Aspects of the reproductive biology of the southern mullet, *Liza richardsoni*, from Algoa Bay, South Africa

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The reproductive biology of the southern mullet from Algoa Bay was studied between June 1978 and October 1980. Gonadosomatic indices and macroscopic and microscopic examinations of the gonads were used to establish the breeding cycle. The period of greatest sexual development extends from September to March and spawning occurred throughout that period. Spawning probably occurs close inshore. *Liza richardsoni* exhibited the phenomenon of group synchronism, two distinct oocyte groups being present within a pre-spawning ovary. The proportion of yolkless oocytes exceeded that of vitellogenic oocytes in ripe fish. However, it was not apparent whether all the vitellogenic oocytes would reach maturity. This highlights the need for quantitative histological studies to accompany fecundity estimates. Histological investigations were useful in the clarification of breeding cycle determinations based on gonadosomatic indices and visual macroscopic assessments.

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Die reproduktiewe biologie van die suidelike harder in Algoabaai is tussen Junie 1978 en Oktober 1980 bestudeer. Gonadosomatiese indekse en makroskopiese en mikroskopiese ondersoeke van die gonades is gebruik om die broeisiklus te bepaal. Die periode van grootste geslagtelike ontwikkeling het van September tot Maart gestrek en kuitskiet het gedurende dié tydperk plaasgevind. Kuitskiet vind heelwaarskynlik naby die kus plaas. *Liza richardsoni* toon groepsinchronisasie met twee afsonderlike groepe oösiete teenwoordig in dieselfde ovarium net voor kuitskiet. In ryp visse is daar meer oösiete wat nie dooier bevat nie as oösiete met dooier, maar dit was nie duidelik of eersgenoemde sou ryp word nie. Dit toon die behoefte aan vir kwantitatiewe histologiese studies wat met beramings van die aantal ryp eiers gepaard moet gaan. Histologiese ondersoeke was waardevol vir die bepaling van broeisiklusse wat gebaseer is op gonadosomatiese indekse en makroskopiese skattings.

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According to Wallace (1974) the distribution of the southern mullet *Liza richardsoni* extends from the Transkei on the east coast to the Orange River on the west coast of southern Africa. It is particularly abundant on the south-west coast from the Cape Peninsula to just beyond Agulhas point, where many millions are landed annually (Smith 1965).

Since the beginning of 1974 monthly catch statistics have been collected by the Division of Sea Fisheries, this being facilitated by the compulsory licensing of all beach seine-set- and drift nets. In 1975 six million mullets were landed by commercial operators between South West Africa and the area to the east of Knysna (Rep. Sea Fish. Brch. S. Afr. 43 1975), the majority of these being *L. richardsoni*. Despite the fact that this species is less abundant east of Agulhas, it was one of the five most abundant species caught in the surf zone of Algoa Bay (Lasiak 1979).

The reproductive biology of mullet is well documented, most of the research emanating from Australia, Israel, Taiwan and the U.S.A. Most effort has been directed at *Mugil cephalus*, particularly with regard to induced spawning (Pien & Liao 1975; Kuo, Nash & Shehadeh 1974; Shehadeh, Kuo & Milisen 1973). Histological investigations have been carried out by Stenger (1959), Abraham (1963), Abraham, Blanc & Yashouv (1966), and Zhitenev, Kalinen & Abayev (1974). The majority of studies have concentrated on the later oocyte stages. In South Africa the only mullet species to have received significant attention is *Liza dumerili*. Descriptions of testicular histology and the breeding cycle of male *L. dumerili* from the Swartkops estuary have been given by Van der Horst (1978) and Van der Horst & Erasmus (1978). The object of the present paper is to describe the breeding cycle of *L. richardsoni* using three major criteria:

(i) visual assessment of gonadal maturity
(ii) changes in gonadosomatic indices
(iii) histological studies of ovarian and testicular changes.

