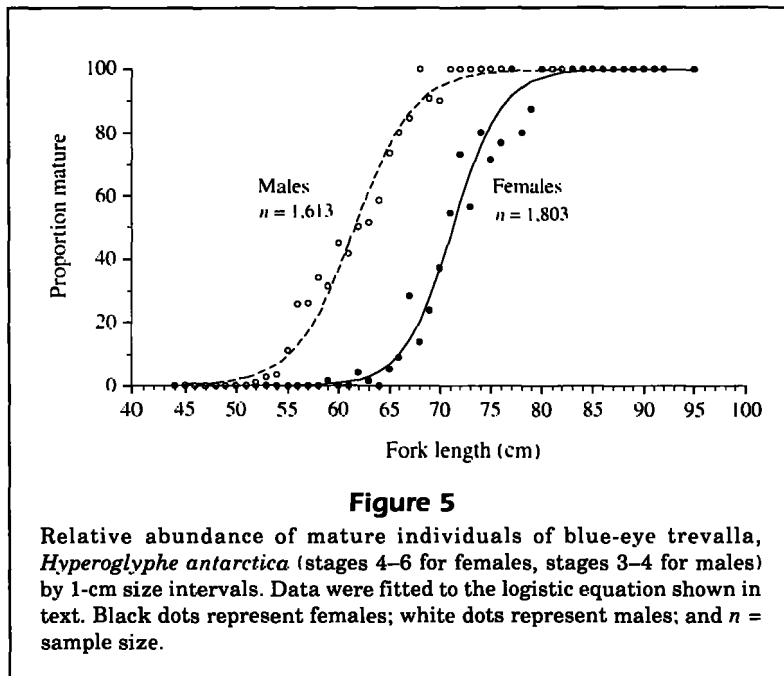
mum abundance occurring in May and June (66.3% of the total 445 postspawning females examined). Thus, maturation of ovaries spanned several months, from October to February, and actual spawning apparently took place from early March to early May.

Size at maturity

The smallest mature female observed during the present study was 59 cm FL, and the smallest mature male was 52 cm FL. The estimated average sizes at maturity were 71.3 and 61.6 cm FL for females and males, respectively (Table 3; Fig. 5). These sizes were very similar to those estimated from data collected in the mid 1950's (Table 3).

Rate of atresia

The rate of atresia for both unyolked and yolked oocytes was generally low (atretic oocytes represented between 1 and 10% of all oocytes when present). However, a few ovaries presented a high level of atresia (about 90%) of their yolked oocytes. These atretic

Figure 5

Relative abundance of mature individuals of blue-eye trevalla, *Hyperoglyphe antarctica* (stages 4–6 for females, stages 3–4 for males) by 1-cm size intervals. Data were fitted to the logistic equation shown in text. Black dots represent females; white dots represent males; and *n* = sample size.

ovaries were of two types. The first type consisted of small ovaries with abundant white oocytes visible macroscopically within a translucent, pinkish mass of unyolked oocytes. Histological examination later revealed that the white oocytes were oocytes at an early stage of yolk formation and were undergoing atresia. This type of ovary was observed in May and June 1992 and 1993, and represented 64% of all yolked ovaries examined during these periods. It was always observed in preadult females at size below the average size at maturity (mean FL=63.6 cm [±3.2 cm SD]).

Only two females presented the second type of atretic ovaries; they had large ovaries (GSI of 6.9 and 8.1) and nearly all fully yolked oocytes were at an early stage of atresia. These atretic oocytes could not be detected macroscopically, but they were recognizable microscopically in preserved samples (Fig. 3, C and D). The two females were caught during the spawning period in March 1993; they represented only 1.2% of all mature ovaries examined histologically.

Occurrence of postovulatory follicles

Postovulatory follicles were found in 16.8% of all mature ovaries examined (*n*=167). They were never found in ovaries at early stage of yolk formation. Both type-1 and type-2 postovulatory follicles were usually present in stage 4*, whereas only type-2

