MATURITY AND SPAWNING OF THE SNAPPER, LUTIANUS KASMIRA (FORSKAL) FROM THE ANDAMAN SEA

K. RANGARAJAN¹

Central Marine Fisheries Research Institute; Unit, Port Blair

Abstract

Lutionus kasmira of the Andaman Sea spawns only once in a year but the spawning period is likely to be spread over a period of four or five months from November to March. The occurrence of mature fish over a prolonged period and high gonadosomatic index during a number of months lend additional evidence for the prolonged spawning season of the fish. The minimum size at first maturity was about 170 mm and fifty per cent maturity was attained when the fish grew to a length of 200 mm. Fecundity was found to fluctuate very widely from 42,100 to 332,620. The sexes were found to be disproportionate in the catches, the males outnumbering the females, which suggests that differential fishing could occur in Lutianus kasmira.

INTRODUCTION

In the Andaman group of islands, the sea-perches form a major fishery contributing about 20-30% of the total fish landed every year. Among the perches, fishes belonging to the family Lutianidae are very common. The Andaman Islands, with a rocky coastline and fairly deep waters, afford an ideal habitat to many species of *Lutianus*, and the blue-and-yellow snapper, *L. kasmira*, is fairly common in these islands occurring almost throughout the year.

Practically no information is available on the various aspects of the biology of *L. kasmira* except the brief mention made by Basheeruddin and Nayar (1962) on the food and size range of the juveniles of this species. Whitehouse (1923) has mentioned about the breeding season and size range of young ones of *L. quinquelinearis* (=*L. kasmira*). Rangarajan (1972) has dealt with the food and feeding habits of *Lutianus kasmira* from the Andaman Sea and the present communication is on the maturity and spawning of the species from the same area.

MATERIAL AND METHODS

A total number of 792 fishes, consisting of 352 females and 440 males, ranging in total length from 70 mm to 303 mm, collected from the Port Blair fish market during 1966-68, was examined for this study. The total length, weight, sex and stage of maturity of each fish were recorded. The ovaries and testes were preserved in

J. Present address: Central Marine Fisheries Research Institute; Sub-station, Madras-8.

5% formalin. As no appreciable shrinkage or swelling of the ova due to preservation was noticed when compared with fresh material, all studies were made on preserved material. A plot of the diameters of the ova obtained from the anterior, middle and posterior regions of the right and left ovary (stage V) showed a similar distribution pattern. However, for the sake of uniformity, portions removed from the middle region of both the ovaries were used for further studies.

MATURITY STAGES

The I.C.E.S. classification of maturity stages (see Lovern and Wood, 1937) was followed in this study. The morphological characteristics of the different stages as observed in *L. kasmira* are given below. Spawning (stage VI) and spent (stage VII) specimens were not available.

Stage I. Immature

Ovaries appear very thin and transparent and occupy less than one third of the body cavity. Ova are not visible to naked eye, irregular in shape and transparent. The diameter of ova ranges from 0.010 to 0.084 mm. Yolk deposition has not yet commenced. Testes are very thin, thread-like and transparent.

Stage II. Maturing

Ovaries are pinkish, occupying about one third of the body cavity. The maximum size of the egg has increased to 0.302 mm and yolk deposition has just commenced in maturing ova. Testes in this stage are narrow, whitish and are of the same size as the ovary.

Stage III. Early mature

Ovaries occupy about half the body cavity and are slightly yellow. Ova are spherical and opaque with deposition of yolk. The maximum size of the egg is 0.454 mm. The first group of mature ova gets separated at this stage from the immature egg stock with a distinct mode at 0.403 mm. Testes in this stage appear creamy white, flat and extend up to half the length of body cavity.

Stage IV. Late mature

Ovaries are distinctly yellow and occupy nearly three-fourths of the body cavity. Ovarian walls are thin and the maximum size of the ova is 0.538 mm. The mode of the largest group of ova fails at 0.403 mm as in the previous stage. Eggs are fully laden with yolk. Males with testes of this stage were not available for study.

Stage V. Ripe

Ovaries are greatly enlarged, turgid and occupy almost the entire body cavity. They are fully packed with large, opaque yellow eggs. The maximum diameter of the egg has increased to 0.655 mm. Mature eggs show a transparent peripheral

K. RANGARAJAN

zone and a number of oil globules measuring 0.034-0.084 mm in diameter are present. Ripe testes were not available for study.

