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Ethology and reproduction of pteroid fishes found in the Gulf of Aqaba (Red Sea), especially *Dendrochirus brachypterus* (Cuvier), (Pteroidae, Teleostei)

by

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24 Figures

Summary. In the framework of the Red Sea coral reefs the pteroid fishes occupy a special position, being predators adapted solely to this habitat, and forming one of the top levels in the local food web. Three species are common here: *Pterois volitans, P. radiata* and *Dendrochirus brachypterus*. The first two species are solitary fishes, dispersed along the coral habitat, each defending his home range against conspecific and congeneric individuals. *Dendrochirus* are always found in groups of 3-4 to 10 individuals together around coral heads or rocky fragments. All three species are crepuscular, being active at sunset and during the evening hours. During these hours they catch food, using different techniques for fishing and for collecting benthic crustacea. Experiments show that they learn fast and so are able to avoid hunts and hunting technique dangerous for them.

With the onset of reproductive behaviour all three species show a tendency to gregariousness and sexual dimorphism in colour pattern as well as in behaviour. The males are much more aggressive than the females, exhibiting agonistic behaviour that includes lateral head shaking, circling display, lateral and frontal confrontation, and mouth to mouth biting. Females are paler, with swollen bellies marking ovarian development. Ovulation occurs between 18.00 to 20.00 hr immediately followed by female receptiveness toward a courting male. The pair swim up, turn their backs down and expel their sexual cells. The spawn floats, formed by two whole mucous balloons, in which the eggs are arranged in one or two layers, each in its own envelope.

Histological and anatomical investigation of the ovaria, showed that these are of special structure, not observed in other fish species. Each ripening ovocyte grows on its own ovigerous branch that brings it close to the ovarium wall which produces the mucous envelope. This process enables the aggregation of egg-mass and the synchronization of spawning.

Riassunto. Nell'ambito delle formazioni coralline del Mar Rosso i Pteroidi occupano una posizione particolare, essendo essi predatori adattati unicamente a questo habitat ed occupando uno dei livelli superiori della locale rete trofica. Tre sono le specie comuni: *Pterois volitans, P. radiata* e *Dendrochirus brachypterus*. Le prime due sono specie solitarie, disperse lungo la formazione corallina dove ciascun individuo difende il suo territorio da altri individui congenerici e conspecifici. *Dendrochirus* è invece gregario e si rinviene in gruppi da 3-4 a 10 individui, in vicinanza di spuntoni corallini e frammenti di roccia.

Le tre specie menzionate sono crepuscolari e sono attive al tramonto e durante le ore serali. In questo periodo catturano il cibo, costituito da pesci e crostacei bentonici, usando differenti tecniche di raccolta.

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Esperimenti hanno dimostrato che questi pesci sono in grado di apprendere rapidamente e quindi di evitare i pericoli derivanti da attività di caccia per loro pericolose. Dal punto di vista del comportamento l'inizio della riproduzione è segnato da una tendenza alla gregarietà e da dimorfismo sessuale per quanto riguarda colorazione e comportamento. I maschi mostrano un'aggressività maggiore che le femmine con un'attività che comporta movimenti laterali della testa, spostamenti in cerchio, « confronto » in posizione frontale e laterale, morsi « bocca a bocca ».

Le femmine sono più pallide, con ventre dilatato, indice dello sviluppo ovarico. L'ovulazione avviene fra le 18.00 e le 20.00, seguita immediatamente dall'accettazione del maschio. La coppia nuota verso l'alto, volge il dorso verso il basso ed espelle i prodotti sessuali. L'ovatura galleggia ed è formata da due sfere mucose nelle quali le uova sono disposte in uno o due strati e ciascuna racchiusa in una propria capsula.

L'analisi istologica ed anatomica degli ovari ha messo in evidenza la loro peculiare struttura, non osservata in altre specie di pesci. Ciascun ovocita in maturazione si accresce nell'ambito del proprio ramo ovigero che lo porta in vicinanza della parete ovariale che produce, a sua volta, l'involucro mucoso.

Questo processo rende possibile la formazione dell'ovatura e la sincronizzazione della deposizione.

Introduction

During the last two decades, extensive papers have been published dealing with biology and behaviour of coral reef fishes. Most of these publications are focused on a limited group of fish families, especially the Pomacentridae (Hiatt & Strasburg, 1960; Abel, 1961; Fishelson 1964, 1970; Hobson, 1965; Randall, 1967; Fishelson, Popper & Avidor, 1974). Of these works only a few deal with the ethology and reproduction in natural environment (Myrberg *et al.*, 1967; Swerdloff, 1970; Fishelson 1970). Observations of this kind have now been performed on the lion-fishes (Pteroidae), the tropical relatives of the widely distributed scorpion fishes. Being typical predators, the lion-fish, form the top level of consumers on some coral reefs, and may play a prominent role in the animal density and species composition on a given place. Being poisonous, these fishes have attracted the attention of scientists for a long time and from this point of view have been investigated extensively (see summary in Halstead, 1970, and Fishelson, 1973).

The work presented here seems to be the first one devoted to the ecology and ethology of lion-fishes and should be a basis for further and more extensive investigations.

Methods

Parts of the investigations summarised here were performed in the Gulf of Aqaba and the Gulf of Suez, within the framework of eco-ethological observations on the shallow water benthic animal communities occurring here (Fishelson, 1971).

Three species of lion-fishes were observed, of which one, the pygmy lion-fish *Dendrochirus brachypterus*, was extensively studied. The two other species partly investigated were *Pterois volitans* and *P. radiata*. Observations were made in the field by snorkling during various times of the day and night, especially after sunset, when the lion-fishes are really active. Additional and detailed observations were made on fishes caught in the Gulf of Aqaba and kept in aquaria of the Marine Section, Department of Zoology, Tel Aviv University. Here the fishes were held in containers of 250 to 750 liters of natural or artificial sea water, with inner sandfilters and with additional aeration. The pH of the water was kept at about ± 8.0 and the temperature varied between 23°C and 26°C. Each of the investigated species was kept separately, and fed daily on living fishes (*Gambusia*, Cichlids, Gupy) shrimps (*Palaemon elegans*) and adult *Artemia salina*. Spawns obtained from these lion-fishes were collected at evening immediately after the spawning, or the next morning, and incubated in aerated and well filtered sea water .Artificial insemination was also performed using the « dry method » of sperm addition to the eggs pressed out from the female belly. To prevent microbial destruction of eggs during the first stages of development, some of the spawns were incubated in water containing some antibiotics: a mixture of Penicillin (1 part) and Streptomycine (10 parts). From this stock solution two droplets were added per liter of water/per day. For histological observations, female gonads were preserved in Bouin's fluid or 10 % neutral formalin, and embedded in paraffin or paraffin-celloidin. Sections were prepared at 2μ, 4μ, 6μ and 10μ thick and stained with Ehrlich's hematoxyline; Mallory azan and Hamalum. Some parts of the gonads were fixed in glutaraldehyde and 2 % osmium-tetraoxide. Those parts were embedded in Epon 812 and from these electron microscopic slides were prepared. Pictures were taken with a Nikon F and Nikonos cameras as well as with a microphotocamera from a Leitz-microsocope. Schematic figures were prepared from photos or from fishes; the larvae were observed in a Zeiss-stereomicroscope. Various aspects of behaviour of adult fishes were also filmed using a Bolex 16 mm camera and a closed circuit TV system.

