Recruitment and Survival of Milkfish Chanos chanos Larvae in the Surf Zone

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Abstract The majority of Chanos chanos larvae collected from the surf zone at Villa and Tigbauan, Iloilo, Philippines, fell within a narrow range for total length (TL; 12.0–15.0 mm in 96% of 2,386 larvae) and had otolith increment counts of 15–20 (78%). The increment counts showed serial increases representing 5–10 days in some samples, at increase rates of 0.5–0.6/day, but such increases were not accompanied by increases in total length. Based on the low frequency (7.3%) of surf-zone larvae possessing food items in the gut, milkfish larvae occurring in the surf zone were considered to be under deficient feeding conditions. Otolith increments were formed at a rate of 1/day in well-fed larvae and 0.4/day in starved, captive larvae, in which stagnation of TL growth was also observed. The retardation of otolith increment formation and overall body growth in the surf zone larvae were considered to have resulted from deficient feeding conditions of a larval group entering and remaining in the surf zone for a certain period and/or from the concurrent recruitment and disappearance of larvae in the surf zone. The maximum duration of stay of the larvae in the surf zone was estimated to be about 10 days, from about day 15 to day 25 after hatching. Consequently, it is necessary for the larvae to move to juvenile nursery grounds within this period.

Larvae of the milkfish, Chanos chanos (Forsskål), which occur in tremendous numbers in inshore waters, have been the sole source of seed supply for the Southeast Asian milkfish aquaculture industry for centuries. The mechanisms associated with their mass occurrences have attracted the attention of fish biologists for years.

Chanos chanos spawns in offshore waters (Senta et al., 1980; Bagarinao and Kumagai, 1987; Leis and Reader, 1991), larvae being carried or moving shorewards as they develop (Kumagai and Bagarinao, 1981; Kumagai, 1984; Taki et al., 1987). Larvae occurring in inshore waters are 10–17 mm total length (TL), the majority being 11–15 mm TL (Senta and Hirai, 1981; Kumagai, 1984). Those beyond the former size range disappear completely from inshore waters.

The disappearance of larvae is considered to be related to their transformation into juveniles, which occurs at about 17 mm standard length (SL) and is accompanied by changes in the mode of life, e.g., from swallowing particulate food organisms to grazing benthic matter (Taki et al., 1987). Larvae may have to migrate to juvenile nursery grounds by this

stage (Taki et al., 1987).

However, little is known of how the larvae spend their time in inshore waters and where they go after staying in the surf zone. The literature on ecology of wild milkfish larvae indicates that larvae occurring in coastal surf zones seem to be under severe feeding conditions (Banno, 1980; Taki et al., 1990), but other aspects, such as age, trophic conditions, growth, survival and duration of stay in such waters, remain largely unknown. As larvae attain the juvenile stage, they change their habitat, allegedly from open shore waters to protected coastal wetlands, such as lagoons, creeks, estuaries and swamps (e.g., Buri et al., 1981). However, juvenile milkfish are hardly seen in nature (Kumagai et al., 1985), and actual data on the occurrence of early juveniles in such habitats are scarce (Kumagai and Bagarinao, 1981; Kumagai et al., 1985).

The present study was conducted to investigate the life of *C. chanos* larvae during their stay in the coastal surf zone. To this end, field sampling of wild larvae was conducted in the Philippines so as to examine occurrence patterns, and age and trophic conditions of the larvae in the surf zone. Rearing

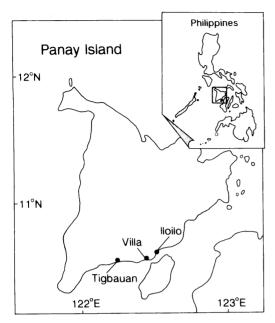


Fig. 1. Map of the Philippines showing the localities mentioned in the text.

experiments using both wild-caught and laboratoryhatched larvae were carried out to supplement data obtained from the field sampling.

Materials and Methods

Examination of wild-caught larvae.—The approximately 9,000 wild-caught Chanos chanos larvae used in this study (Table 1), were collected from the surf zones along the sandy beaches at Villa and Tigbauan, Iloilo, Philippines (Fig. 1), from 10 August 1987 to 5 August 1989, using fry-sweepers. The latter, a kind of push-net comprising a V-shaped bamboo frame with wing nets and a pouch of fine-mesh net (opening about 3 m), is operated by moving back and forth along the shore line in waist- to chest-deep water

Table 1. Wild-caught Chanos chanos larvae used in the study

Year	Collection site	Range of TL (mm)	No. of larvae	
1987	Tigbauan	6.45-15.45	481	
1988	Villa	10.90-15.80	242	
1989	Villa Tigbauan	11.60-16.05 11.94-15.67	ca. 7,000 ca. 1,700	

(Kawamura et al., 1980). Larvae collected were fixed in 10% formalin for abundance and gut content analyses, in 75% isopropanol for otolith observations, or kept alive for rearing experiments at the Brackishwater Aquaculture Center (BAC), University of the Philippines in the Visayas, Leganes, Iloilo, and the Aquaculture Department, Southeast Asian Fisheries Development Center (SEAFDEC AQD), Tigbauan, Iloilo.