Materials and Methods

Between June 1978 and October 1980 *L. richardsoni* were obtained by seine-netting within the surf zone of Algoa Bay. Two specific areas were sampled, King's Beach (33°58′S/25°39′E) and Bluewater Bay (33°52′S/25°41′E). A total of 777 individuals were examined, 528 males and 249 females. Random subsamples of these were used for

subsequent analyses. Total length, standard length and mass of the fish were recorded. A mid-ventral incision of the abdomen was used to expose the gonads. A visual assessment, based on macroscopic features, was made of the maturity state of each fish (Hjort 1910). The paired gonads were dissected out from the body and weighed to the nearest 0,01 g. The mean monthly gonadosomatic index (GSI) was estimated for the separate sexes.

To verify the maturity stages assigned by visual methods, monthly subsamples were examined microscopically. Small pieces of gonadal tissue from the anterior and posterior regions were fixed in Bouin's solution. Once fixed the material was stored in a 70% ethanol:glycerol solution (95ml:5ml). Subsequently the tissue was routinely dehydrated, embedded in Histosec and sectioned at 5 – 7 μm. Sections were stained in Delafield's haematoxylin or modified Mayer's haematoxylin and counterstained with eosin. D.P.X. or Clearmount was used as mounting medium.

Ovarian development was assessed using a combination of the classification systems of Yamamoto (1956) and Braekevelt & McMillan (1967), as adopted by Van der Horst (1976) in a study of the groovy mullet *L. dumerili*. Follow-

Table 1 Morphological characteristics of oocytes in the southern mullet, *L. richardsoni*

Developmental stage	Cell diameter (μm)	Nuclear diameter (μm)	Nuclear characteristics	Cytoplasmic characteristics	Membranous coverings of oocyte
Chromatin nucleolus oocyte (CNO)	18,9 ± 0,5 (17,2 – 30,1)	12,0 ± 0,3 (0,4 – 8,6)	Nucleus is roughly spherical, it contains one or more distinct chromatin nucleoli. Nucleus forms the major proportion of the cell.	Small cells, spherical to oval in shape. Cytoplasm stains brick red, clearly distinguished from other cells.	Cell membrane apparent
Early perinuclear oocyte (EPO)	43,0 ± 1,03 34,4 – 64,5	24,1 ± 0,5 (8,6 – 21,5)	Spherical nucleus containing 2 – 15 nucleoli of varying size and shape. Chromatin threads are visible in the nucleus. Nucleoli are situated along nuclear periphery.	Cytoplasm is homogenous and highly basophilic. Occasional vesicles are found irregularly scattered throughout the cytoplasm.	Cell membrane apparent
Late perinuclear oocyte (LPO)	77,4 ± 1,1 (60,2 – 103,2)	47,3 ± 0,7 (34,4 – 60,2)	Nucleoli more numerous than earlier stage 8 – 25 nucleoli being distributed along the periphery of of the nucleus.	Cytoplasm is less basophilic, some cells have 'granular' cytoplasm. A few cells show cytoplasmic zonation — a thin less basophilic peripheral zone contrasting with the inner granular area.	Cells showing cytoplasmic zonation are bounded by a very thin poorly stained layer
Yolk vesicle oocyte (YVO)	Early stage 105,8 ± 1,2 (86,0 – 146,2)	62,8 ± 0,9 (55,9 – 81,7)	Nucleus, as in the previous stage, with 9 – 23 nucleoli distributed peripherically.	A thin layer of 'granular' basophilic cytoplasm lies inside the zona radiata, similar cytoplasm is dispersed irregularly about the nucleus. In the early phase a ring of yolk vesicles appears in the cytoplasm, along the nucleus. As development proceeds rings of yolk vesicles appear at the periphery, and eventually the cytoplasm is full of yolk vesicles.	A distinct, thin, acidophilic layer, the zona radiata appears around the oocyte's periphery. External to this is a basophilic layer, the follicular granulosa.
Primary yolk oocyte	198,7 ± 2,7 (133,3 – 249,4)	78,3 ± 1,4 (55,9 – 77,4)	Nucleoli are basophilic, majority are still situated along nuclear membrane, 8 – 23 nucleoli being observed in a cross-section. Lamp brush chromosomes are visible in the nucleus.	Yolk vesicles fill the entire cytoplasm. In the early stages tiny basophilic yolk globules appear, seem to be confined to the periphery and are situated within the yolk vesicles, i.e. they are intravesicular. As development proceeds yolk globules increase in size and abundance until virtually all vesicles are occupied. There is a tendency for yolk globules to be larger close to the nucleus. Thin layer of lightly basophilic cytoplasm is still visible inside the zona radiata, it is devoid of yolk vesicles and globules.	Zona radiata appreciably thickened · > 1,4 μm in diameter. The follicular granulosa is prominent.
Secondary yolk oocyte	275,2 ± 2,8 (223,6 – 322,0)	82,6 ± 1,3 (77,4 – 107,5)	4 – 14 nucleoli in a cross-section. Nucleus is still relatively spherical, poorly stained, a few lamp brush chromosomes visible. Some nucleoli appear vacuolated.	Cytoplasm is full of large extravesicular eosinophilic yolk globules. Yolk vesicles still present. Lightly basophilic cytoplasm layer at periphery has decreased in thickness.	Zona radiata has increased in thickness, mean diameter 3,4 μm. Cross striations, indicating the radial canals are visible. Follicular granulosa is one layer of cells thick.
Tertiary yolk oocyte	413,0 ± 5,1 (350 – 490)	93,8 ± 2,5 (84 – 91)	Nucleus is still centrally positioned, 5 – 18 nucleoli observed in cross-section.	Cytoplasmic characteristics similar to those of secondary yolk stage. Yolk vesicles beginning to coalesce, yolk globules have increased in size. Further decrease in thickness of peripheral lightly basophilic cytoplasm.	Zona radiata has increased to a mean diameter of 11,2 μm. Not only cross striations are visible, zona radiata also has a laminate appearance.
Migratory nucleus oocyte	> 400 μm		Nucleus moving towards one side of cell, almost spherical in outline. 6 – 10 faintly stained nucleoli are situated peripherically.	Cytoplasm is packed with yolk globules. 3 – 6 large fat droplets present.	Zona radiata thickened further, mean diameter of 17,3 μm. Cells of follicular granulosa are separated by vesicle-like structures.