General Remarks about the Fishes

In the northern part of the Red Sea, along the shallow subtidal around the Sinai Peninsula, three species of lion-fishes are found:

1. *Dendrochirus brachypterus* (Fig. 1), the so-called pygmy lion-fish, is usually found in small groups of 3 to 6 individuals inhabiting dispersed small rocks or dead coral fragments, often far away from dense coral growth. In the Gulf of Aqaba, they are common in the most northern part, close to the shore line, and over muddy substrates, where other lion-fishes are seldom observed.

2. *Pterois volitans*, the common lion-fish (Fig. 2) is a solitary reef dweller, usually found along the forereef region. Here it hides in shadows below and behind overhanging coral colonies. They usually occur singly, scattered on the reef, entering the backreef region and the shallow water lagoon at high water. Only during the initial stages of courtship behaviour do they gather together in groups of 3 to 8 for a short time. On rocky shores, where coral growth is absent, the common lion-fish occurs in crevices and caves of this habitat.

3. *Pterois radiata* (Fig. 3) is less common and more solitarily dispersed than the former species. This species is also more restricted to the forereef habitat, especially to regions covered by branching, living coral colonies.

All 3 species observed are nocturnal fishes, that hide during the daytime and become active at sunset, which in our latitude usually occurs at 6.00 to 6.30 p.m. In the shallow water of the Gulf of Aqaba this is the time of the

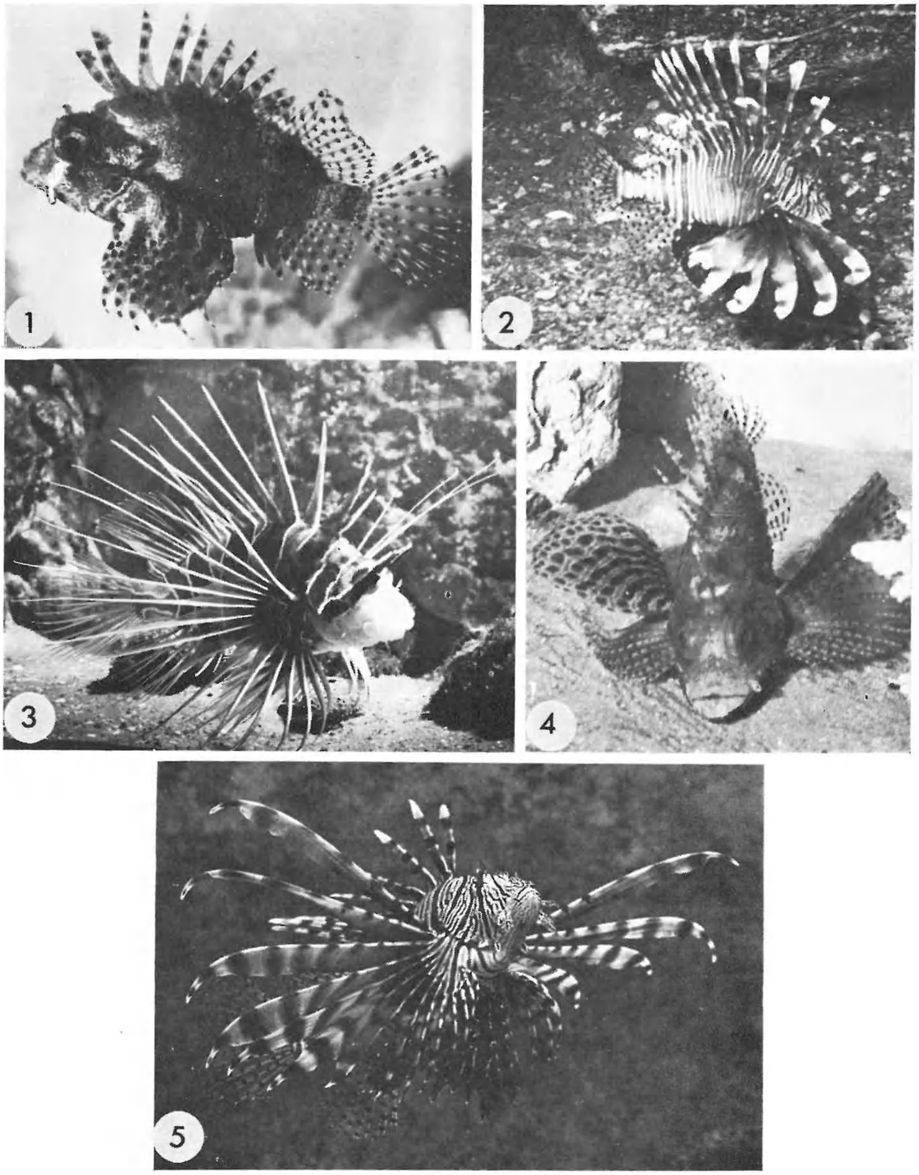

FIG. 1-5. 1) Dendrochirus brachypterus - *female, with a white subocular line, extending on the dermal wart;* 2) Pterois volitans - *a dark coloured male in agonistic posture;* 3) Pterois radiata *female searching for food on the bottom;* 4) D. brachypterus *male feeding above the substrate*; 5. P. volitans *hunting below the water surface.*

night-day change over, during which the day active reef fishes and invertebrates descend slowly, seeking cover for the approaching night, whereas the nigth active animals vacate their covers, moving out for feeding and mating. This is also the time of the highest species diversity observed on a chosen coral reef (Table 1). On such occasions optimal conditions are formed for predators such as

TABLE 1. *Number of animal species that may serve as food for lion-fishes observed on isolated coral knolls near Eilat, at various times during a two-week period.*

Taxonomic unit	12.00	22.00	18.00
Teleost fishes	21	9	39
Brachyuran crustaceans	3	5	5
Shrimp crustaceans	2	6	8
Gastropod molluscs	6	8 *	10 *
Polychaet worms	1	3	5
TOTAL	32	31	58

* 4 mollusc species were naked snails usually not consumed by predators.

the lion fish, to collect their diet with minimal energy investment. During this twilight time, the lion-fishes leave their cover and propel themselves by slow and undulating motions of the caudal and posterior, soft parts of the dorsal and anal fins. They glide, usually moving upwards, above the rocky surfaces and so emerge between and on the rocks unexpectedly and at once begin their feeding activities (Fig. 4).

FEEDING BEHAVIOUR

Common to all 3 species observed is the manner in which they move during hunting. Fixing on a prey, a chosen fish or group of fishes, they move slowly towards them, using the wide open colourful pectoral fins as a shield that prevents the prey from seeing the propulsive motion of the caudal fin (Fig. 5). This, together with the cryptic striped pattern of head and fins, reduces to a minimum the alarm of the prey. Such cryptic etho-morphological composition is especially effective in the diminished light, as the hunting fish moves slowly between the branches of coral or the spread, striped arms of the night-active feather-stars (RUTMAN & FISHELSON, 1968) and the long spines of the sea urchin *Diadema setosum*. The actual catching of the prey is performed with one strong gulp, during which the victim is sucked in by the large and wide-open mouth. Water sucked in on such occasions leaves through the opercular slits, and the large serrated and dense gill rakers occurring here prevent the prey from being swept away with the current. The swallowing is so quick and unobtrusive that the hunting fish don't disturb the area. This allows them to hunt fishes from a group, as in the case of cardinal fishes (APOGONIDAE) one by one without frightening them into any escape response.

Except for this general pattern of feeding, there are also types of feeding behaviour specific to different species of lion-fishes:

D. brachypterus mostly feeds on animals that carelessly approach his resting place. It seems that behaving cryptically he acts like a cat; normally the victims are small fishes that, looking for shelter or nipping the substrate, approach the spot on which the fish rests. Sometimes *Dendrochirus* was observed to wait until such prey approached close enough to be swallowed; on other occasions the predator was observed to glide slightly toward the prey and catch it. On several occasions, 3 to 4 pygmy lion-fishes were observed to rest around a sea urchin among whose spines a group of *Paramia bipunctata*-cardinal fishes were hiding. The lion-fishes wait till one of the *Paramia* move out from among the spines, close enough to be snapped up.

