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Morphological Aspects of the Development of Swimming and Feeding Functions in the Milkfish *Chanos chanos*

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Abstract Development of swimming and feeding abilities based on morphological development of larval and early juvenile *Chanos chanos* was investigated. In larvae smaller than about 6.5 mm SL, mechanical supports of fins and branchial arches were in a primordial stage of development. Supports and rays of the vertical fins and branchial arches rapidly developed from 6.5 mm SL, and all components appeared by about 10.5 mm SL. Thereafter body depth proportion changed and the supports and rays of the paired fins and gill-rakers developed. These developmental events were nearly or totally completed by about 17 mm SL, and we concluded that the larvae transformed to juveniles at this size. By this time, the mode of swimming of the fish shifted from undulating locomotion to caudal propulsion and that of feeding from swallowing particulate food to filtering and concentrating substrate food matters using gill-rakers and the epibranchial organ. One of the most characteristic, and well-known, phenomena in the life history of *Chanos chanos* is the mass occurrence in the surf zone of postlarvae of a limited size range. In view of the scheme of the development of mechanical supports of the body and fins, they may acquire a swimming ability strong enough to move against the current only upon reaching about 10.5 mm SL, and if active shoreward migration of the larvae occurs, it is only during the late period of their journey from the spawning grounds to the shore. The sudden disappearance from the surf zone of larvae larger than 15–16 mm SL is obviously related to a change in food habit.

Larvae of the milkfish, *Chanos chanos* (Forsskål), falling within a narrow range of body size (10–16 mm, modally 12.5–14.5 mm TL, cf. Kumagai, 1984) occur seasonally in tremendous numbers along shorelines of certain areas in the tropical and subtropical Indo-Pacific. Observations of the growth of laboratory-hatched larvae of the species (Vanstone et al., 1977; Liao et al., 1979) have shown that the above-mentioned modal size is attained under laboratory conditions within three to four weeks after hatching. Kawamura and Washiyama (1984) estimated the age of wild larvae occurring in southern Japan at 18–20 days old on the basis of the number of daily growth increments on the otolith.

The mechanism of the shoreward transport of larvae from the spawning grounds is open to question; they may be carried shoreward by currents and winds (Kumagai and Bagarinao, 1981; Kumagai, 1984), or migrate actively to the shore (Buri et al., 1981; Buri and Kawamura, 1983; Kawamura, 1984), or a combination of both of these mechanisms could be employed. After occurring in the surf zone as postlarvae, juvenile *Chanos chanos* occur in estuaries, coastal lagoons, mangrove swamps, etc. (e.g. Schuster, 1952; Tampi, 1958; Senta and Hirai, 1980; Kumagai and Bagarinao, 1981; Villaluz et al., 1982). However, ecological information concerning *C. chanos* juveniles is scarce (Kumagai and Bagarinao, 1981; Kumagai et al., 1985). Although there are elaborate discussions on the ecology of the species (Buri, 1980; Buri et al., 1981; Buri and Kawamura, 1983), we are still in need of accumulation of actual data on the morphological, functional and ecological development of the fish in order to elucidate its life history.

The purpose of this study is to examine developmental processes of swimming and feeding functions of *Chanos chanos* during the larval and early juvenile stages based on the development of morphological characters concerned with these functions. Osteological development of fin-supports in *C. chanos* has been described in our previous paper (Taki et al., 1986) and is only summarized in this paper.

Material and methods

Fertilized egges of *Chanos chanos*, spawned

naturally at the Igang Substation of the SEAFDEC Aquaculture Department, Iloilo, Philippines, on 12 June 1983, were transferred to a 0.5-ton circular plastic tank at the Tigbauan Research Station of the Aquaculture Department also located in Iloilo. The eggs hatched on June 14. Hatched larvae were provided as food with the rotifer, *Brachionus plicatilis*, at a concentration of 5–10 individuals/*l* of water from two days after hatching (day 2) and with *Artemia* nauplii from day 14. Aside from the laboratory-hatched material, larvae were captured from the shore water at Tigbauan on 11 June 1983 and reared in a 0.5-ton circular plastic tank fed with *Artemia* nauplii at the same station. Incubation and rearing were done in natural sea water (31–33% S) at ambient temperatures (25.5–30.0°C). Ten specimens were sampled every day from day 0 to day 21 from the laboratory-hatched batch and every other day from the day of capture to the 32nd day from the wild-captured batch. All these specimens were measured of their TL and SL immediately after sampling and then preserved in 5% freshwater formalin.

Sixty-four specimens of the laboratory-hatched larvae, 4.6–12.1 mm SL, and 32 specimens of the wild-captured/reared larvae and juveniles, 11.2–27.0 mm SL, were stained either with alcian blue and alizarin red S following the methods of Dingerkus and Uhler (1977) or with alizarin red S according to the methods of Taylor (1967). All these stained specimens have been used in Taki et al. (1986).

Range and mean of TL and SL of each sample were based on 10 specimens. Measurement was made to the nearest 0.05 mm. Methods for measuring the angle of flexion of the notochord end followed Kohno et al. (1983). Other methods are the same as in Taki et al. (1986).