DEVELOPMENT OF OVA TO MATURITY

Ovaries typical of the five stages, i.e. stage 1 to stage V, were selected for this study. The diameters of 500 ova from the middle region of each ovary were measured and the average percentage for each micrometer division (m.d.) calculated. The frequencies at three-micrometer division intervals have been presented in Fig. 1.



FIG. 1 Ova-diameter frequency polygons of ovaries of Lutianus kasmira in different stages of maturity.

The first batch of mature ova gets separated from the general egg stock with a distinct mode at 0.403 mm in stage III. In stage 1V, besides an increase in the maximum size of ova, a rise in the percentage of ova at the 0.403 mm mode has been seen, although the mode itself remains stationary. As the ovary passes on to stage V, which represents a fully ripe ovary, two distinct modes are seen in the mature group of ova. The first mode which was noticed at 0.403 mm in the previous stage has advanced to 0.504 mm and another has appeared at 0.403 mm. The mode at 0.504 mm evidently constitutes the group of eggs which are to be spawned in the ensuing spawning season. The ova under the mode at 0.504 mm were fully yolked and showed a transparent peripheral zone. Moreover a number of oil globules were also seen scattered in the cytoplasm indicating that the ova were fully ripe. The ova of mode 0.403 mm were also fully yolked and mature but did not show a transparent peripheral zone or oil globules. The total range in size of the intra-ovarian eggs was from 0.084 to 0.655 mm. All the ova above 0.303 mm in diameter were fully yolked and in the same stage of maturity.

SPAWNING.

As already seen, in the mature ovary of *L. kasmira* (stage V), there are only two groups of eggs, namely the immature egg stock and the mature group. The mature group of ova is represented by two distinct modest, one at 0.403 mm and another at 0.504 mm. Since these two modes are quite close and not fully separated from each other it may be inferred that the mode at 0.403 mm would advance to further maturity before spawning commences and the fish would spawn only once in a year. The absence of ova which have undergone half the maturation process in the stage V ovary suggests that there may not be a second spawning in the same year. However, since spawning and spent individuals have not been examined it is difficult to draw definite conclusions on the frequency of spawning.

The percentage occurrence of fishes with gonads in different stages of maturity during different months was determined to fix the spawning season. A total of 290 fishes of both sexes during 1966, 237 during 1967 and 265 during 1968 were examined. The data relating to females are presented in Table 1, and the occurrence of different stages of males was more or less similar to that of females.

The data indicate that generally mature fishes were common in the catches from August/September to March. High percentage of mature fishes occurred during October and November, showing a general decrease thereafter. The occurrence of mature fishes of *L. kasmira* over a period of four or five months indicates that the species has a prolonged spawning season extending from November to March.

Males beyond stage III were not encountered in the collections during the three years of investigation. The reason for the absence of advanced stages of males in inshore waters is not clear. Probably it might indicate that the process of maturation in males is completed in offshore areas.

Whitehouse (1923) noticed a continuous arrival of small fishes of L. quinquelinearis (=L.kasmira) measuring 3.5 to 4.5 cm into the Silvathurai lagoon, Tuticorin, over a fairly long period from September to March and concluded that the species might have a prolonged spawning period of nearly three months. The present observations agree with those of Whitehouse (1923).

GONADO-SOMATIC INDEX

The relative ovary weight or the gonado-somatic index (ovary weight $\times 10^3$ / fish weight) has been employed by various workers to explain the state of maturity in fishes. Since this index may be useful to indicate the maturity and periodicity of spawning, the Gonado-somatic index of 352 females has been analysed. The weight of individual fish was recorded. The ovaries after preservation in 5% formalin were carefully dissected out, excess moisture and surroundig tissues removed and weighed to the nearest milligram.