Pterois radiata, like the former species, feeds mostly close to the substrate. Spreading latero-ventrally the wing-like pectoral fins, these fishes swim obliquely, head down, their eyes searching the substrate, and snap from there any moving animal. Frequently, individuals of this species were seen to stay motionless among a dense cover of feather-stars and from this position to catch small fishes passing by.

Pterois volitans showed an additional way of fishing: Emerging from their crevices, they move out into the open water and ascend towards the surface. Here they remain motionless, 20 to 30 cm below the water, watching the surface. At this time schools of the sardina-like *Allanetta* (*Atherina*) *forskali* are hunted by various fishes, among them the belonid fish *Ablenes hians*, *Strongilura crocodilus* and by the hemirhamphid fishes *Hyporamphus* spp. The schools of small fishes, escaping from the swift predators, move jumping over the water surface, often falling back into the water to land exactly above the *Pterois* waiting in ambush. At such moments the predator with a single stroke of the tail jerks forward catching some of the escaping fish. Not all the attempts are successful, and so the fish remains in the same spot looking for additional jumpers (Fig. 5). The feeding of all three species occurs as the light decreases and the groups of diurnal active fishes, like *Anthias squamipinnis* and *Abudefduf azysron* descend gradually towards their rocky covers. On such occasions also they are being hunted by the lion-fishes.

The feeding on various invertebrata, involves an entirely different type of behaviour. Hunting for small benthic animals, the lion-fishes glide with their open pectoral fins over the substrate, palpitating with the vibrating free ends of fin rays. This movement sets in motion the various inhabitors of the epilithic algae, such as amphipods, isopods, palaemonid and alpheid shrimps and some molluscs. The escaping animals are very carefully picked out by the lion-fishes. Preliminary checks of stomach contents of the fishes investigated, revealed that *P. volitans* which is a typical fish-eater, feeds also on shrimps, whereas, *P. radiata* and *D. brachypterus* are typical carcinovorous species, occasionally feeding on smaller fishes. The various types of feeding continue till complete darkness (7.00 or 7.30 p.m.) but the lion-fishes remain over the rocky surface all night long, and only at sunrise do they move into shadowed parts of the habitat. Du-

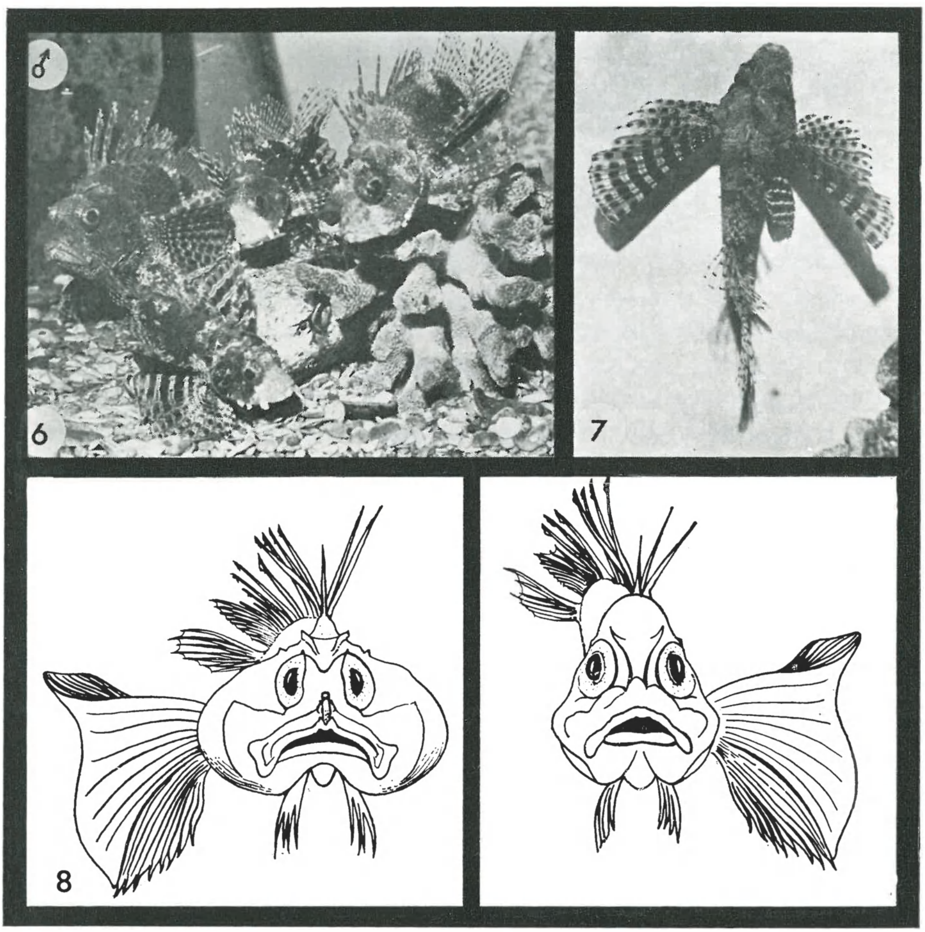

FIG. 6-8. 6) *Group* of D. brachypterus *composed of the dominating male (left, uniformly coloured) and three females;* 7) *Male of* D. brachypterus *in agonistic posture approaching another male;* 8) *The shape of a « normal » and displaying head in male of* D. brachypterus *(according to photos).*

ring moony nights, as the visibility in water is high, pteroids were observed to continue to collect food also during later hours.

During feeding movements, the lion-fishes often meet each other, especially along the reef front. On such occasions they behave agonistically, spread their spiny dorsal fins towards each other and retreat. Occasionally *P. volitans* was observed to chase another individual that invaded its place. In such instances the attacking fish turns darker, whereas the escaping fish flees folding his pectoral fins. Although there is evidence that each *Pterois* occurs permanently on one place and defends it against conspecific fishes, real long term territoriality has not been established till now. As for *Dendrochirus brachypterus* that occurs in groups of several individuals, the larger fish are always the dominating ones as they move for food collection. Consequent sectioning of dominating animals showed that these are always males and it was found that such groups of *Dendrochirus* consist of one dominant male, some females and some small males (Fig. 6).

Reproduction

As most of the reproductive behaviour occurs in almost total darkness, especially in the *Pterois*-species, the majority of observations were performed in captivity, supported by additional data collected in nature. In aquaria the main fish that served for detailed observation was *Dendrochirus brachypterus* of which 60 specimens were observed during the last year. Comparative observations performed on *Pterois*-species showed that generally they behave very much like the pygmy lion-fish. For this reason, only some parts of their reproductive behaviour will be mentioned.

Sexual Dimorphism

As mentioned above, in all 3 lion-fish species, as in most of the scorpion-like fishes, the colour pattern is a cryptic one, based on stripes, lines and blotches. These are usually yellow white or red on a brown or reddish-brown background. This enables the fishes to merge with the environment as do numerous coral fishes (Eibl-Eibesfeld, 1962). Differences between sexes becomes apparent mostly toward courtship and these are morphological and ethological. As for *D. brachypterus* the males could be recognized during daytime by their more robust heads and slightly longer pectoral fins. In females these fins hardly reach the caudal peduncle bearing 4 to 6 light colour bands on them (Fig. 1). In males the pectoral fins usually reach the base or middle of the caudal peduncle and bear 6 to 10 coloured bands (Fig. 7). During courtship and reproduction the differences between males and females become more pronounced. Males turn darker and are more uniformly coloured, especially in their anterior region. Females become paler at this time especially those with ripening eggs. In these the belly becomes whitish and swollen (Fig. 10) and the branchial region and mouth silvery-white. Especially silvery and shining is a line extending from the eyes down and continuing on a dermal wart-like extension on the mandible (Fig. 1). Even in darkness, such females can easily be located and this could be used for « signalling » towards the male. The non-ripe female remains with the usual banded colouration of the trunk.