Results

Growth. The growth in TL and SL of laboratory-hatched larvae from day 0 to day 21 is shown in Fig. 1. Day-0 larvae about 6 hours after hatching measured 4.05–4.5 mm (mean 4.3 mm) TL. The larvae absorbed yolk rapidly and the growth from day 0 to day 2 was very rapid compared with the growth thereafter. Feeding was evident on day 3. The larvae reached in mean values 5.8 mm TL and 5.5 mm SL on day 7, 8.6 mm TL and 7.8 mm SL on day 14, and 13.05 mm

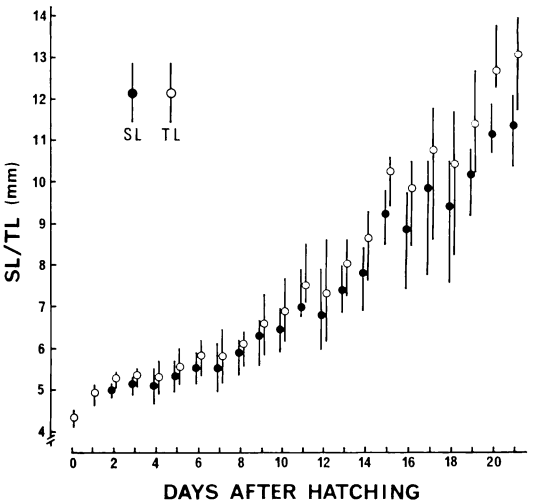

Fig. 1. Growth of laboratory-hatched/reared larvae of *Chanos chanos*. Range (vertical line) and mean (open or solid circle) of TL and SL are shown for each daily sample of 10 individuals.

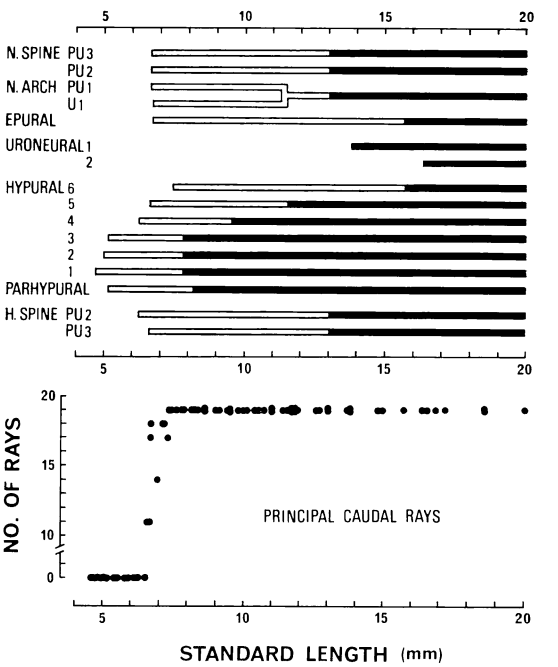

Fig. 2. Scheme of the development of the components in the caudal complex and development in number of principal caudal fin-rays in reared *Chanos chanos*. Open bar: cartilaginous state; solid bar: ossified state. H., haemal; N., neural; PU_{1-3}, preural centra 1–3; U_1, ural centrum 1.

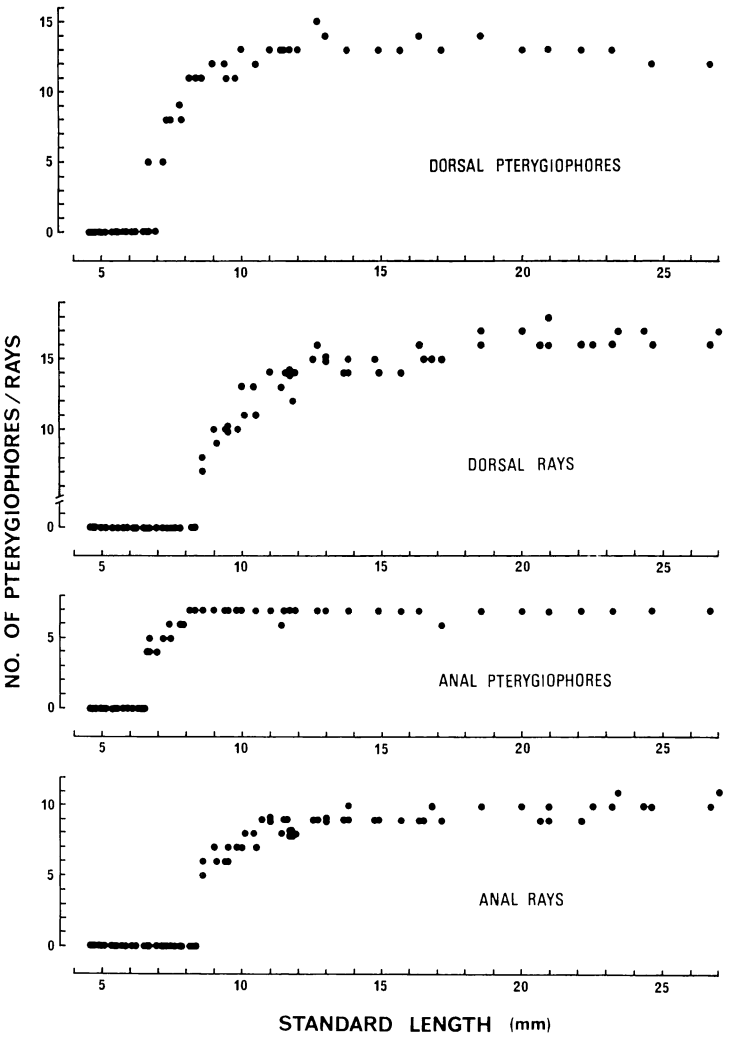

Fig. 3. Development in number of pterygiophores and fin-rays in the dorsal and anal fins in reared *Chanos chanos*.