ing these systems eight developmental stages were observed as indicated in Table 1. To assess seasonal variations in the proportion of oocytes at a particular stage 200 – 400 oocytes were classified per section on the basis of their morphological appearance. Oocyte diameter, nuclear diameter and thickness of the zona radiata were measured for a minimum of 30 oocytes at each morphologically defined stage, using an eyepiece micrometer. Only cells which had been sectioned through the nucleus were measured, the diameter of ovoid oocytes was estimated from the mean of the long and short axes. The number of nucleoli present was also recorded for each developmental stage. Results are expressed as the mean ± S.D.

Testicular maturation was assessed using the classification system based on the presence and relative proportions of the various spermatogenic cells. Such schemes have been adopted by Gokhale (1957), Hyder (1969), Hiroi & Yamamoto (1970), Ruby & McMillan (1970) and Van der Horst (1978).

Results

The sex ratio for the 777 specimens examined was 2,1 male:1 female. This skewed ratio reflects the fact that on several occasions large schools of male fish were encountered. The fish ranged in size from 23,0 to 39,0 cm total length. The length frequency histograms for the separate sexes are shown in Figure 1, from which it is apparent that the males tended to be smaller than the females.

Gonadosomatic indices

Figure 2 shows monthly variations in gonadosomatic indices. Similar cyclic variations are apparent in the gonadosomatic indices of male and female mullet. The period of greatest sexual development extends from September to March and spawning probably occurs during most of this period. The ovary attains a greater mass than the testis, maximum GSIs of 23,71 and 6,42 being recorded for females and males respectively. Lowest gonadosomatic indices were recorded between May and August and this reflects a period of sexual inactivity. The pre-spawning period, August to September, and the post-spawning period, March to May, were of relatively short duration.