From the ethological point of view the outstanding characteristic of a male is its agonistic behaviour towards other males. During reproduction, introduction of another male into the aquarium, or in the sea by bringing in a captured male from a nearby rock, elucidates an immediate negative reaction from the possessor (P) towards the intruder (I). This negative reaction occurs in several stages, and as in blennys and in other fishes (FISHELSON, 1963, 1971) each stage seems to present a certain part in the agonistic hierarchy, during which the fishes move from low intensity acts into higher intensity acts. The attack of one fish on the other is the high point of this behaviour.

1. *Approaching*: With widely spread fins the P-fish swimming slightly above the bottom, approaches the I-fish (Fig. 7) at the same time turning uniformly darker. Upon drawing closer to I-male, an undulating alternating motion of the frontal dorsal spines begins, during which the spines of P-male move in unison or in apposite directions. The I-male becomes paler and reacts by lowering its anterior body parts towards the substrate (Fig. 9) and the approaching male.

2. *Lateral Display*: P-male moves back and forth in front of the I-male, bending the body and pointing the dorsal spines obliquely towards him. The branchial region slightly lifted.

3. *Frontal Facing*: P-male rests before the I-male face to face. Its pectoral fins are strongly coloured, spread out and undulating, their ventral parts trembling as during food collection; dorsal fin strongly erect and spines moving.

4. *Lateral Head Shaking*: Close to the I-male, the possessor stops and moves its anterior parts sideways slowly or very quickly several times together. This movement is usually accompanied by strong lifting up of the branchial region, which gives the head an enlarged appearance (Fig. 8).

5. *Head Biting*: This is a final and very quick motion, during which, with a strong jerk the P-fish tries to grasp the intruder's frontal head parts into its

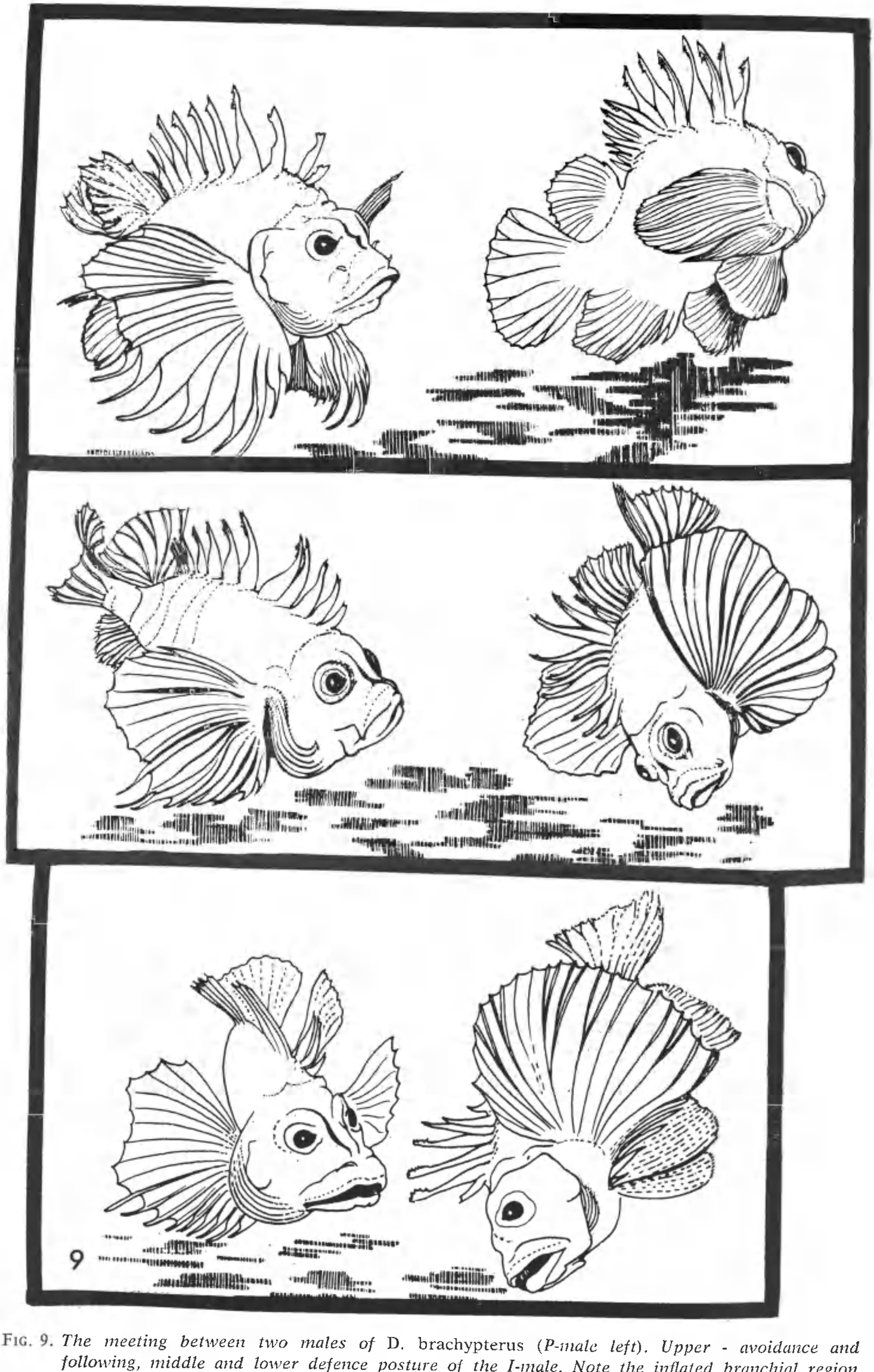

FIG. 9. *The meeting between two males of* D. brachypterus *(P-male left). Upper - avoidance and following, middle and lower defence posture of the I-male. Note the inflated branchial region of the P-male (according to photos).*

wide open mouth. Succeeding, it may shake the I-fish vigorously in a sideways direction. On several occasions after such confrontations the premaxilla and mandible of such attacked fish were seen to be torn away.