- BT-									1967				· .		1968		:
· INO.	1	П	ш	IV	.v	No.	1.	, II	ш	IV	v	No.	1	Ш	III	IV	. V
·	_	:	· –	_	_	13	61.5	·	38.5	— .	' <u> </u>	14	71.4	14.3	7.1	7.1	′. <u> </u>
_		. ** 	<u> </u>	— [′]	_	5	20.0	80.0	_	<u> </u>		9	22.2	66.7	_	-	11.1
·. <u> </u>	_	· 	_		_	9	33.3	22.2	44.4	_	<u> </u>	3	66.7	—	33.3	—	. —
14	71.4	21.5	7.1	.	_	15	93.3		6.7	·		~8	100.0	· <u> </u>		_	: .
15	80.0	- 20.0	_	_	_	. 9	66.7	33.3	_	 ;;	_	1	100.0	·			· _
20	85.0	15.0		_		9	22.2	77.8		_		14	21.4	35.7	35.7	7.1	
15-	53.3	40.0	6.7	_	_		_	_	_	— (_	20	90.0	5.0	5.0	<u> </u>	
<u>`9</u>	88.9	. —		_	11,1	20	65.0	25.0	10.0	_		5	80.0	·		20.0	_
29	48.3	20.7	13.8	-	17.2	3	_	100.0	<u> </u>	. —	_	12	25.0	75.0	—	. —	_
9	22.2	11,1	44.4	22,2	_	6	-16,7	83.3	. —	— , ,	_	3	—	. 33.3	66.7	_	_
11	54.5	27.3	18.2	_	—	23	30.4	26.1	43.5	` — ,	—	8	·	100.0	_	<u> </u>	_
8	—	50.0	12.5	25.0	12.5	3	100.0		_	_	_	10,	80.0	20.0	<u> </u>	— .	_
				$\begin{array}{cccccccccccccccccccccccccccccccccccc$													

TABLE 1. Percentage occurrence of different stages of maturity in the females of L. kasmira in various months

118

K. RANGARAJAN

.

The immature ovaries revealed an index up to 2.0 and maturing ovaries from 2.0 to 10.0. The mature ovaries showed an index above 10.0 and it progressively increased with maturity reaching a maximum of 67.0 in a fully mature ovary. The average gonado-somatic index for different months is given in Table 2. It is generally seen that the higher values were recorded from September to December in 1966, January to March, August and November in 1967 and January to March, August and November in 1967 and January to March, August and November in 1967 and January to March, August and November in 1968. The fact that the index is fairly high during the period August/September to March lends further evidence that the fish has a prolonged spawning period.

	1	966	. 1	967	1968			
Months	No.	G.S.I.	No.	G.S.I.	No.	G.S.I.		
January		_	13	5.87	14	4.32		
February			5	2.10	9	7.82		
March			9	9.57	3	9.56		
April	14	1.81	15	3.82	8	1.20		
Мау	15	1.21	9	2.26	1	1.43		
June	20	1.05	9	2.84	14	11.60		
July	15 -	3.04		_	20	2.31		
August	9	5.65	20	4.91	5	8,88		
September	29	13.44	3	2.39	12	2.21		
October	· 9 [·]	17.40	6	2.79	3	13.42		
November	11	5.72	23	7.37	8 ·	2.98		
December	8	19.80	3	1. 91	10	1.13		

 TABLE 2. Average gonado-somatic index (G.S.I) in L. kasmira during different months.

In order to find out whether the gonado-somatic index has any relationship with the feeding intensity of the fish, the data at Table 3 were analysed. It may be seen from the table that in the case of immature fish (below 200 mm length), high relative ovary weight coincided with high feeding intensity in the months of March and November 1967 and October 1968. However it was also noticed that during certain months, especially September and December 1966, May, September and December 1967, March and August 1968, when the relative ovary weight was high the feeding intensity was poor. In the case of mature fish (above 200 mm length) also no direct relationship could be found between the gonado-somatic index and feeding intensity. The analysis showed that in *Lutianus kasmira* the variations of gonado-somatic index were not related to the feeding intensity.

CONDITION FACTOR

The condition factor or ponderal index (Thompson, 1943; Hile, 1936) was calculated by applying the formula $K=100 \text{ W/L}^3$, where K represents the condition factor, W the weight of the fish in grams and L the length of the fish in centimetres.

K. RANGARAJAN

Since the purpose of the study is to trace the condition cycle of the fish throughout the year in relation to maturity and feeding, they were classified into two groups, namely immature (below 200 mm) and mature (above 200 mm). The average values of condition factor, gonado-somatic index and volume of food for immature and mature fish during different months are given in Table 3.