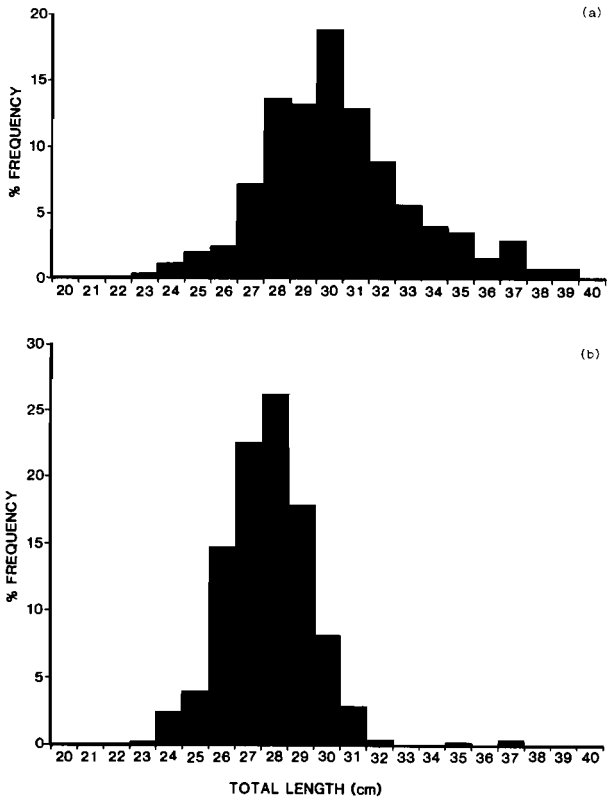

Figure 1 Length frequency histogram for (a) female and (b) male *L. richardsoni* from the surf zone, King's Beach.

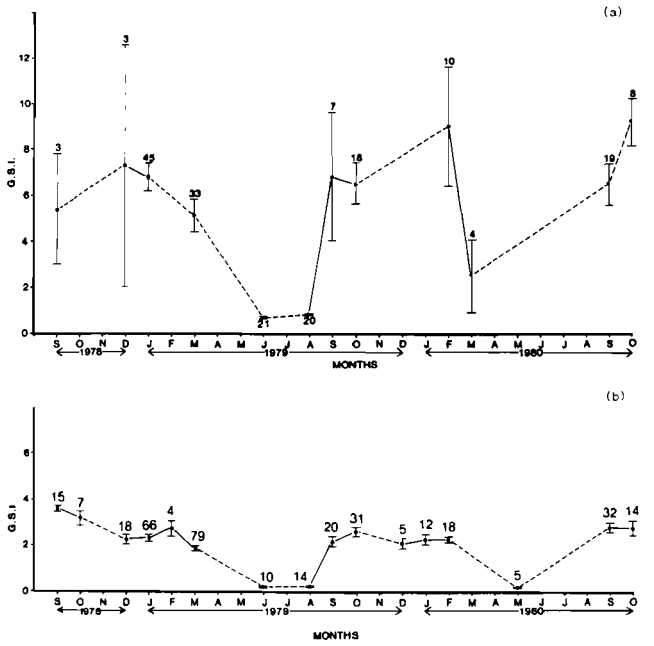

Figure 2 Seasonal variations in the gonadosomatic indices of (a) female *L. richardsoni* and (b) male *L. richardsoni*. Data are given as mean ± S.E.M. calculated on a monthly basis. Numbers denote sample size.

Variations in the occurrence of maturation phases during the breeding cycle

The percentage of fish with gonads in different maturation phases, as determined on a visual basis, is given at monthly intervals in Figure 3. Comparison of these histograms with the cyclic variations in GSI shows that in the early stages of sexual development (September to October) the majority of mullet were classified as active or ripe in the case of females, with the males being mainly in the active phase. The later stages of sexual development were characterized by ripe and ripe-running individuals of both sexes. The proportion of spent animals had increased by this stage (February to March). At the beginning of the period of sexual inactivity (May to August) spent males predominated, whereas in August inactive males and females at the early recovery stage were prominent.