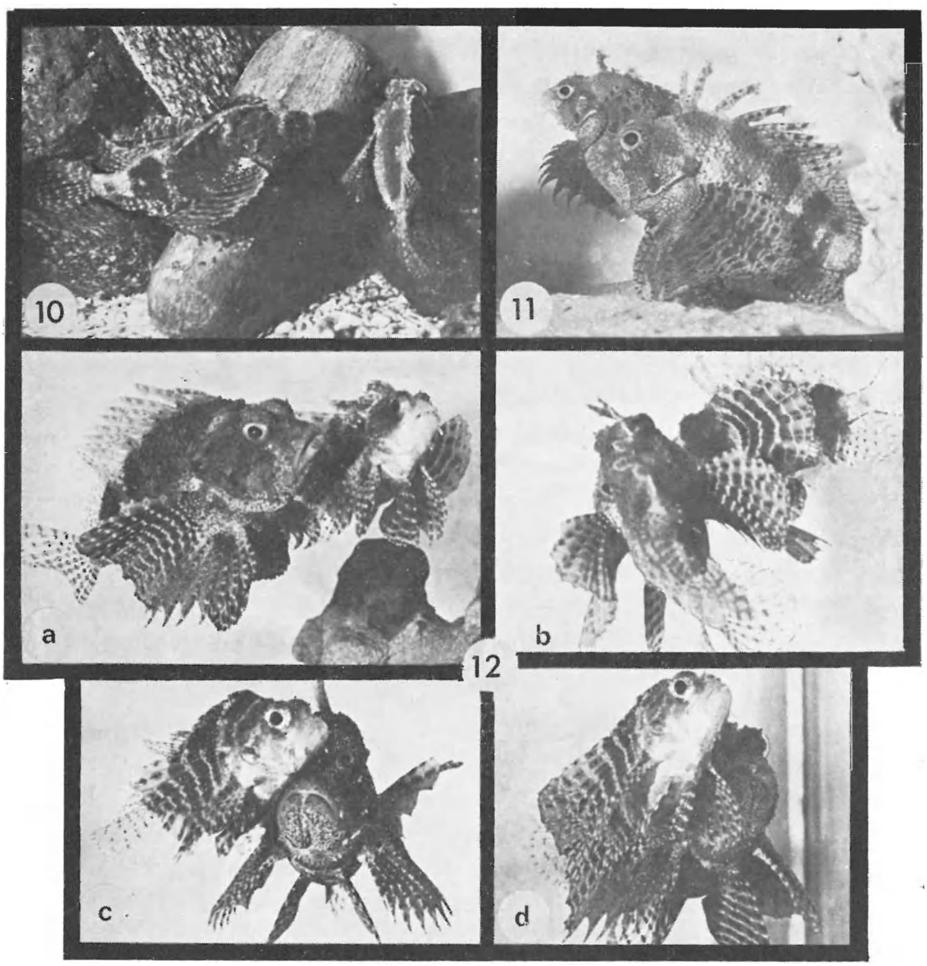

FIG. 10-12. 10) *A ripe female (right) of* D. brachypterus *followed by the female;* 11) *The male (in front) and female ascend together;* 12) *Various stages of pre-spawning pairing: male larger, head darker;* a) *rising;* b) *and* c) *lifting;* d) *from behind as if carrying up.*

On several occasions the intruder has been observed to flee from the attacker and then chasing occurs, that in the aquaria, if not stopped may lead to a fatal end. In nature such fleeing males were observed to escape speedily to a distance of 1.5 to 2.5 m from the pursuing male.

The intruder male's reaction could also be different (Fig. 9): being attacked, it manages to lower its head and expose the sharp dorsal spines to the attacker at such a speed, that the attacking fish collides with them and is badly stung. On at least three occasions such males remained for some seconds impaled on these spines and only by strong caudal strokes managed to free themselves. Such experiences did not change the behaviour of the attacking fish at all.

These events did not change the general picture of behaviour and in all instances the intruded male had to be removed from the container otherwise it was killed. Behaviour like this was also observed in males of *Pterois*-species especially in nature. Being more mobile than *Dendrochirus*, *Pterois volitans* were observed to swim out high in the water against intruding (or intruded) males and after displaying, circling around and head to head facing, chases the new fish out from the vicinity, to a distance of 3 to 4 m.

It is interesting to note that in all instances the stronger male of the lion-fish becomes darker coloured approaching the other individuals, male or female. Such agonistic fishes exhibit the same behaviour also towards man if approaches them while snorkeling. Often, with such a display they accompany the man till he swims out from their region-territory.

Only recently it was observed that the courting males of *P. volitans* are especially aggressive: being disturbed during courtship they even try to sting our camera and so use the defensive weapon of their fins as an offensive organ. Possibly most of the stings caused by lion-fishes during swimming were inflicted by such active males. Females of all the three species observed do not exhibit agonistic behaviour towards each other. Only rarely, during unexpected meetings, do they raise the dorsal fins and for a short time turn them towards the other individual.

Courtship Behaviour

In all cases observed, courtship begins 20 to 30 min before dark and is always initiated by the male. During this part of reproductive behaviour in *Dendrochirus brachypterus*, several stages could be observed.

Male

1. *Searching* — The male moves slowly from female to female approaching those with a silvery-shine on the ventral parts of their heads (Fig. 10). Sometimes the male remains close to one female for a while, or without stopping, moves over to another. The females with « normal » colouring remain unnoticed.

2. *Head Up* — Resting on the bottom close to a female, the male raises himself on the ventral fins and looks up towards the water surface. Sometimes this

position is immediately followed by swimming up towards the surface and descending back towards the same female. On other occasions, after a head up, the male swims towards another female and repeats the act.

3. *Circling* — The male fish moves slowly around the female, sometimes in small jerks; during this circling the pectoral fin on its female-near side is folded toward the body, whereas the fin on the other side is wide open and undulating.

4. *Leading Up* — Stopping the circling, the male ascends slowly, usually followed by the female.

Female

1. *Side Winding* — Supporting herself alternately on the ventral and pectoral fins, the female moves laterally away from a courting male during his circling behaviour. This laterally directed movement may change over to swimming, during which the female leaves the active male. In such cases the male may in turn swim after the female (Fig. 10).

2. *Following Up* — Ascending towards the water surface, the female closely follows the ascending male (Fig. 11). During such rising, the female trembles with pectoral fins in a mode as described for males. Such following can be repeatedly performed for 10 to 15 min, during which the pair repeats again and again the various stages of courtship, without spawning.

Spawning

The pair remain close to the water surface, swimming around without descending. The male often presses his body to that of the female, raises her higher, pushing upwards (Fig. 12). Frequently he also nips the silvery, shining, wart-like protuberances on the female's mandible. Finally, the act of spawning occurs marked in the beginning by the momentary enlargement of the female's genital pore. The extrusion of the spawn is accompanied by a jerk as the pair swim upside-down close to the surface. The pair may also spawn while swimming normally, in such instances lifting up their caudal parts.

The Spawn

Each female produces two hollow mucus tubes, that remain afloat below the surface (Fig. 13). After 15 to 20 min these tubes fill up with sea water and change to oval transparent balls of 2.0 to 5.0 cm in diameter. The eggs are embedded in this transparent mucus, forming one or two layers. Each egg is separated from the surrounding eggs by a sheet of denser mucus. In 70 spawns that were counted, it was found that the number of eggs per ball varied between 2,000 (in small females) and, in larger individuals up to 15,000.

As the eggs are expelled, the male expells the sperm, which could be detected on the mucus ball forming many miniature islets of spermatozoa. Immediately