It may be seen from the data that the condition of the immature fish during June, July and August 1966 was lower than the weighted average for the whole year. For the mature fish in the same year the condition was lower during April, May, July and November than the weighted average for the whole year. During 1967 the lower values were obtained in January-April and November for both immature and mature fishes. In 1968, January, May, August and December showed lower values for the immature fish and January-March and August for the mature fish. It should be pointed out that the number of mature fish contributing to each mean is small in many months and hence great reliance cannot be placed on such values.

Variations in condition of different fishes have been attributed to various factors by earlier workers. In *Pleuronectes platessa* high and low condition are found before and after spawning respectively (Thompson, 1943). Hickling (1945) found the condition low before spawning and high after spawning in *Sardina pilchardus* which was explained as due to sexual cycle and the availability of food respectively. Qasim (1957) suggested that the increase and decrease of condition in the shanny, *Blennius pholis* are probably due to general building up and loss of reserves respectively. In *Thyrsites atun* it was not possible to correlate the changes in condition either to sexual cycle or the intake of food and they may depend upon several other factors (Biackburn, 1960).

In the case of L. kasmira, although the condition of immature fish differs from that of mature fish in various months, it may be seen that in immature fish also the condition was high during the spawning season, indicating that probably factors other than sexual cycle may be responsible for the variations in the condition. Again, it was not possible to correlate the variations in condition both in the immature and mature fishes with the feeding intensity. Hence it could be said that in L. kasmira changes in condition are not related to the reproductive cycle or feeding intensity but may be due to other environmental factors.

SIZE AT FIRST MATURITY

To determine the minimum size of fish at first maturity a total of 352 females and 440 males collected during 1966-68 was grouped sex-wise into 10 mm size groups and the percentage occurrence of fish of various maturity stages in each size group was calculated.

All the females up to 139 mm in total length were in the immature stage. From 140 mm onwards the percentage of immature fish steadily decreased with a corresponding increase of mature fish. A small percentage of fish (1.5%) was found

120

		Imm	ature	1966		Ма	ture			1967 Immature Mature						Immature			1968 Mature					
Months N	No.	K	G.S .1	l Vol.	No	. к	G.S.I.	Vol	. N	0. K	G.S.I	. Vol.	No.	K	G.S.I.	Vol.	No.	K	G.S.I.	Vol.	No	K	GSI	Vo
Jan.	-	_		_	_	_	_		15	1.44	2.45	0.37	7	1.50	6.50	0.22	19	1.39	1.15	0.44	5	1.38	8.87	0.00
Feb.	_	—	_	_	_	—	_	—	11	1.61	1.14	0.22	_		_	_	17	1.51	1.3 9	0.64	8	1.44	7.07	0.08
Mar.	_		-	-	_	_	_		10	1.37	4.56	1.55	14	1.41	3. 9 4	1.57	4	1.50	7.27	0.57	6	1.39	1.96	0.00
Apr.	18	1.46	0.28	0.60	9	1.37	2.85	0.7 9	19	1.39	1.31	0.51	10	1.47	4.12	_	30	'49	0.56	1.00	_	—	-	—
Мау	35	1.48	0.56	0.51	5	1.49	1.76	1.29	17	1.51	0.99	0.86	3	1.53	2.55	_	5	1.45	0.52	0.14		_	-	_
June	42	1.41	0.60	0.50	9	1.59	0.58	2.03	22	1.59	1,35	0.79	_	_	_	_	14	1.51	5.08	0.35	25	1.51	4.22	0.95
Jul	26	1.38	1.41	0.39	10	1.44	1.78	1.60	_	_	<u> </u>	_	_	_	_	_	40	1.52	1.33	0.42	8	1.55	0.87	0.00
Aug.	25	1.40	0.39	0.43	4	1.54	12.46	0.10	28	1.51	3.43	0.57	11	1.65	1.41	2.37	9	1.47	4.98	0.39	5	1.42	0.66	3.75
Sep.	28	1.47	7.50	0.35	17	1.50	11.82	0.39	6	1.54	1.05	1.07	5	1.61	0.61	0.00	28	1.51	1.13	0.45	_			_
Oct.	17	1,49	7.17	0.45	10	1.52	5,16	0.96	11	1.56	1.68	0.10	_	-	_	_	2	1.62	8.55	0.71	6	1.64	4.48	0.07
Nov.	11	1.51	3.16	0.34	3	1.37	9.78	0.17	30	1.43	3.11	0.53	8	1.45	10.36	0.58	14	1.5	5 1.82	0.51		_		
Dec.	11	1.45	10.94	0.05	10	1.57	4.53	0.31	8	1.51	1.02	0.54	2	1.56	0.46	0.05	20	1.32	2 0.71	0.19	-	—	_	_
Fotal weighted	213				77]	77				60				202				63		•	
average		1.44				1.50				1.49				1.51				1.48			1	1. 49		

TABLE 3. Average values of condition factor (K), gonado-somatic index (G. S. I.) and volume offood (vol.) in immature and mature Lutianus kasmira

.