TL and 11.35 mm SL on day 21.

Larvae collected from the wild measured 13.0–15.5 mm (mean 13.95 mm) TL and 11.5–13.7 mm (12.4 mm) SL on the day of their capture. Samples of the 2nd and 4th days after capture showed negative growth, with a mean TL of 13.5 mm and a mean SL of 11.35 mm on the 4th day. Thereafter the larvae grew exponentially, attaining in mean 17.5 mm TL and 14.95 mm SL on the 10th day, 23.5 mm TL and 19.15 mm SL on the 20th day, and 31.45 mm TL and 24.95 mm SL on the 30th day.

Development of characters concerned in swimming function. The summarizations of the development of fin-supports given below are based on the same material that was used in our previous work (Taki et al., 1986).

Caudal fin-supports and fin-rays: Developmental process of the caudal fin-supports is summarized in Fig. 2. The development of the caudal complex started at 4.7 mm SL at hypural 1, and all components except for uroneurals 1 and 2 were present at 7.45 mm SL. By 16.35 mm SL the two osseous uroneurals appeared, and all other elements partially ossified. Principal caudal fin-rays (10+9) were formed in a narrow SL range from 6.6 to 7.35 mm.

Dorsal and anal fin-supports and fin-rays: In the

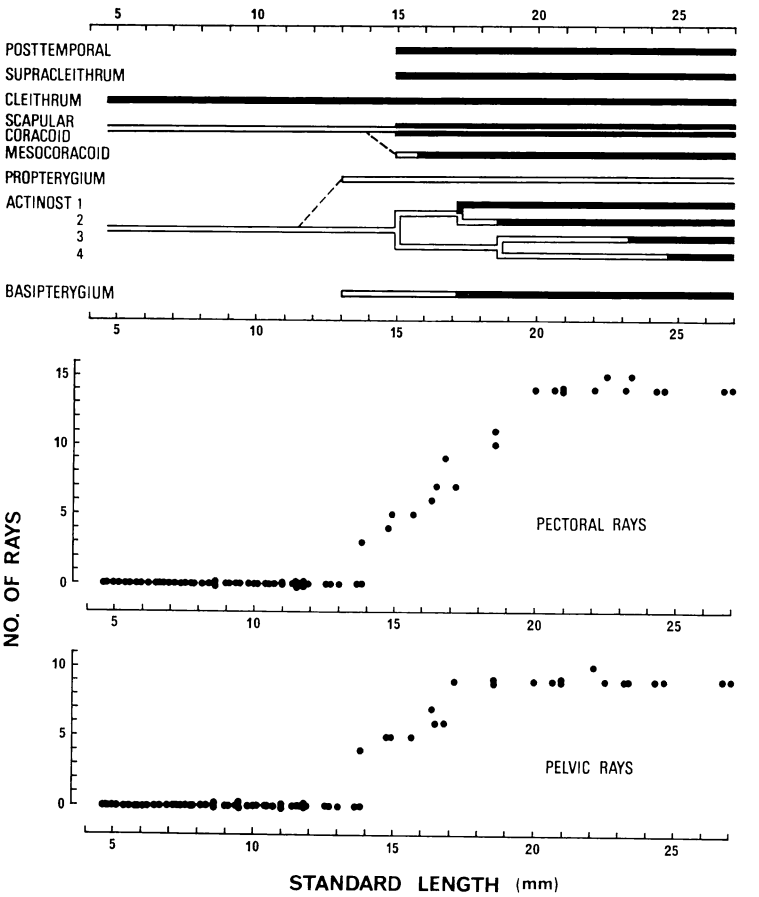

Fig. 4. Scheme of the development of the components in the girdles and development in number of fin-rays in the pectoral and pelvic fins in reared *Chanos chanos*. Open bar: cartilaginous state; solid bar: ossified state.

dorsal fin, pterygiophores first appeared at 6.7 mm SL. The minimum adult count of 11 pterygiophores was attained at 0.15 mm SL and the number of pterygiophores was stabilized between 12 and 15 from about 9–10 mm SL (Fig. 3). At this size the pterygiophores were all composed of proximal and distal radials except for the anteriormost one which consisted of a proximal radial only. Ossification started at 16.35 mm SL in all proximal radials. Development of dorsal fin-rays was noticed for the first time at 8.6 mm SL. The minimum adult count of 13 rays was acquired at 10.0 mm SL, and the fin-ray count levelled off from about 12.5 mm SL with 15–17 rays.