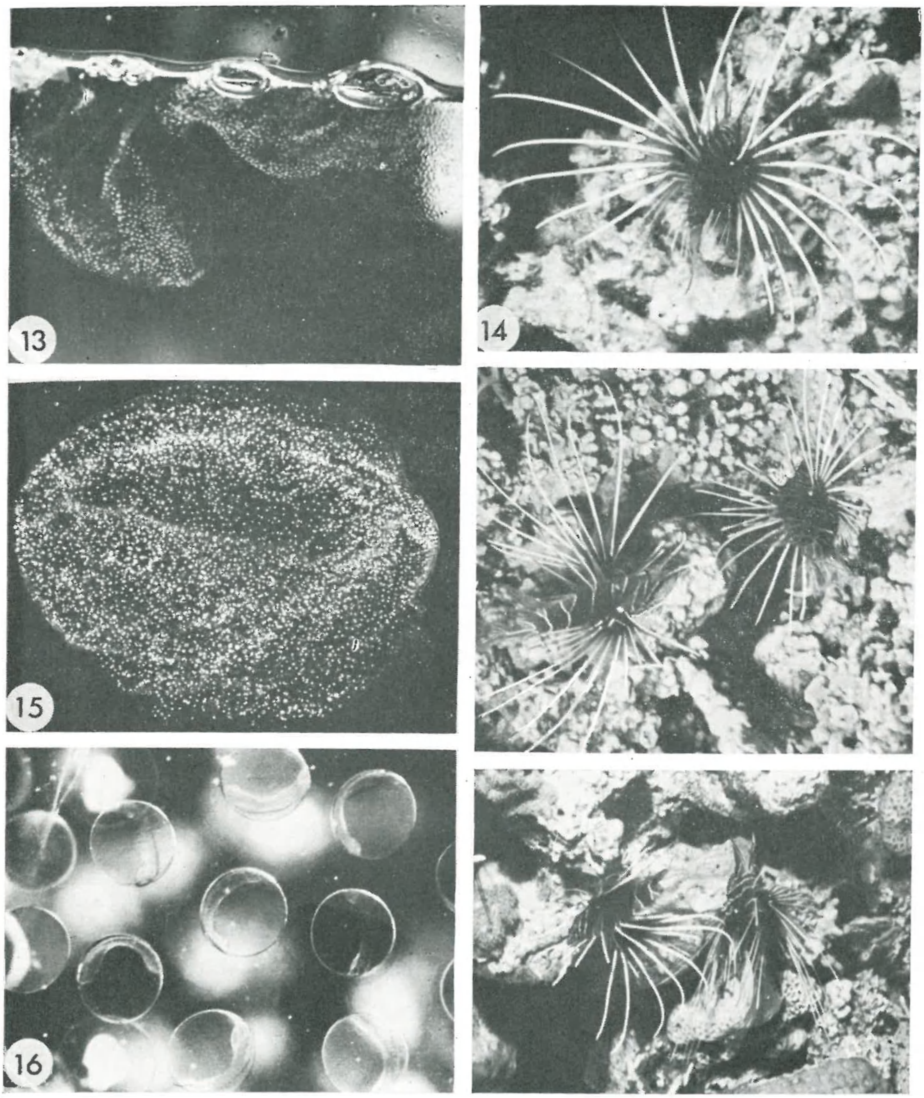

FIG. 13-16. 13) *Two floating spawns of* D. brachypterus; 14) *Courtship in* Pterois radiata *along the coral reef at Eilat; upper) the diplaying male; middle and down) male (larger one) circles around female;* 15) *The developing spawn of* D. brachypterus; 16) *the same, 12 hours after fertilisation (x 30).*

after spawning the spent female descends and the male swims down searching for other females ready to spawn. Thus a single male was observed to lead three females to spawning during 35 min and so six egg-balls were produced and fertilised. In aquaria a fertile female will spawn even if a male is not found. In some cases this causes a delay of spawning and afterwards atrophic eggs are found mixed with normal ones. The same females will spawn again some days later and so, this may continue for months uninterruptedly. In nature, ripe females were observed and collected from June till December. Those brought to the aquaria during this season and kept in standard conditions spawned a week later.

As for the *Pterois*-species, parts of their reproductive behaviour observed in nature and captivity showed great similarity to that of the pygmy lion-fish. Also in these species the courtship occurs shortly before total darkness and makes observations difficult. Here also the males are more darkly coloured than the females (Fig. 14) and they actively search for ripe females. Males of *P. volitans* were observed in nature to travel around widely, forming sometimes aggregations with females of 3 to 8 individuals together. In nature and captivity, male courtship movements such as searching, head-up, circling and lateral pressing, which were observed in pygmy lion-fish, were also seen in males of *P. volitans* and *P. radiata*. Also in those fishes males were observed to lead ripe females toward the surface for spawning. As in the pigmy lion-fish also in *Pterois*-species the spawn is in the form of mucus-balls floating below the water surface.

Development and Behaviour of Larvae

The data provided here concern spawns of *Dendrochirus brachypterus*, kept under a temperature of ± 26° and aerated. Various meristic characters are illustrated in Fig. 17 and 18, and dimensions are summarized in Table 2. The

Table 2. *Dimensions of the developing larvae of* Dendrochirus brachypterus (*in mm*).

Age	Total Length	Yolk Sac	Head Anus distance	Head Length	Pectoral fin
1 day	1.0-1.25	0.5-0.6	0.6-0.7	0.12-0.14	—
2 days	1.3-1.5	0.25-0.30	0.7-0.8	0.18-0.21	—
3 days	1.6-1.75	0.11-0.12	0.75-0.85	0.26-0.3	0.2-0.25
4 days	1.75-1.83	—	0.85-0.9	0.45-0.5	0.3-0.37
5 days	1.80-1.85	—	0.85-0.90	0.5-0.6	0.35-0.40
6 days	1.8-1.9	—	»	»	0.4-0.42

development of larvae occurs within the floating spawn and could be easily observed under a microscope (Fig. 15). From fertilisation till the 6 day old larvae the following changes were observed:

6 hours after fertilisation the blastodermic cup is formed on the animal pole of the egg. Peridermal tissue begins the expansion over the yolk sac.

12 hours after fertilisation the embryo is in the first stages of formation; its caudal and anterior parts widen and slightly rise above the yolk sac (Fig. 16). In the central part of the trunk 4 to 6 segments are visible.

18 hours after fertilisation 16 to 22 segments are visible in the trunk region. End of caudal part slightly freed from the yolk sac. Head enlarged, eye cups under formation, without pigmentation.

36 hours after fertilisation hatching occurs. Larvae wriggling with their tails, move around. Being motionless they sink toward the bottom and then ascend again. These first day larvae (Fig. 17, A) are fully segmented with signs of melanine granules on the yolk sac. The first contractions of the heart primordium are observable. The iris is almost closed and 2 otoliths are visible in the auditory vesicle. The intestine duct sets in formation and the liver primordium is located above the dorsal part of the yolk sac. The mucus walls of the spawn fall apart and as observed under a microscope, they are invaded by infusoria and bacteria that degrades them.

In a 2 day old larvae the pectoral fins' primordia are visible (Fig. 17, B), located above the middle of the yolk sac. The entire intestine can now be traced, and above its bent posterior part, the urinary vesicle is visible.

The heart beats are distinct and signs of blood-flow are traceable. Granules of melanin and iridescent guanin appear in the ventral parts of the eyes. The yolk sac is now occupied by a large oil droplet with only small remnants of yolk. Signs of the caudal rays appear in the fin primordium.

Three days old larvae swim much more regularly, supported by movements of pectoral fins' primordia, which are distinguished by the beginning of dark pigmentation along their margin (Fig. 17, C). The mouth is open and the mandible moveable, with signs of cartilage development and pharyngeal muscles. Development of the stomach and intestinum differentiation has advanced. On the caudal part of the body a row of melanophores emerged.

Four days old larvae are good swimmers and start feeding, catching small ciliates. Their pigmentation is much stronger, occurring on the mouth and mandible; as a black margin on the pectoral fins, and a diffuse black band before the urostylar part of the cauda (Fig. 17, D). Four very large and laterally protruding neuromasts are visible on the trunk (Fig. 18, D).

Larvae 6 days old showed migration of mesenchymatic cells into the fin primordium, thus marking the onset of development of the dorsal and anal fins (Fig. 17, E). Head region, pectoral fins and intestinum are much more developed. The pigments on the preurostylar part of the trunk form a dense black band (Fig. 18, E).