121

K. RANGARAJAN

to be mature in the 160-169 mm group. In the 170-179 mm group, while the greater percentage of the fish (56.8%) were still in the maturing stage, 4.6% of fishes had attained maturity. About 20% of fishes were mature in the 180-189 mm group and about 42% in the 190-199 mm group. All the fishes in the 200-209 mm group were either in maturing or mature stage. Nearly 59% of the fishes were mature at this size group. From this size group onwards the percentage of mature fish increased rapidly and all the fish above 220 mm were mature. From these data it is clear that the minimum size at first maturity in *L. kasmira* was about 170 mm and fifty per cent maturity was reached at about 200 mm.

In the case of males all fishes measuring up to 159 mm in total length were found to be immature. The first mature specimen was noticed in the 160-169 mm size group as in the case of females. From 170-179 mm size group onwards the percentage occurrence of immature fish decreased steadily with the corresponding rise in the percentage occurrence of maturing fishes. In the 200-209 mm size group only 20% of the fishes were immature while the remaining were either maturing or mature. As earlier pointed out males in advanced stages of maturity were not available for study. However, since the first mature male was noticed in the 160-169 mm size group, it may be said that the minimum size at first maturity in the male was about 170 mm which was the same as that of the female.

TABLE 4.	Range and average gonado-somatic index in L. kasmira under
	different size groups

Size groups	N7.	Range of relative	Average relative			
	No.	ovary weight	ovary weight			
90 — 99	2	0.10 - 0.12	0.11			
100 - 109	5	0.06 — 0.39	0.13			
110 119	6	0.14 — 1.28	0.67			
120 129	13	0.05 - 1.04	0.48			
130 — 139	20	0.17 - 2.38	0.86			
140 — 149	44	0.16 - 8.26	1.55			
150 — 159	28	0.26 5.67	1.51			
160 — 169	66	0.28 - 43.03	2,52			
170 — 179	44	0.25 - 36.09	3.56			
180 — 189	40	0.28 - 59.69	8.13			
190 - 199	38	0.42 45.06	11.37			
200 209	29	1.98 67.34	16.05			
210 — 219	15	7.63 - 49.93	20.93			
2 20 — 22 9	2	4.83 24.38	14.60			

The range of fluctuation in gonado-somatic index may also indicate the size of the fish at first maturity since the fluctuation will be very wide in mature fishes. The range of gonado-somatic index and the average value are given in Table 4. The range of fluctuation in relative ovary weight was small up to 159 mm. A wide

122

fluctuation was noticed in the relative ovary weight in the size group 160-169 mm which seems to correspond with the size group in which first maturity was noticed. The range of fluctuation in the gonado-somatic index was very high in fishes measuring above 160 mm. The maximum fluctuation in the value was noticed in the size group 200-209 mm coinciding with the size group in which fifty percent maturity occurred.

FECUNDITY

A total of 21 mature females ranging in total length from 169 to 219 mm was examined for fecundity. The excess moisture from the ovaries was removed with a filter paper and were weighed to the nearest milligram. From the central portion of the left and right ovary a small piece was cut out and its weight determined accurately. All the ova in each piece were teased out completely and the mature ova counted.



FIG. 2 Relationships between fecundity and length of fish, weight of fish, length of ovary and weight of ovary.

The total number of mature ova in the left and right ovary was calculated by taking into consideration the number of mature ova in the sample, the weight of the sample and the total weight of the ovary.