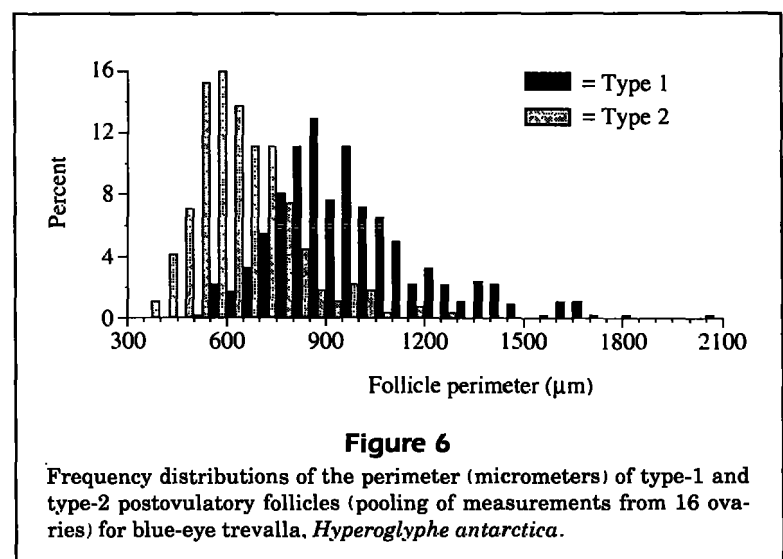postovulatory follicles were found in hydrating ovaries (stage 5*) (Fig. 6).

Measurement of whole oocytes

As maturation progressed, a clear gap appeared between unyolked and yolked oocytes (Fig. 7, A–D), showing that the fecundity of blue-eye trevalla is determinate. The recruitment of oocytes from the reserve of unyolked oocytes was completed when the average diameter of yolked oocytes reached about 650 μm (Fig. 7E). Unyolked oocytes present in these ovaries were at stage 2 and had a diameter of less than 100 μm (the gap in size between unyolked and yolked oocytes was clear and unyolked oocytes were no longer measured in most advanced ovaries). The diameter of yolked oocytes then increased slightly to about 700 μm (Fig. 7G) before migration of the nucleu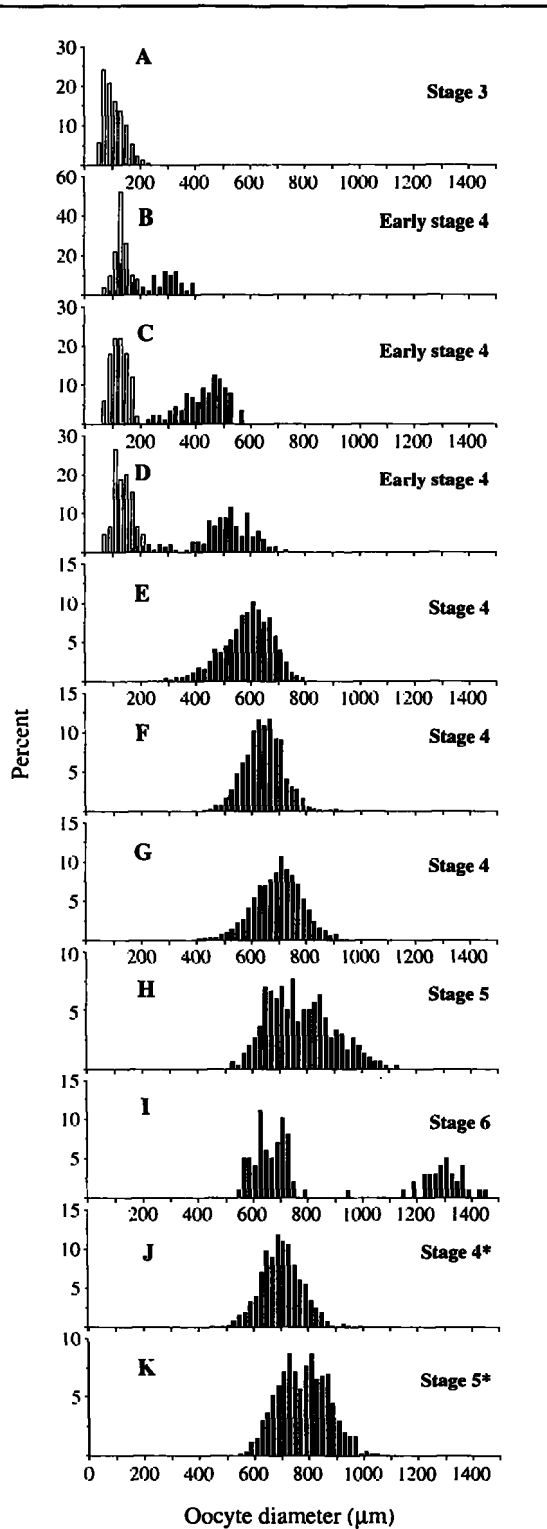s and hydration began (Fig. 7. H–I). After a batch was spawned, formation of a new batch began from the remaining pool of yolked oocytes, showing migration of nucleus and hydration (Fig. 7, J–K). The mean oocyte diameter of stage-4 ovaries used to construct graphs E to G ranged from 500 to 770 μm (having an overall mean of 640 [±60 SD] μm, *n*=81). Hydrating oocytes observed during the present study were about 1.3 mm (Fig. 7I).