Anal pterygiophores were first seen at 6.65 mm SL, and the number of the pterygiophores became constant at 7 from 8.15 mm SL (Fig. 3). As in the dorsal fin, all the pterygiophores save for the anteriormost one, which was composed of a proximal radial, consisted of proximal and distal radials at the stage of the completion of the full complement of the pterygiophores. All proximal radials began to ossify at 16.35 mm SL. Anal fin-rays started to develop at 8.6 mm SL, and the specific counts of 9–11 rays were attained at 10.7 mm SL.

Pectoral and pelvic fin-supports and fin-rays: The osseous cleithrum, coraco-scapular cartilage and blade-like cartilage (fin plate cartilage, future actinosts) were already present at 4.65 mm SL. Development of other pectoral-girdle components was much retarded; none of them was seen till 14.9 mm SL excepting the propterygium. At 14.9 mm SL, the osseous possttemporal and su-

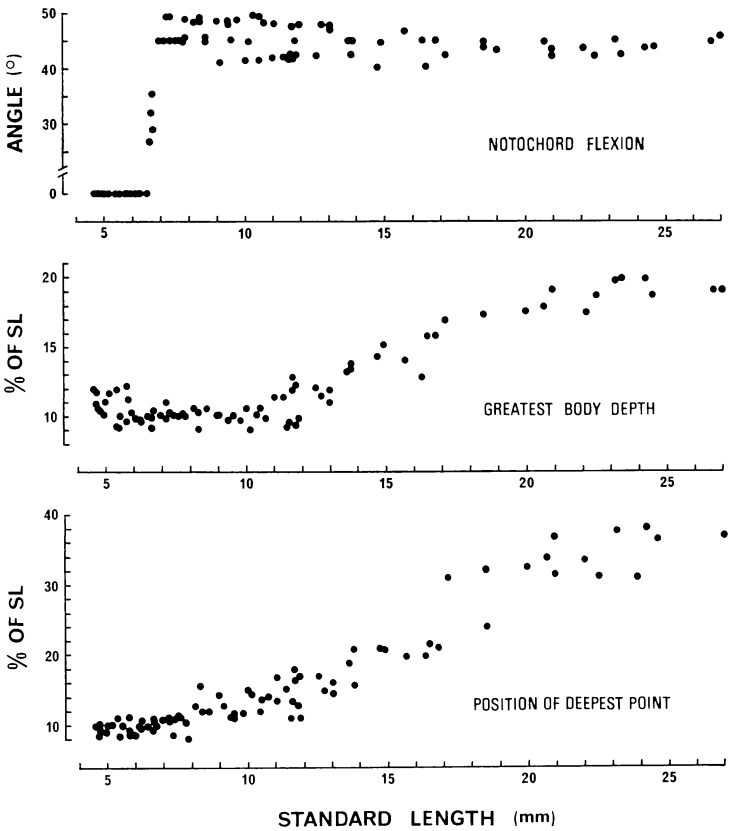

Fig. 5. Transition of the angle of flexion of notochord end, greatest body depth in percent of SL, and the position where the greatest body depth occurs expressed by the distance in percent of SL from the tip of the snout to the deepest point of the body in reared *Chanos chanos*.

pracleithrum and cartilaginous mesocoracoid started to develop, the scapula and coracoid began to ossify, and the blade-like cartilage began to split (Fig. 4). A complete set of pectoral-girdle elements was first evident at 18.55 mm SL. Ossification of actinost 4, the last to ossify in the pectoral girdle except for the propterygium, started at 24.6 mm SL. Pectoral fin-rays appeared from 13.8 mm SL, and their count became stabilized at 14–15 rays from about 20 mm SL.

The basipterygium of the pelvic girdle developed from 13.0 mm SL and started to ossify at 17.15 SL (Fig. 4). Pelvic fin-rays began to develop simultaneously with pectoral fin-rays, but the full complement (9–10 rays) was attained much earlier than in the pectoral fin, at 17.15 mm SL.

Flexion of notochord end: The caudal end of the notochord started to flex at 6.6 mm SL. The angle of flexion increased abruptly and reached 40–50° at about 7 mm SL, wherefrom the angle tended to decrease slightly and then stabilized at around 45° (Fig. 5).

Greatest body depth: The greatest body depth ranged from about 9 to 12% of SL in larvae smaller than 6 mm SL (Fig. 5). Thereafter the ratio maintained a constant level at around 10% of SL to about 10.5 mm SL and increased gradually and nearly reached a plateau at about 17 mm SL, completely levelling off at 18–20% of SL from about 20 mm SL. The greatest body depth occurred at anterior 9–11% of SL (head region) in specimens smaller than 8 mm SL. From this size the position where the greatest depth occurred gradually moved backward to about 17 mm SL, at which size the deepest point of the body abruptly shifted further backward to the trunk region. The positions of the deepest points were situated at anterior 31–38% of SL in specimens larger than