The fecundity of L. kasmira fluctuated very widely and was found to vary from about 42,100 to 332,620. Since the fish reveals a prolonged spawnig season the fecundity computed indicates only the potential stock of eggs present in various individual fish and not the number of eggs that will be shed during a spawning burst

The relationships between fecundity and length of fish, weight of fish, length of ovary and weight of ovary are shown in Fig. 2. The equations depicting these relationships are as follows:

Fecundity (Y) and length of fish (X) : $\log Y = -0.6154 + 2.5038 \log X$

Fecundity (Y) and weight of fish (X) : $\log Y = 1.5983 + 1.7065 \log X$

Fecundity (Y) and length of ovary (X) : log $Y = -1.3744 + 3.9565 \log X$

Fecundity (Y) and weight of ovary (X) : $\log Y = 4.2329 + 1.3628 \log X$

The correlation coefficients (r) for the above relationships were 0.77, 0.83, 0.84 and 0.95 respectively which indicate that a high degree of correlation exists for the relationship between fecundity and weight of ovary.

SEX RATIO

The size range considered for working out the sex ratio was from 70-79 mm to 300-309 mm. The percentage occurrence of sexes in different months for three years is given in Table 5. The ratios of females to males for the three years 1966, 1967 and 1968 were found to be 1:1.23, 1:1.06 and 1:1.48 respectively

Months	No.	Females:	Males	No.	Females:	Males	No.	Females:	Males
January		_	_	22	59.1	40.9	24	58.3	41.7
February		-	<u> </u>	11	45.5	54.5	25	36.0	64.0
March	_	-	_	24	37.5	62.5	10	30.0	70.0
April	27	51.9	48.1	29	51.7	48.3	30	26.7	73.3
Мау	40	37.5	62.5	20	45.0	55.0	5	20.0	80.0
June	51	39.2	60.8	22	40.9	59.1	39	35.9	64.1
July	36	41.7	58.3	_			48	41.7	58.3
August	29	31.0	69.0	39	51.3	48.7	14	35.7	64.3
September	45	64.4	35.6	11	27.3	72.7	28	42.9	57.1
October	27	33.3	66.7	11	54.5	45.5	8	37.5	62.5
November	14	78.6	21.4	38	60.5	39.5	14	57.1	42.9
December	21	38.1	61.9	10	30.0	70.0	20	50.0	50.0

TABLE 5. Sex Ratio of Lutianus kasmira in the commercial catches

indicating the general predominance of males over females. The sex ratio figures suggest that differential fishing could occur in *L. kasmira*, the males being fished more than the females.

Based on size groups, the males were predominant up to 99 mm. In the range 100-169 mm the females were predominant. From 170 mm onwards males were again predominant. A complete absence of females above 230 mm was noticed. It may be inferred that females above 230 mm may move out of the inshore waters to other areas probably for the purpose of spawning.

ACKNOWLEDGEMENT

The valuable suggestions and help received from Dr. S. Jones during the investigation are gratefully acknowledged.

REFERENCES

- BASHEERUDDIN, S. AND K.N. NAYAR. 1962. A preliminary study of the juvenile fishes of the coastal waters off Madras city. *Indian J. Fish.*, 8 (1): 169-188.
- BLACKBURN, M. 1960. A study of condition (weight for length) of Australian barracouta, Thyrsites atun (Euphrasen). Austr. J. mar. Freshw. Res., 2 (1): 14-41.
- HICKLING, C.F. 1945. The seasonal cycle in the Cornish pilchard, Sardina pilchardus Walbaum. J. mar. biol. Ass. U.K., 26: 115-138.
- HILE, R. 1936. Age and growth of the Cisco, Leucichthys artedi (Le Sueur) in the lakes of the northeastern highlands, Wisconsin. Bull. U.S. Bur. Fish., 48: 211-317.
- LOVERN, J.A. AND H. WOOD. 1937. Variations in the chemical composition of herring. J. mar. biol. Ass. U.K., 22: 281-2+3.
- QASIM, S.Z. 1957. The biology of Blennius pholis L. (Teleostei). Proc. zool. Soc. London., 128(2): 161-208.
- RANGARAJAN, K. 1972. Food and feeding habits of the snapper, Lutianus kasmira (Forskal), from the Andaman Sea. Indian J. Fish. 17: 43-52 (1970).

THOMPSON, D.AW. 1943. On growth and form. 2nd ed. University Press, Cambridge.

WHITEHOUSE, R.H. 1923. A statistical study of young fishes from Silvathurai lagoon, Tuticorin. Madras Fish Bull., 17 (3): 49-103.