Fecundity

Because fecundity was found to be determinate, annual fecundity was estimated from the standing stock

Figure 6

Frequency distributions of the perimeter (micrometers) of type-1 and type-2 postovulatory follicles (pooling of measurements from 16 ovaries) for blue-eye trevalla. *Hyperoglyphe antarctica*.

Figure 7

Frequency distribution of oocyte diameter by stage of maturity (measurements from several ovaries pooled in each graph) for blue-eye trevalla, *Hyperoglyphe antarctica*. White and black bars represent independent measurements of unyolked and yolked oocytes, respectively (unyolked oocytes were not measured in stage-4 ovaries from graph E). * = partially spent ovaries.

of yolked oocytes in stage-4 and stage-5 ovaries (Fig. 7, E–H). The fecundity (*F*) ranged from 1.3 to 11.0 million oocytes per fish, and although varying considerably at given length (Fig. 8), it showed a significant exponential increase with the length (FL) of females, following the equation
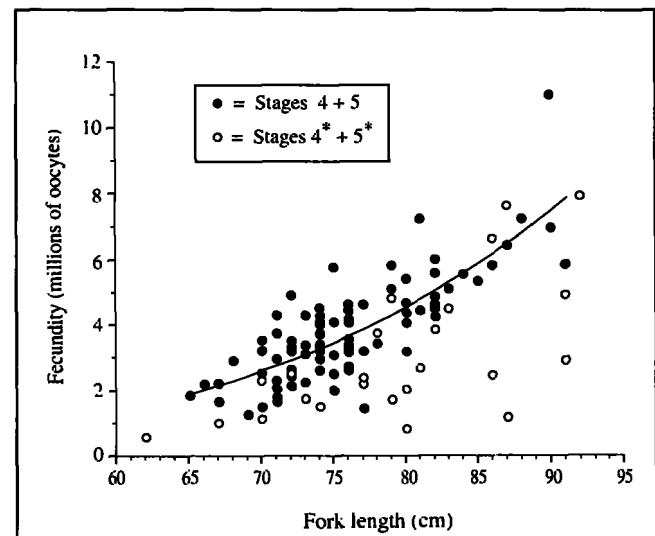
$$F = 4.2 \times 10^{-8} \times FL^{4.22},$$

where *F* is in millions and *FL* in cm. The linear regression between log-transformed data was statistically significant: F=110.6, df=82; P<0.001, R^2=0.57. Multiple regression analysis showed that the variation in average diameter of yolked oocytes between mature females (as illustrated in Fig. 7, E–H) did not affect fecundity estimates (Table 4). The average relative fecundity was 480 oocytes (±125 SD) per g (gutted weight) and did not show clear trends with the size of fish.

Batch fecundity estimated for ripe females ranged from 0.5 to 2.4 million oocytes (*n*=8) and also increased with length (Fig. 9). The number of yolked oocytes left in partially spent ovaries ranged from 0.6 to 7.9 million (Fig. 8), with a median value at 2.4 million (*n*=24).

Spawning aggregation

The bulk of the commercial catch for blue-eye trevalla consisted of small (<55 cm FL), immature fish year

Figure 8

Annual fecundity estimates (black dots) and power relationship between annual fecundity and size of females (line drawn from equation $F = 4.2 \times 10^{-8} \times FL^{4.22}$) for blue-eye trevalla, *Hyperoglyphe antarctica*. Fecundity estimated for partially spent ovaries is also shown (white dots) but was not included in the regression analysis.

Table 4

Multiple regression between log-transformed annual fecundity, fork length (FL, cm), and mean oocyte diameter (micrometers) for blue-eye trevalla, *Hyperoglyphe antarctica*. Sample size = 84, SE = Sampling error.