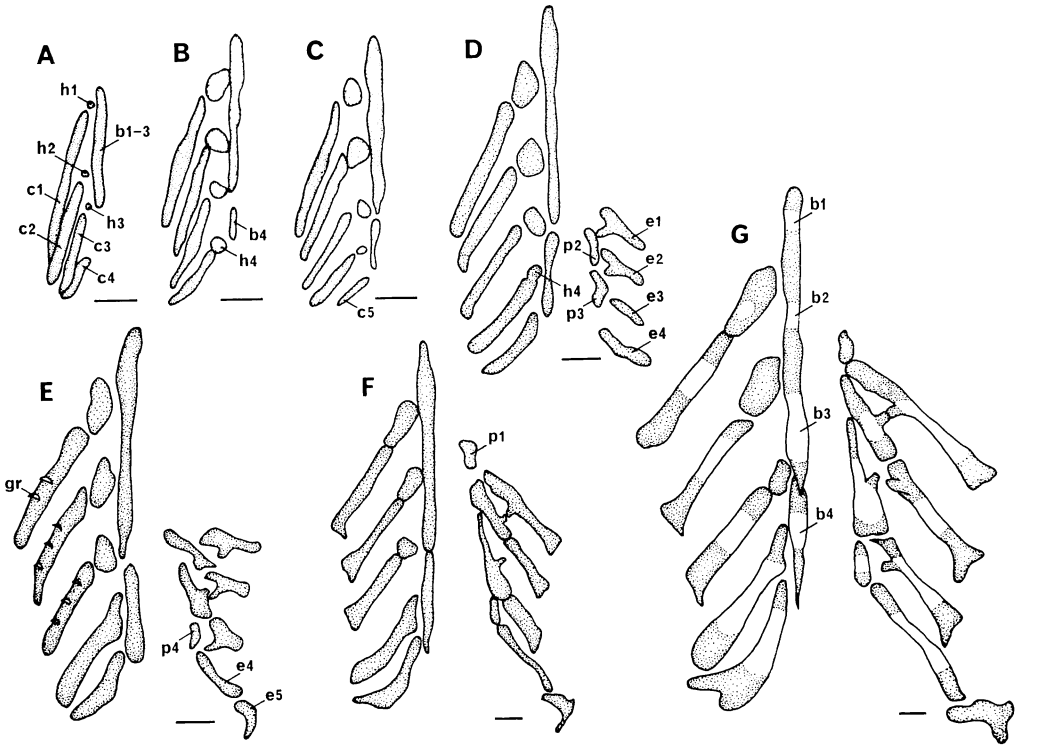

Fig. 6. Development of branchial arches in reared *Chanos chanos*. Dorsal view of left lower arches and dorsal view of right upper arches are shown. A, 5.75 mm SL; B, 6.65 mm SL; C, 7.35 mm SL; D, 9.0 mm SL; E, 10.0 mm SL; F, 12.7 mm SL; G, 13.8 mm SL. b_{1-4}, basibranchials 1–4; c_{1-5}, ceratobranchials 1–5; e_{1-5}, epibranchials 1–5; gr, gill-raker; h_{1-4}, hypobranchials 1–4; p_{1-4}, pharyngobranchials 1–4. Scale bar, 0.1 mm.

20 mm SL.

Development of characters concerned in feeding function. Branchial arches: Our smallest 4.6 mm SL specimen already had the rod-shaped basibranchial (future basibranchials 1–3), small, globular hypobranchials 1–3, and rod-shaped ceratobranchials 1–4. No upper branchial arch element was discernible at this size. A similar state of development was seen till 5.75 mm SL (Fig. 6A), though weakly stained hypobranchial 4 was seen in some specimens below this size. Basibranchial 4 was added as a ball-shaped, weakly stained cartilage at 6.65 mm SL (Fig. 6B). Ceratobranchial 5 was visible for the first time at 7.35 mm SL as a rod-shaped cartilage smallest of all ceratobranchials (Fig. 6C). Hypobranchial 4 and ceratobranchial 4 became fused at 7.8 mm SL. The upper branchial arches composed of epibranchials 1–4 and pharyngobranchials 2 and 3 were first evident at 8.15 mm SL (Fig. 6D for a 9.0 mm SL specimen). Gill-rakers were first perceived at 10.0 mm SL, two on ceratobranchial 1, three on ceratobranchial 2, and three on ceratobranchial 3 (Fig. 6E). At this size pharyngobranchial 4 and epibranchial 5 were added. Pharyngobranchial 1 started to develop at 10.5 mm SL. A process was formed on each of epibranchial 1 and pharyngobranchials 1 and 2 at 12.7 mm SL (Fig. 6F). Gill-rakers now developed on all the hypobranchials, ceratobranchials and epibranchials, and also on connective tissues adjacent to the hypobranchials as extensions of the rows of rakers on the hypobranchials. Signs of ossification were seen for the first time at 13.8 mm SL in basibranchials 1–4, hypobranchial 1, ceratobranchials 1–5, epibranchials 1–4, and pharyngobranchials 2–4 (Fig. 6G). Hypobranchials 2 and 3, epibranchial 5 and pharyngobranchial 1 started to ossify at 15.7 mm, 17.2 mm and 18.55 mm SL, respectively.