Histological study of gonadal maturation

The morphological criteria used in oocyte classification are summarized in Table 1. Staging was based on changes in nuclear and cell diameter, nucleus, cytoplasm and membranous coverings of the oocyte.

The histological features defining each of the seven

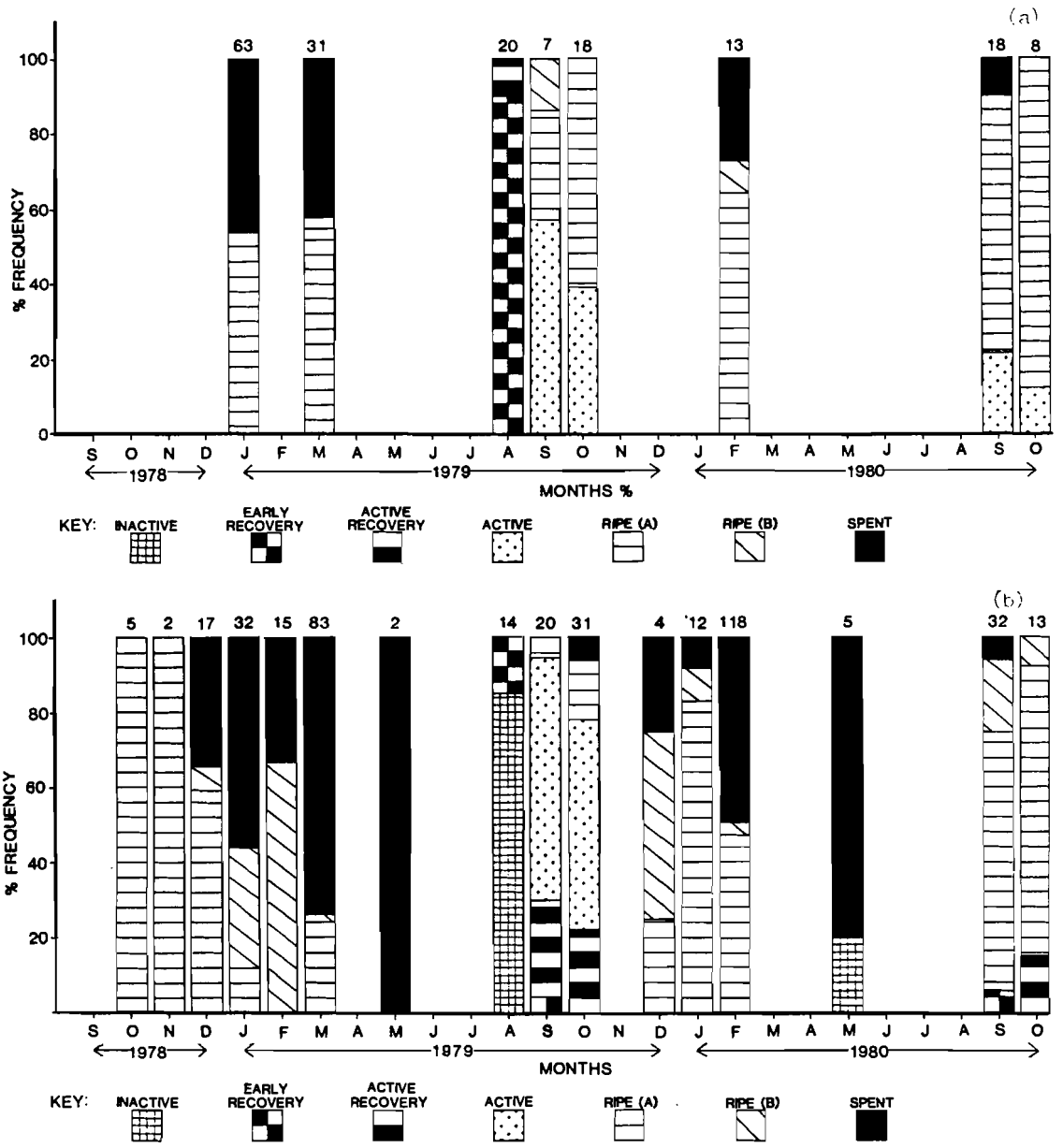

Figure 3a and b. Percentage of fish with testes and ovaries corresponding to maturity states based on visual assessment. Data are expressed as a percentage of the total number of fish examined monthly. Number of fish examined is given above each histogram.

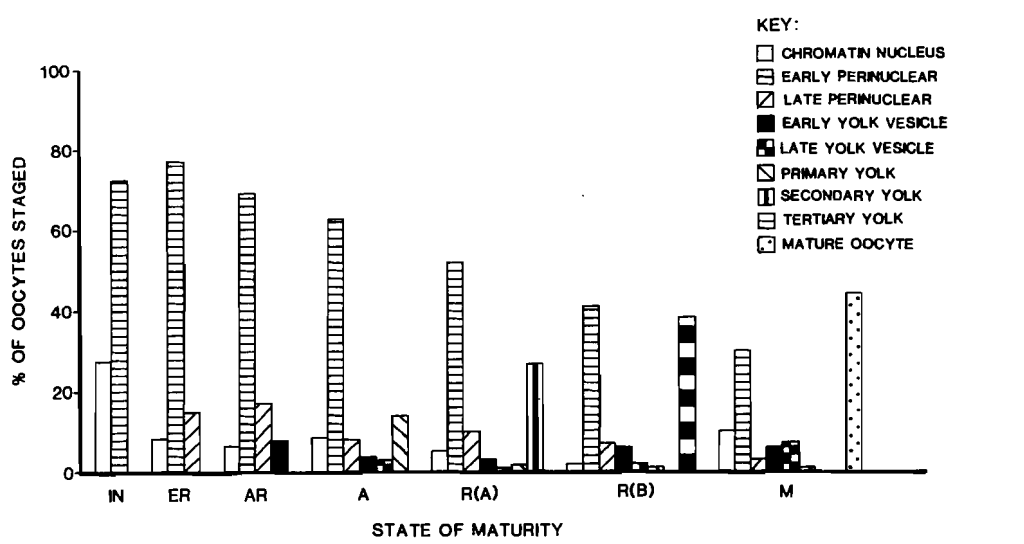

Figure 4 Variation in the distribution of nine oocyte types according to stage of maturity in the southern mullet, *L. richardsoni*. (IN, inactive; ER, early recovery; AR, active recovery; A, active; R(A), early ripening; R(B), late ripening; M, mature condition.)

maturation phases recognized in male and female *L. richardsoni* are presented in Table 2. Distinctions between the maturation phases were based on the presence or absence of particular spermatogenic or oogenic cells. This does not necessarily imply that the most advanced oocyte stage characteristic of each maturation phase is the numerically predominant feature of that histological section. The mean percentage, standard error about the mean and range of oocyte types at each maturation phase are presented in Table 3. A visual interpretation of these data is given in Figure 4. Early perinuclear oocytes were observed in all maturation stages and were invariably the most abundant type of oocyte present. The proportions present ranged from 77,0% at early recovery to 41% in ripe individuals. The proportion of non-yolky oocytes as a whole decreased steadily as maturation proceeded and they gave rise to more advanced

Table 2 Histological characteristics in relation to reproductive phases in the gonads of *L. richardsoni*