Source	Partial coefficient	SE	t	P (2-tail)
Constant	−3.942	2.263	−1.742	0.086
Log (FL)	4.059	0.437	9.291	0.000
Log (oocyte diameter)	0.228	0.302	0.757	0.451

Figure 9

Linear relationship between batch fecundity and size of females for blue-eye trevalla, *Hyperoglyphe antarctica*. Line drawn from the equation Batch Fec.= 0.097 × FL − 6.28 (F=20.2, df=5, P<0.001, R^2=0.80. R^2 increased from 0.65 to 0.80 when the outlier was excluded from the regression).

round, and the proportion of larger fish increased during the breeding season (Fig. 10). The proportion of these large fish (both sexes) increased in catches from 31.1% during the "nonspawning period" (May to December) to 61.3% during the "spawning period" (January to April).

Examination of size composition and sexual maturity data for females >55 cm FL allowed broad distinction of three groups of fish in commercial catches during the breeding season (Fig. 10): 1) preadult females at size below the average size at maturity (i.e. <69 cm FL), most in the developing stage of maturity, but only a few of which would spawn during the current spawning period; 2) females just reaching size at maturity (i.e. between 69 and 75 cm FL), ranging from developing to ripe stages of maturity, about half of which would spawn for the first time during the current spawning period; and 3) large females (i.e. >75 cm FL), most in the fully developed stage of maturity and likely to spawn. Preadult females were caught all around Tasmania from November to May; first-time spawners were caught mainly off the northeast coast of Tasmania and were more abundant between January and April; largest females were also caught primarily off the northeast coast of Tasmania but only during a brief period, from early March to early May, and quickly disappeared from catches afterward (very few were caught in postspawning condition).

For males, several groups could also be distinguished (Fig. 10), although not as clearly as those for females, because of their generally more compact length-frequency distributions.

Preadult females (<69 cm FL) represented as much as 45.6% of all three groups defined above. Similarly, 31.5% of males >55 cm FL had not reached the average size of sexual maturity. In addition, first-time spawners (i.e. mature females at ≤75 cm FL and mature males at ≤65 cm FL) represented as much as 56.7 and 75.9% of all mature females and males, respectively.
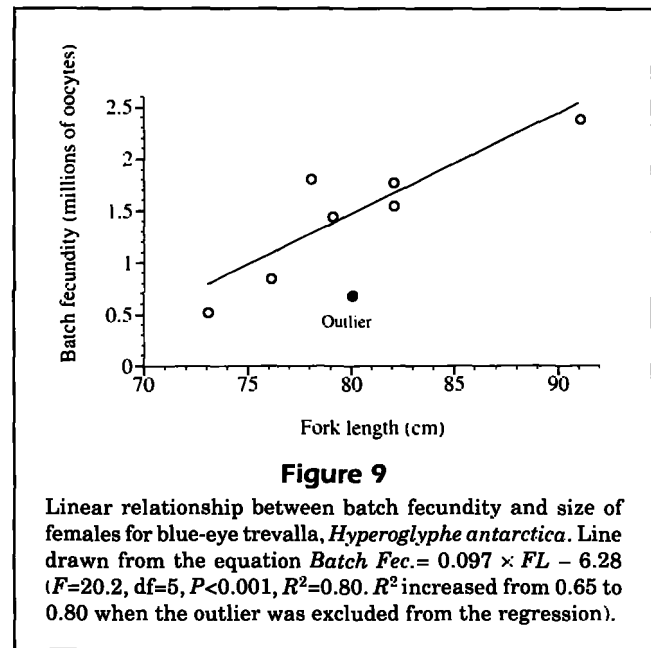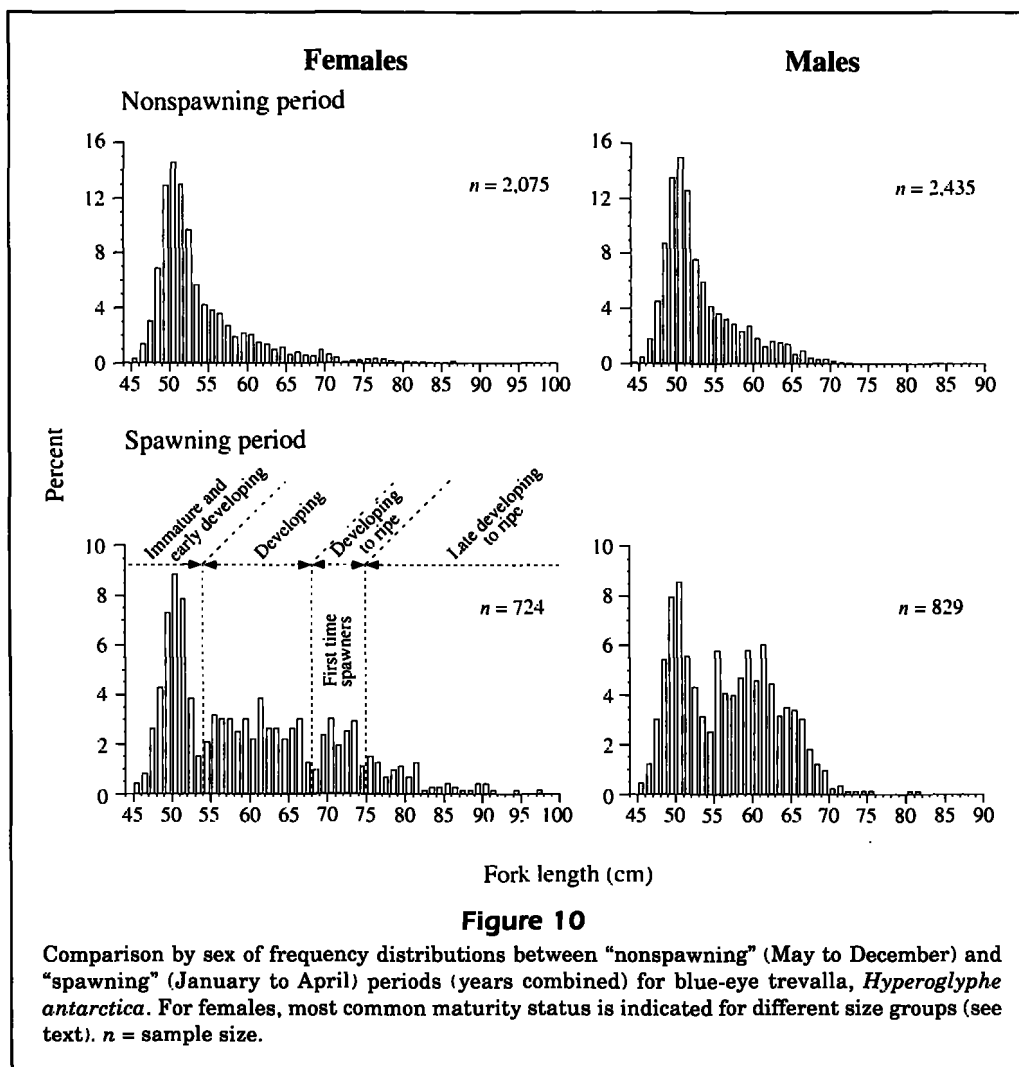
Discussion