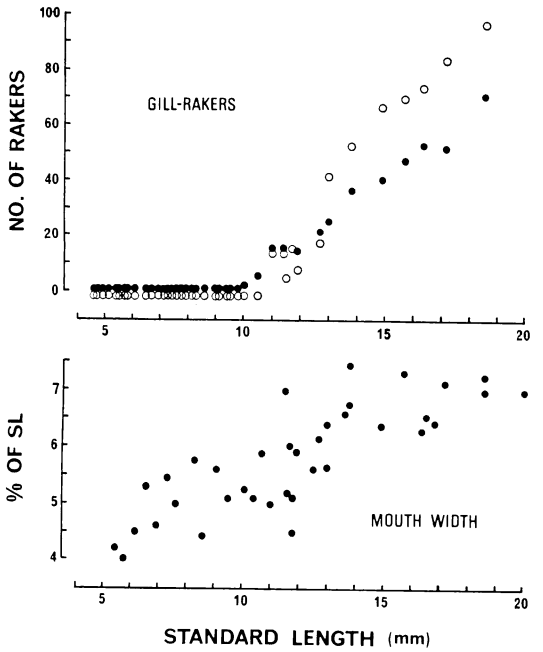

Fig. 7. Development in number of gill-rakers (solid circle: gill-rakers on the first arch; open circle: those on the components in the epibranchial organ) and transition of mouth width in percent of SL in reared *Chanos chanos*.

Number of gill-rakers: *Chanos chanos* has a paired epibranchial organ which serves as an accessory to the digestive system (Bertmar et al., 1969; Kuwatani and Kafuku, 1978). Development in number of gill-rakers participating in the structure and function of the organ, i.e. those on ceratobranchials 4 (inner row) and 5 and epibranchial 5, as well as those on the first arch (hypobranchial 1, ceratobarnchial 1 and epibranchial 1), was examined (Fig. 7). The smallest specimen possessing appreciable gill-rakers was 10.0 mm SL, with two rakers on the first arch. Gill-rakers in the epibranchial organ were first seen in an 11.0 mm SL larva, which had 14 gill-rakers on the epibranchial organ elements. The number of gill-rakers both on the first arch and on the branchial organ elements increased rapidly from about 13 mm SL.

Mouth width: Due largely to the difficulty in measuring accurately the width of the mouth of larval specimens, the plots of the measurements of mouth width in percent of SL were scattered widely (Fig. 7). Even so, a tendency to gradual increase of the relative width with growth was recognized. Relative width of the mouth stabilized at about 6–7% of SL from 13–14 mm SL.

Discussion

Growth and development of laboratory-hatched larvae of *Chanos chanos* has been described in detail by Liao et al. (1979). Compared with their results, our laboratory-hatched larvae showed an almost identical growth pattern up to about day 15 (6.4–11.8 mm TL on days 14–15 in Liao et al.; 6.8–9.9 mm SL on day 15 in this study). Thereafter, the growth of our larvae was retarded through to day 21 (13.5–16.5 mm TL on day 21 vs. 11.7–14.0 mm TL and 10.3–12.1 mm SL on day 21). This difference in growth seems attributable to differences in feeding and other rearing conditions between the two studies.

Developmental events observed in this study agree in both age and size of larvae with the descriptions by Liao et al. (1979) except for the development of fin-rays in the vertical fins and that of the pelvic fins. Fin-rays of the caudal, dorsal and anal fins were seen from days 6–7 (5.0–6.2 mm TL) in Liao et al., while they were first evident on day 9 (5.8–7.3 mm TL, 5.55–6.6 mm SL) in our material. This discrepancy may be due at least partially to the differences in the conditions of the specimens observed, i.e. probably in live or fresh state in Liao et al., cleared and stained in our study. The pelvic fins developed on day 21 (13.5–16.5 mm TL) or even earlier in Liao et al., but our day-21 larvae (11.7–14.0 mm TL, 10.3–12.1 mm SL) had no pelvic fins. Our smallest specimens possessing discernible pelvic fin-rays was a wild-captured/reared larvae eight days after collection, with a body size (15.9 mm TL, 13.8 mm SL) that corresponds to the length of the day-21 larvae of Liao et al. Vanstone et al. (1977) have shown that in their laboratory-hatched larvae of *Chanos chanos* the pelvic fins started to develop between day 31 (14–15 mm TL) and day 35 (20.1–22.6 mm TL). Liao et al. (1977) observed the appearance of the pelvic fins in wild-captured larvae from the 5th–7th day after capture (13.5–15.5 mm FL), and Kawamura and Hara (1980) on the 6th day (length of larvae not indicated). From these facts, it is likely that development of the pelvic fins at a younger age in Liao et al. (1979) is due to rapid growth of their larvae.