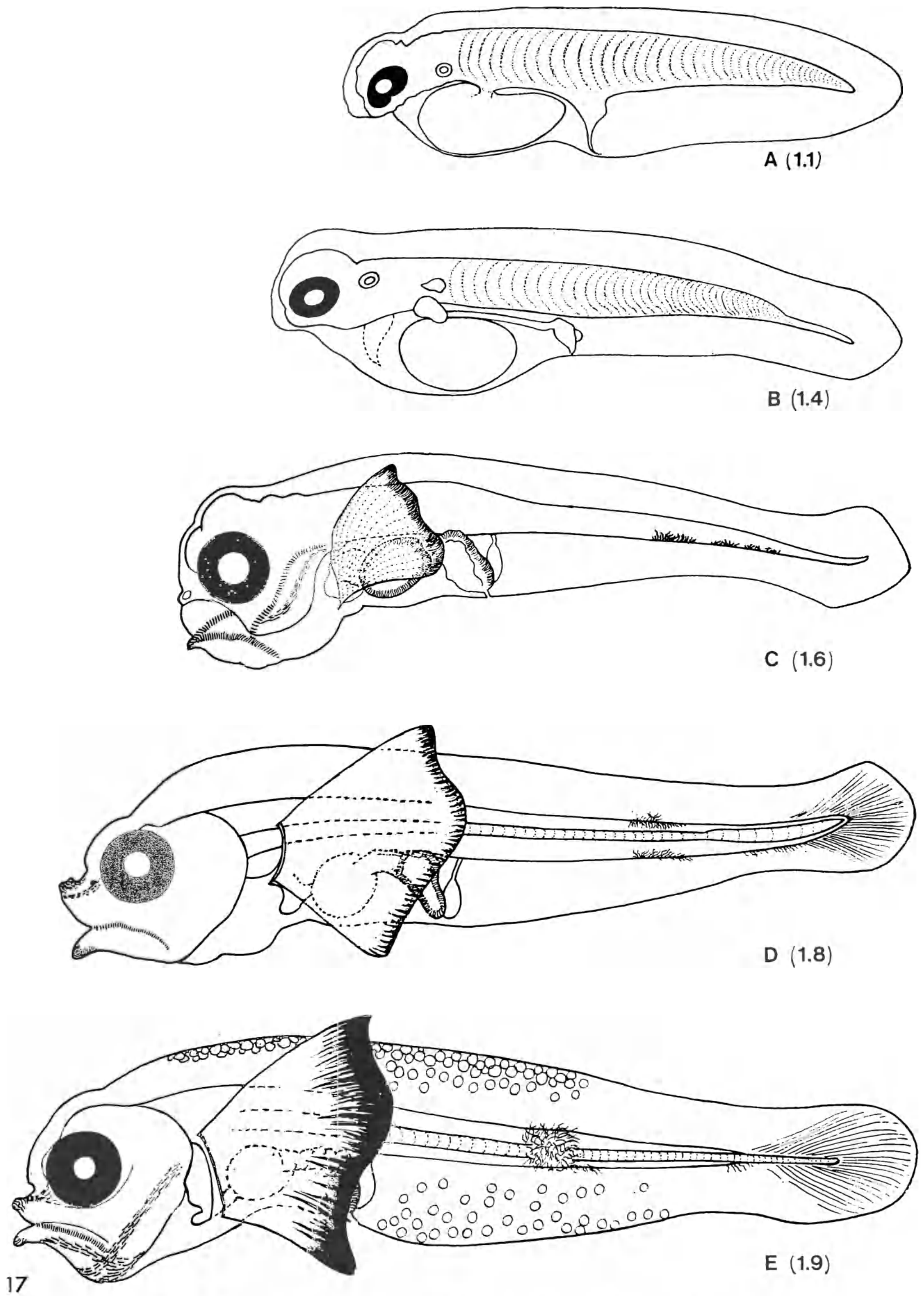

FIG. 17. *Larvae of* D. brachypterus *(in parentheses, their length in mm).*

This stage was the last one observed. A day after, all the larvae were found dead, possibly from starvation. It looks as though the density of ciliates per volume of water was not enough to support the larvae population. We will try again. During all of the week-long development the larvae behaved phototropically, gathering in the illuminated parts of the containers.

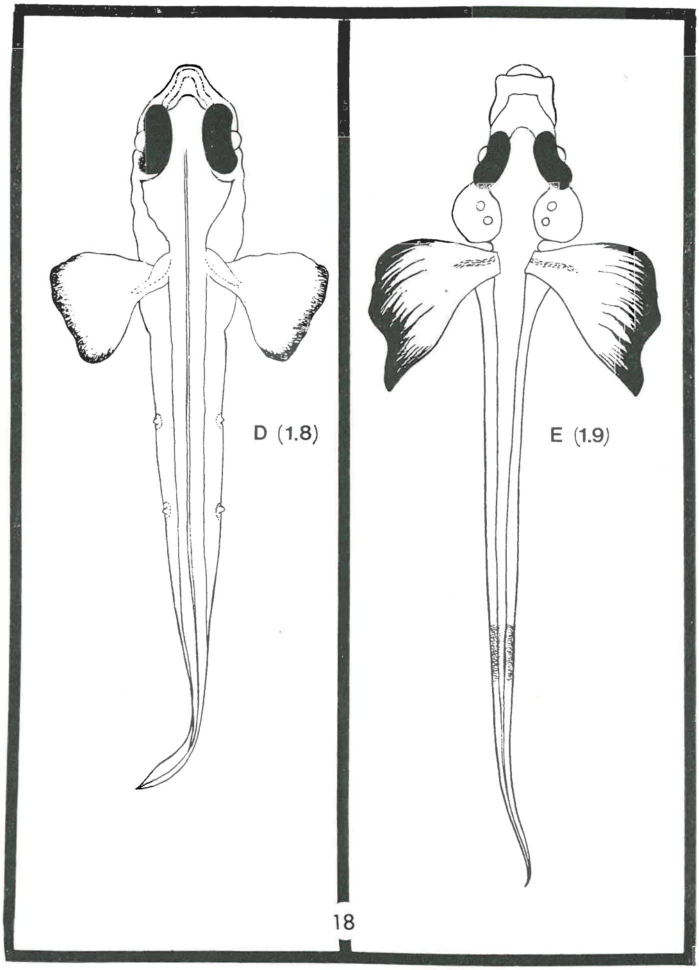

FIG. 18. *As Fig. 17.*

As for larvae from the *Pterois*-species, up till now we have not succeeded with fertilisation in captivity. But comparing several of the smallest juvenile *Pterois* collected and observed in nature, it was possible to detect one of their larvae in plankton. This larva was 6 mm long, distinguished by the long rays that form the pectoral fin (Fig. 19). Observing this living larva it was found that here also we are dealing with a phototropic stage. It seems that in these fishes the change to photophobism and benthic life occurs after the metamorphosis to a juvenile form. Pteroid juveniles of 10 to 12 mm body length were found hiding among pebbles and stones, or sea-urchin spines. In such stages their morphology and feeding behaviour resembles that of adult fishes.

Ovary and Ovulation

Although this part of the investigation will be summarised in more detail in the near future, it seems worthwhile to finish the paper by bringing up some points about the ovogenesis. In general terms the shape and form of spawn described here was also found in other scorpion-like fishes (Sparta, 1941; Moser, 1967) and the question arose how such a spawn could be produced by the ovary and this precisely synchronized with the courtship activities that, as mentioned, continue only about 30 to 45 min. It seems that the special type of ovary found in the pteroid fish is well adapted for this. Dissecting the females it was found that the ovary is formed by two sacs that caudally join to form the oviduct (Fig. 20).