Ovary maturation, spawning frequency, and fecundity

Maturation of ovaries appears to be group-synchronous for blue-eye trevalla, spanning from spring to summer (October–February) and followed by a brief spawning period in late summer–autumn (early March–early May). As observed for other fish species (Hunter and Macewicz, 1985b), the occurrence of atretic ovaries marks the end of spawning. The timing of spawning coincides well with the discovery, in June 1991 and May 1993, of a few juvenile blue-eye trevalla among floating seaweed off the Tasmanian east coast (Last et al., 1993). These juveniles ranged in size from about 30 to 60 mm standard length and were estimated to be about 2.5 to 3 months old on the basis of daily ring counts of otoliths (Proctor[3]).

Blue-eye trevalla reach sexual maturity at a large size, and according to yet unvalidated age data,[4] females are about 11–12 years old and males about 8–9 years old at sexual maturity. The bulk of immature fish in commercial catches are about 3 to 4 years old. Analysis of data collected in the 1950's showed

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[3] Proctor., C. 1994. CSIRO, Division of Fisheries, Hobart, Tasmania. Personal commun.

[4] Morison, S. 1995. Victorian Fisheries Research Institute, Department of Conservation and Natural Resources, P.O. Box 114, Queenscliff 3225, Australia. Unpubl. data.

Figure 10

Comparison by sex of frequency distributions between "nonspawning" (May to December) and "spawning" (January to April) periods (years combined) for blue-eye trevalla, *Hyperoglyphe antarctica*. For females, most common maturity status is indicated for different size groups (see text). n = sample size.

that there had been no changes in the size at maturity of blue-eye trevalla since the fishery began.