Reproductive phase	Histological features	
	Testis	Ovary
Inactive	No indication of lobular organization. Primary spermatogonia are dispersed amongst the connective tissue fibres. Sperm remaining from the previous breeding cycle were present in the main sperm duct.	Characterized by the presence of oogonia, chromatin-nucleolus oocytes and early perinuclear oocytes.
Early recovery	Testes clearly organized as lobules, comprising spermatogonia. Latter have increased markedly in number.	The ovigerous folds of the lamellae contain oogonia and oocytes of the inactive condition plus late perinuclear oocytes.
Active recovery	Spermatocytogenesis has taken place. Testes are composed of cysts mostly containing spermatogonia, as well as some primary and secondary spermatocytes.	Yolk vesicle oocytes become apparent.
Active	All spermatogenic cells are present. Lobules are full of cysts, comprising primary and secondary spermatocytes, and spermatids. Rupture of cysts releases sperm into the lobule lumen.	Primay yolk oocytes are present.
Ripe	Up to 50% of the lobules contain sperm, main sperm duct also filled with sperm. Few cysts remaining contain spermatocytes.	Secondary and tertiary yolk oocytes are present.
Spawning	Spermatogenesis is complete, testes are full of sperm. Only peripheral lobules show other spermatogenic cells. Main sperm duct maximally distended.	
Spent	Lumen of lobules show emptying, lobule walls apparently thickening owing to invasion by collagen fibres. Spermatogonia present in great numbers.	Lamellae show empty follicles, some atretic oocytes are present. Only early stages are otherwise apparent i.e. up to and including early perinuclear oocytes.

Table 3 Variations in the proportions of nine oocyte developmental stages associated with prominent ovarian maturity phases observed in *Liza richardsoni*. Data is given as the mean percentage ± standard error and the range is given in parenthesis. *N* is the number of samples examined at each maturation phase, *T* is the number of oocytes staged

Oocyte development stage	Maturation phase							
	Immature $N=1$; $T=610$	Inactive $N=1$; $T=687$	Early recovery $N=6$; $T=3096$	Active recovery $N=5$; $T=2429$	Active $N=6$; $T=2478$	Ripe (A) $N=3$; $T=1563$	Ripe (B) $N=9$; $T=2203$	Mature $N=2$; $T=281$
CNO	9,7	27,7	8,3 ± 0,5	6,5 ± 1,2	8,5 ± 14	5,4 ± 2,2	2,6 ± 0,8	9,9
			(6,9 – 9,8)	(2,2 – 9,6)	(4,8 – 14,4)	(1,3 – 8,5)	(0,8 – 7,2)	(2,3 – 17,5)
EPO	90,3	72,3	76,7 ± 2,9	69,3 ± 3,8	62,7 ± 2,8	52,2 ± 4,9	40,9 ± 3,4	29,8
			(68,6 – 84,2)	(57,1 – 79,0)	(53,4 – 68,4)	(42,7 – 59,2)	(23,1 – 54,5)	(21,4 – 38,2)
LPO			15,2 ± 3,0	17,2 ± 2,7	7,9 ± 1,1	9,8 ± 1,6	7,2 ± 1,2	2,7
			(7,6 – 24,3)	(8,8 – 22,7)	(4,1 – 11,9)	(7,0 – 12,5)	(2,5 – 14,5)	(1,9 – 3,4)
EYVO				3,9 ± 0,6	3,7 ± 0,8	3,6 ± 0,6	6,5 ± 1,1	6,0
				(2,5 – 15,6)	(0,4 – 5,7)	(2,5 – 4,3)	(1,9 – 12,4)	(2,9 – 9,0)
LYO					3,4 ± 1,7	0,6 ± 0,1	2,1 ± 0,6	6,8
					(0,3 – 11,2)	(0,3 – 0,8)	(0,6 – 6,6)	(0 – 13,6)
1°YO					13,9 ± 3,3	1,7 ± 0,5	1,5 ± 0,7	0,6
					(2,2 – 22,5)	(1,0 – 2,7)	(0,0 – 7,0)	(0 – 1,1)
2°YO						26,9 ± 4,8	0,4 ± 0,2	0,0
						(20,7 – 36,3)	(0,0 – 1,8)	
3°YO							38,7 ± 3,6	0,0
							(21,0 – 54,4)	
MO								44,4
								(42,7 – 46,1)

oocytes. The proportion of primary yolk oocytes declined rapidly as they matured into secondary oocytes. Similarly, the proportions of secondary oocytes decreased from 27,0% to 0,41% between the two ripe phases. The enormous number of cells present in testes and the difficulty in making accurate counts preclude similar quantitative histological analyses in males.