In *Dendrochirus brachypterus* the length of the unexpended ovaria are 10 to 12 mm, while during ovulation they extend to a length of 25 to 28 mm (in a female of 110 mm TL), and 12-13 mm maximum width. In *Pterois*-species the ovaria are much larger. The ovigerous tissue hangs in the central part of the ovarium, attached to a mesenchymatic hilus, within which the arterio-venous system of the germinative organs are found (Fig. 20). As in *Sebastodes*-fishes (Moser, 1967), some Cichlid fishes (Polder, 1971) and amphibia (Hoar, 1969) the inner epithelial layer of the ovarian sac of pteroid fishes does not produce ovocytes. In those fishes this epithelial layer is formed by special types of elongated secretory cells that participate in the production of the mucus envelope around the eggs (Fig. 21). The dissection of the ovarial cover exposes an unusual type of ovogonic tissue in which each developing ovocyte hangs on a special ovigerous peduncle (Fig. 22). These peduncles develop and elongate gradually with the ripening of the ovocytes. Thus the riper the cell is, the higher is its position above the place of origin (Fig. 23, 24). Mature ovocytes, that before spawning are approximately $\pm$ 500 μ in diameter, are enveloped in their follicular membranes. They are attached to their peduncles and pressed towards the secreting epithelium of the ovisac.

The development of a peduncle resembles that observed in birds (Franchi, 1969). All around these ripe ovocytes occurs the formation of the mucus envelopes, that seem to originate from the inner epithelial tissue of the ovisac as well as from follicular cells. The checking of females at various hours of the day, showed that this process of cell ripening and peduncle extension continues

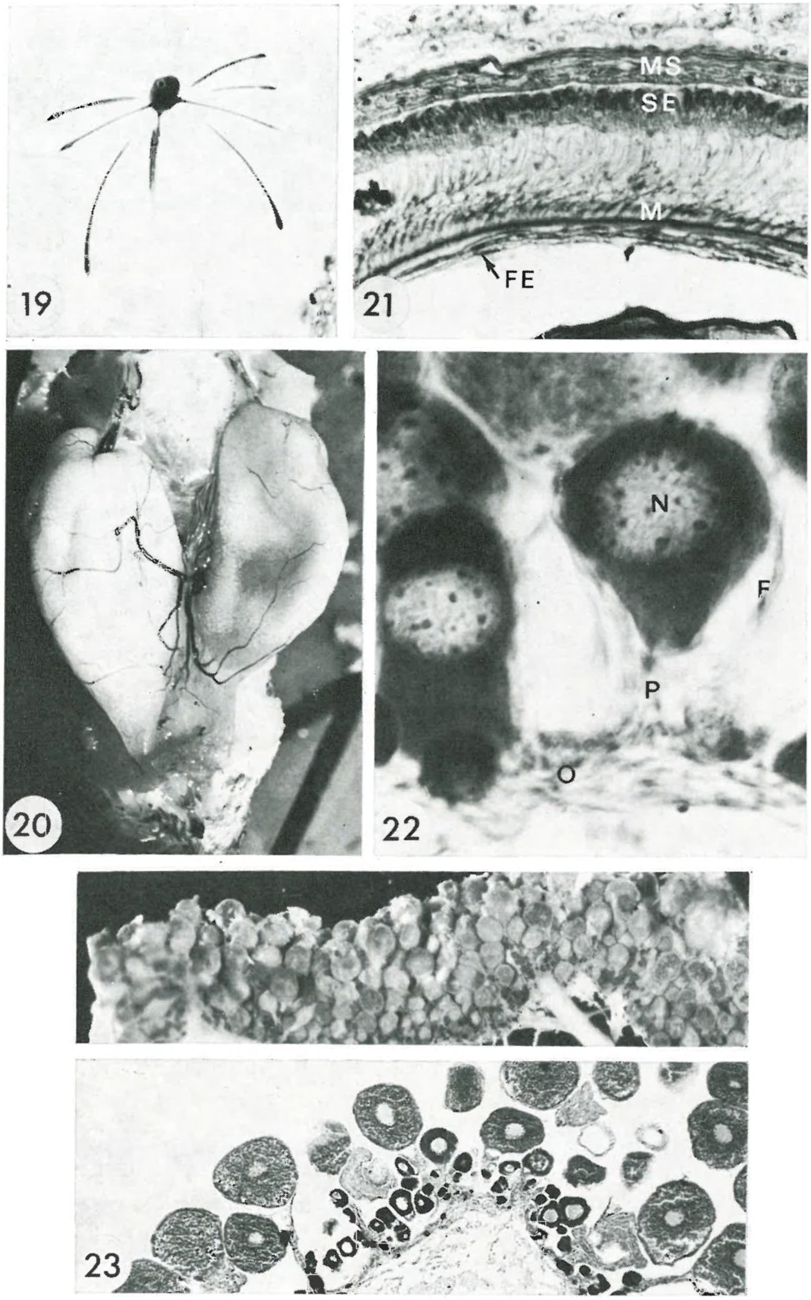

FIG. 19-23. 19) *The larva of* Pterois *sp.;* 20) *Ovaria of* D. brachypterus - *note the hilus and blood vessels entering the gonad, and the ripe eggs visible through the ovisac;* 21) *Ovary wall and a part of egg membrane (x 120):* MS) *muscular layer;* SE) *inner secretory epithelium;* M) *mucus around the egg;* FE) *follicular envelope of the ovulated egg;* 22) *Juvenile ovocyte and peduncle (x 800):* N) *nucleus with nucleoli;* F) *follicular cells;* P) *penduncle;* O) *ovogonic tissue;* 23) *Cross-section of an ovary: above-total; below- 10 μ (x 40), showing the lumen of the hilus with blood vessels and eggs in various stages of development.*

all day, being very accelerated in the afternoon. Experiments with artificial insemination showed that the real ovulation occurs during the time of courtship behaviour, s.c. within 15 to 20 min. Females that were prevented from spawning during this period remained with eggs in their ovaria and those on the next day, begin to be atrophied and degraded.

So it seems that there is a limited and short period of correlation between the light condition, courtship behaviour and ovulation, with consequent spawning.

From the physiological point of view, as in Cichlid fishes, the prolonged and fractionated spawning expresses the innate ability of the ovary to produce eggs (FISHELSON, 1966). Under stable thermal conditions and by good feeding, *D. brachypterus* females spawned every 6 or 8 days over a period of at least 8 months. As each female produces 2 egg-balls in each spawn, in which the average number of eggs range from 3 to 6 thousand, this makes the total amount of eggs produced by a female in captivity — 200,000 to 400,000. This is a very high number compared with the ovary dimensions. The gradual in-growth of ovocytes, carried away from the ovogenic tissue toward the ovosac by the extending pedunculi prevents egg-crowding and produces space for additional ovogenesis. This mechanism enables the maximisation of the physiological capability of the ovary and enables the achievement of this goal-production of numerous eggs in a short period of time.

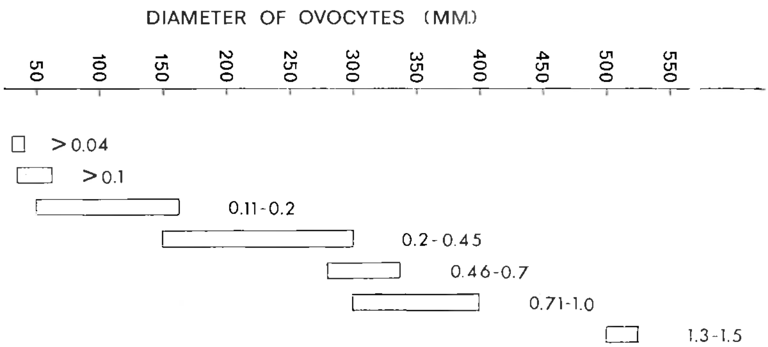

FIG. 24. *Ovocyte dimensions in* D. brachypterus: *numbers above columns indicate the distance from the place of origin and length of pedunculi (mm).*

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