The scheme of the development of the char-

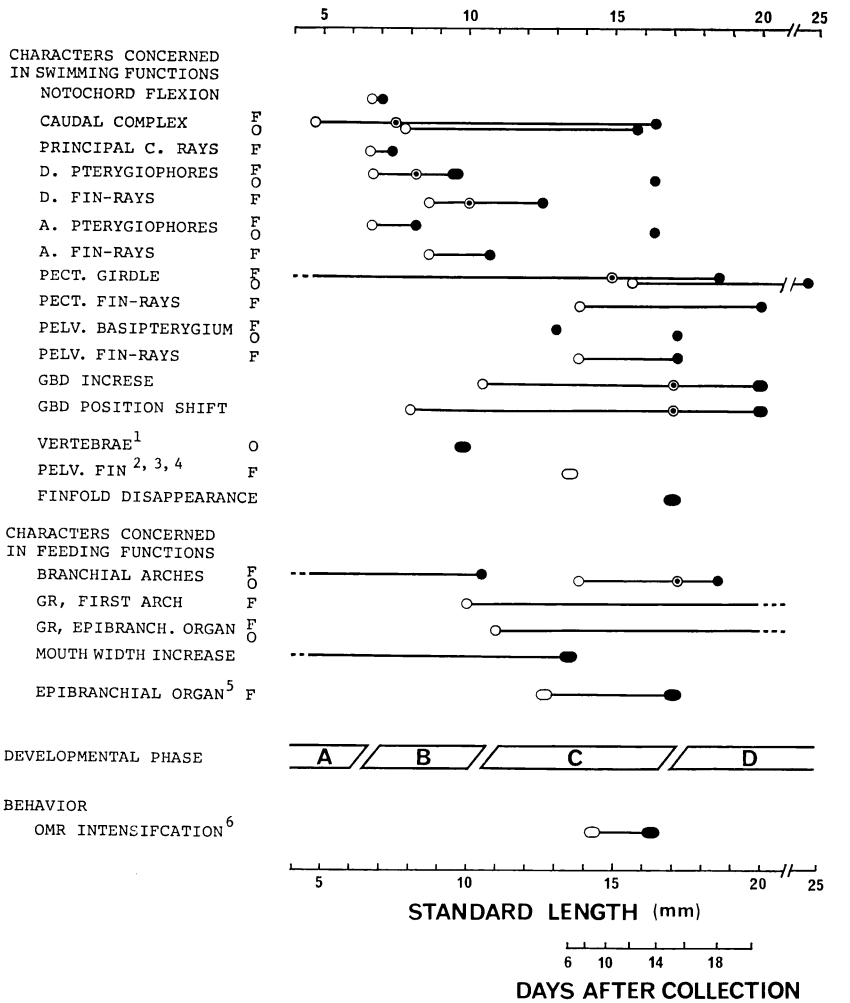

Fig. 8. Schematic representation of the development of characters concerned in swimming and feeding functions in reared *Chanos chanos*. Open circle: start of developmental event; double circle: near completion of event; solid circle: completion of event. A, anal: D, dorsal; GBD, greatest body depth; GR, gill-raker; OMR, optomotor reaction; PECT, pectoral; PELV, pelvic. Superscripts 1–6: based on Senta and Kumagai, 1977 (1); Liao et al., 1977 (2); Vanstone et al., 1977 (3); Liao et al., 1979 (4); Kafuku and Kuwatani, 1976 (5); Kawamura and Hara, 1980 (6). F, formation; O, ossification. For developmental phases A–D, see the text.

acters associated with the swimming and feeding functions of *Chanos chanos* during its early life can be described as follows and diagrammatically represented as in Fig. 8. Larvae smaller than about 6.5 mm SL had the notochord straight at its caudal end and only primodial structures of the caudal complex, pectoral girdle and branchial arches. From about 6.5 mm SL the vertical fins and branchial arches developed rapidly. Of the vertical fins, the caudal fin developed first, immediately followed by the dorsal and anal fins. All fin-supports (partly osseous only in the caudal) and fin-rays in these fins and all compounents of the branchial arches were formed by about 10.5 mm SL. Vertebrae ossify at the end of this developmental phase (at about 11 mm TL, Senta and Kumagai, 1977). From about 10.5 mm to about 17 mm SL, the larvae underwent a rapid change in morphology, this time mainly in the paired fins, body proportions and gill-rakers: the girdles

developed and ossified and fin-rays developed in the paired fins; mouth width increased; body became deeper and the position of the deepest point of the body moved backward to the trunk region; branchial arches nearly completely ossified; and gill-rakers developed and increased rapidly in number. Ossification of the fin-supports in the vertical fins was also completed. The epibranchial organ fully develops late in this developmental phase (by 19 mm TL, Kafuku and Kuwatani, 1976). Developmental events that remained unfinished at about 17 mm SL were the differentiation of actinosts 3 and 4, completion of fin-ray formation in the pectoral fins, complete stabilization of body depth proportions and ossification of the small pharyngobranchial 1.

On the basis of the scheme of development as described above, the early stages of *Chanos chanos* can be devided into four phases in terms of the development of swimming- and feeding-related characters: A) The initial phase which corresponds to the preflexion larva of Kendall et al. (1984), the period in which mechanical supports of the fins and branchial arches have not yet developed; to about 6.5 mm SL. B) The phase in which principal structures in the vertical fins, vertebrae and branchial arches are developed; to about 10.5 mm SL. C) The phase in which mechanical supports in the paired fins, gill-rakers and epibranchial organ are developed and the body form attains juvenile proportions; to about 17 mm SL. D) Juvenile stage; beyond 17 mm SL. We conclude that, from a functional morphological standpoint, *C. chanos* reaches the juvenile stage at around 17 mm SL (about 20–21 mm TL), though the full fin-ray complement of the species is attained at 20 mm SL when the pectoral fin-rays acquire the adult count.