The fecundity of blue-eye trevalla is clearly determinate; several batches of ripe oocytes are formed successively from a standing stock of yolked oocytes. Comparison of annual and batch fecundities suggests that females spawn all their oocytes in 3 or 4 large batches. Several studies (e.g. Macewicz and Hunter, 1993; Oda et al., 1993) have shown that postovulatory follicles usually persist in fish ovaries for short periods (days). The cooccurrence of postovulatory follicles and ripe oocytes in ovaries of blue-eye trevalla also suggests that hydration and ovulation of successive batches could take place within a short period. However, multiple samples taken at short intervals during spawning would be required to age postovulatory follicles accurately.

The average relative fecundity of blue-eye trevalla appears to be fairly high when compared with other middle slope species (e.g. hoki, *Macruronus novaezelandiae* off southern Australia [520 oocytes/g[5]] and sablefish, *Anoplopoma fimbria* off Oregon [110 oocytes/g [Macewicz and Hunter, 1994]). The rate of atresia in ovaries appears to be negligible, and, in the present study, it did not affect fecundity estimates (although this would not necessarily be true for all spawning seasons). The fact that female blue-eye trevalla are partial spawners constitutes more of a problem for estimating fecundity, even more so because spawning batches are large. Partially spent females cannot be identified macroscopically, and to avoid underestimating annual fecundity, it is necessary to check microscopically for the presence of postovulatory follicles in every female before estimating the number of oocytes.

Composition and dynamics of the spawning aggregation

Blue-eye trevalla in spawning condition were mostly caught off the northeast coast of Tasmania, which may be a major spawning ground. However, the occasional occurrence of mature blue-eye trevalla on nearly all other Tasmanian fishing grounds, including an offshore seamount 120 miles south of Tasmania (data not included), and the presence of spawning aggregations off New South Wales (Rowling[6]) and South Australia (Jones[7]) indicate that spawning takes place on several grounds within southern Australia. The fact that no genetic difference was found between blue-eye trevalla collected off New South Wales, Tasmania, and South Australia (Bolch et al., 1993) further supports the view of a widely distributed spawning activity. Horn and Massey (1989) also believed that blue-eye trevalla spawned on many grounds in New Zealand.

During his work on hoki spawning aggregations, Langley (1993) identified several spawning groups arriving successively and then leaving the spawning ground. The situation is different for blue-eye trevalla, where the three groups of females identified in the summer aggregation seemed to correspond to progressive arrivals of different size (or age) groups and not to commuting spawning groups, spawning taking place at the end of summer. Older females join the aggregation just before spawning and leave shortly after; younger females (first-time spawners) aggregate earlier and stay on the grounds for some time after spawning.

The presence of preadults in the aggregation (i.e. at size below the average size at maturity and, thus, not all capable of spawning) suggests that this summer aggregation off northeast Tasmania is related to both feeding and spawning behaviors. Blue-eye trevalla feed mainly on the pelagic tunicate *Pyrosoma atlanticum* (Winstanley, 1978), and Cowper (1960) noted a maximum incidence of *Pyrosoma* in the stomachs of blue-eye trevalla during the summer. As observed for Atlantic cod, *Gadus morhua* (Swain, 1993), it is possible that blue-eye trevalla off northeast Tasmania migrate between deeper wintering grounds and shallower feeding and spawning summer grounds. The presence of preadult fish on other Tasmanian fishing grounds during spring and summer

indicates that feeding aggregations are not restricted to the northeast coast of Tasmania. Winstanley (1979) also noted that blue-eye trevalla off Victoria probably move from deeper to shallower depths in spring.

The spawning population observed in commercial catches was young and the majority were first-time spawners. Larger fish used to be caught by drop-line in the early years of the fishery (Baelde, unpubl. data), and it is not known whether their low proportion in current catches reflects a lower vulnerability to line fishing (owing to age- or size-specific change in distribution and aggregating behavior), or reflects a significant decline in abundance owing to fishing. In addition, it is believed that there is one stock of blue-eye trevalla in southern Australia, and, as shown for other fish species with a wide geographic distribution (Schaefer, 1987; Bell et al., 1992; Rijnsdorp, 1993; Clark et al., 1994), size at maturity, spawning season, and fecundity could vary significantly between areas. Differences in the time of spawning and the size of spawners have already been observed between New South Wales and Tasmania.[6]

This study points out that a proper estimate of the spawning biomass of blue-eye trevalla stock off southern Australia would require fishery-independent surveys (i.e. identification of other spawning grounds and analysis of the age-specific movements of fish during spawning) to determine more accurately the structure and abundance of the spawning population.

Acknowledgments

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