Discussion

The lack of confirmed observations on the spawning behaviour of members of the Mugilidae has led to controversy over the location of spawning sites. Referring to the situation pertaining to the grey mullet, *Mugil cephalus*, Kesteven (1953) states 'it is believed that the fish spawn on the coast, in the surf zone, but this has not yet been confirmed for this or any allied species anywhere in the world'. Bromhall (1954) pointed out that many observers considered the spawning grounds of *M. cephalus* to be situated at the heads of rivers rather than on the sea coast. This debate has still not been settled (Van der Horst & Erasmus 1981).

During the present study two mature individuals of *L. richardsoni*, characterized by massive ovaries containing large (mean diameter 954 μm) translucent ova, were obtained from the surf zone at King's Beach. These individuals had gonadosomatic indices of 22,99 and 23,71 and were caught in September 1979 and February 1980 respectively. Mature females of the allied species *L. dumerili*, with gonadosomatic indices exceeding 20, were also recorded from the surf zone at King's Beach (Lasiak, Van der Horst & McLachlan unpubl.). Such observations, accompanied by the prevalence of ripening and at a later stage spent individuals in the surf zone suggest that spawning takes place close inshore in *L. dumerili* and *L. richardsoni*. The apparent rarity of mature individuals may be a reflection of the rapidity of final maturation and the consequently lowered probability of capturing mature fish. However, it may also be indicative of spawning further offshore.

Reviews of spawning time in various members of the Mugilidae by Thomson (1966), Abraham *et al.* (1966), and Van der Horst & Erasmus (1981) indicate that these fish reproduce under several temperature regimes. In Algoa Bay *L. richardsoni* spawns during spring and summer, with marked gonadal development taking place between September and April. This is in close agreement with Marais (1976) who classed *L. richardsoni* as summer spawners in the Swartkops estuary. The closely related species *L. dumerili* was considered by Van der Horst & Erasmus (1978) to spawn during the summer period in the Swartkops estuary. However, Wallace (1974) gives the spawning period of *L. dumerili* from Natal estuaries to be during the winter and early summer. The spawning period of *L. richardsoni* may also vary according to the temperature regimes.

Table 3 indicates that even in ripe individuals of *L. richardsoni* the proportion of yolkless oocytes exceeds that of vitellogenic oocytes, early ripe individuals (Ripe (A)) having a mean of 67% yolkless oocytes, and 33% vitellogenic oocytes. Late ripe individuals (Ripe (B)) had a mean of 51% yolkless and 49% vitellogenic oocytes. However, it is not evident from histological studies whether all these vitellogenic oocytes finally mature, consequently the proportion of oocytes contributing to the fecundity in a particular breeding season may well be less than 49%. This compares well with the 42% of the oocytes in pre-spawning individuals of *Mugil capito* being at the primary to tertiary yolk stage (Abraham *et al.* 1966). In the same study 75% of the oocytes observed in *M. cephalus* at the beginning of the spawning period were at the secondary and tertiary yolk stage. Van der Horst (1976) gives the proportion of vitellogenic oocytes in an early ripe individual of *L. dumerili* as 55%.

Histological studies result in a clearer definition of the breeding cycle, and are of particular relevance in the estimation of fecundity and investigation of breeding synchronism. Standard methods of fecundity estimation as given in Bagenal (1978) rarely take into account the fact that not all oocytes reach maturity that season. Neither is any allowance made for abortive or atretic oocytes. The use of quantitative histological studies in conjunction with fecundity estimates may result in more accurate estimates of the number of eggs produced by synchronous spawners.

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