Kawamura and Hara (1980) found that the optomotor reaction (OMR) of *Chanos chanos* larvae captured from the wild was greatly intensified during a period from 8 to 13 days after capture (length of larvae not indicated). Based on their observation that the pelvic fins developed on the 6th day after capture and the finfold completely disappeared on the 15th day, they considered that the transformation of the larvae to juveniles occurred bretween the 6th and 15th days after the collection of the larvae from the shore water, and the OMR of the larvae underwent a great change during this transition period. Our wild-captured larvae measured on the average 19.2 mm TL and 16.2 mm SL on the 14th day after capture and 21.1 mm TL and 17.4 mm SL on the 16th day. Assuming that the growth of the larvae did not differ greatly between the present study and Kawamura and Hara (1980), their results agree well with our conclusion that the larvae of *C. chanos* transform to juveniles at about 17 mm SL.

In natural waters, fertilized eggs of *Chanos chanos* are distributed from surface to a depth of at least 20 m, with even vertical distribution (Senta et al., 1980), or more abundantly in shallower layers (Kumagai, 1981, cited by Kumagai, 1984). Yolk-sac larvae are uniformly distributed from the surface to about 40 m (Kumagai, 1984). Post-larvae smaller than 9–10 mm TL also occur in midwaters, rising to the surface once they attain this size (Kumagai, 1984). Judging from the above-described developmental process of the mechanical supports of the body and fins, larvae smaller than 9–10 mm TL (about 8–9 mm SL) do not seem to have a swimming ability strong enough to swim for a long distance against current. As the state of developement of the swimming- and feeding-related characters suggests, the mode of wsimming at this size is undulation and that of feeding is swallowing of particulate food (present observation). Larvae may be carried by midwater current toward the shore and/or in other directions. Kumagai and Bagarinao's (1979) drift card experiments indicate that surface currents are not the major factor in the shoreward transport of *C. chanos* larvae.

Upon arriving in the surf zone, the larvae of *Chanos chanos* already have speeds as high as 9–11 cm/second (Kawamura and Hara, 1980; Kumagai et al., 1980; Komaki, 1981, cited by Kawamura, 1984; Buri and Kawamura, 1983), though they still retain the undulating mode of swimming. The larvae may acquire such an efficient swimming ability upon reaching around 10.5 mm SL (11.5–12 mm TL) as the vertebrae and major components of the caudal skeleton develop and ossify. It may follow that, if the larvae actually perform active migration toward the shore, it is probably only during the late period of their journey to the surf zone.

In the size range of the larvae found in the surf zone, the increase in the relative width of the mouth is nearly or totally completed, but gill-

rakers and the branchial organ are still just beginning to develop, indicating that the larvae still retain basically the swallowing mode of feeding. We have observed that the locomotion of the larvae shifts to caudal propulsion at about 15 mm SL, the size at which the caudal skeleton almost completely ossifies and the body form is in the course of transition from larval to juvenile proportions. However, larvae of that size are no longer found in the surf zone. In short, *Chanos chanos* larvae disappear from the surf zone in the middle of their transition from larvae to juveniles.

Juveniles of *Chanos chanos* inhabit coastal wetlands such as lagoons, estuaries, creeks and mangrove swamps. They feed on a variety of food matters on the bottom including detritus, blue-green algae, diatoms, vascular plant debris, animal matter, etc. (Kumagai et al., 1985). The morphological changes we have observed in the branchial region suggest that the changeover of food habit to such substrate feeding takes place at around 17 mm SL, the size at which the structures for filtering and accumulating food matters fully develop, and that the larvae have to reach their new habitats by the time they attain this size. The sudden disappearance from the surf zone of late postlarvae larger than 15–16 mm TL is obviously related to this change in food habit. However, the life of *C. chanos* in the later half of the transition stage from larva to juvenile is little known, and how the larvae succeed, or fail, in entering and establishing themselves in those nursery grounds remains obscure.

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形態からみたサバヒー仔稚魚の遊泳・摂餌機能の発達

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仔稚魚の形態に基づいて，サバヒー *Chanos chanos* の遊泳・摂餌機能の発達を検討した．約 6.5 mm SL 以下の仔魚では，鰭支持骨と鰓弓は発達原初期の段階にあり，脊索末端も未だに屈曲していなかった．垂直鰭の支持骨・鰭条と鰓弓は約 6.5 mm SL から急速に発達し，約 10.5 mm SL で全要素が出現した．それに続いて体高の変化と対鰭の支持骨・鰭条，鰓耙の発達が始まり，これらの変化・発達は約 17 mm SL でほとんどあるいは完全に完了して稚魚期に入った．この時までに遊泳様式は S 字型遊泳から尾鰭推進に，摂餌様式は微粒餌料の呑込みから鰓耙と上鰓器官を用いた底生餌料の沪過・集積へと変化した．サバヒー仔魚は砕波帯に大量に出現するが，形態・機能発達からみて，産卵場からの来遊が，少なくとも着岸間近までは，仔魚の積極的回遊によるものとは思われない．15–16 mm TL 以上の仔魚の砕波帯からの完全な消失が食性の変化と関連していることは明らかである．

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