Examination of laboratory-hatched larvae.—Fertilized eggs, spawned spontaneously at the Igang Substation of SEAFDEC AQD from 22 May to 21 June 1987 and from 5 to 10 August 1988, were transported to the Tigbauan Station of that department, in Iloilo, for hatching and subsequent rearing experiments. About 3,000 larvae were reared for observations on growth and otolith increment formation.

Total length conversion.—Total lengths were measured on both formalin and isopropanol-fixed specimens, and converted to equivalent fresh state TL's, using the following formulae: for isopropanol specimens, TL = 3.417 + 0.814Li, and for formalin specimens, TL = -0.367 + 1.055Lf, where TL is total length of fresh specimens, and Li and Lf are those of isopropanol and formalin specimens, respectively.

Abundance of larvae in the surf zone.—Collections of larvae for abundance assessments were made between 05:00–12:00 hrs (mostly 08:00–11:00) from 10 May to 28 June 1989, some 1,700 larvae being obtained. For these collections, each pushing operation of the fry-sweeper was made for a distance of 67 m along the shore line, and the abundance of larvae expressed as number collected per haul.

Feeding conditions of wild larvae.—Gut contents were examined in 993 of the 1,700 larvae used for the abundance assessments. Feeding conditions of the larvae were expressed by the following two indices: feeding incidence rate (percentage of larvae containing organisms or any other substances in the gut over the total number of larvae examined), and gut fullness index (index 0, gut empty; 1, items ingested were contained in less than 20% of the entire length of the gut; 2, 20% to less than 40%; 3, 40% to less than 60%; 4, 60% to less than 80%; 5, 80% or more).

Otolith examination.—Examination of otoliths (sagittae) included the following: the number of increments in wild-caught larvae on the day of capture, using 2,386 larvae collected from Villa and Tigbauan at 05:00-12:00 from 10 August 1987 to 29 July 1989; increment formation in wild larvae

after their capture under different feeding conditions, using larvae collected from Villa on 28 June 1989 and reared at SEAFDEC AQD; increment formation in laboratory-hatched larvae under feeding and nonfeeding conditions, using larvae hatched on 5 August 1988 at BAC.

For the examination of increment formation in wild-caught larvae kept in captivity, the larvae were placed in 80-ppm alizarin-complexone (ALC) solution for 20 hours to stain the otoliths (Tsukamoto, 1987), immediately after their initial collection. After ALC staining, four samples of 370 larvae each were reared in 3-l containers under different feeding conditions, as follows: (1) fed with Artemia nauplii (twice a day, 1 nauplius/ml of water) from day 0 after ALC staining (day 1 after capture); (2) ditto, from day 4; (3) ditto, from day 6; (4) not fed. Water temperatures ranged from 25.7 to 28.8°C and salinity was maintained at 25.0%. Twenty larvae from each treatment were sampled daily from the third day after ALC staining and preserved in isopropanol. The number of increments deposited outside the ALC-marked increments was counted.

For the examination of otolith increment formation in laboratory-hatched larvae, two samples, each containing about 3,000 larvae, were reared separately in 200-l tanks, at water temperatures of 26.0–30.7°C and salinities of 31.0–33.0%. Larvae in one tank were fed with rotifers, *Brachionus plicatilis*, at a density of 5 individuals/ml of water each day from the onset of feeding, 10–20 larvae being sampled daily, whereas those in the second tank remained unfed, 10 larvae being sampled on 3 and 5 days after hatching.

For otolith observations, sagittae were removed from the left side of the cranium, and mounted on microscope slides with epoxy resin or "Euparal." The total number of otolith increments was counted at least three times, under photo microscope (unstained otoliths) or fluorescent microscope (ALC-stained otoliths) at magnifications of $\times 100-500$.

Delayed feeding experiments.—Seven larval samples, ranging from 140 to 890 specimens, were collected from Villa from 19 June to 10 July 1989, at 3-to 6-day intervals, and reared at water temperatures of $23.7-29.2^{\circ}$ C and a salinity of 25.0%. Larvae of the first- and last-collected samples, kept in 2-l containers, were either fed with *Artemia* nauplii, at a density of 1 nauplius/ml, from the day of capture (day 0) to day 12 (2 replicates, comprising 81 and 88 larvae, respectively), or starved until days 6 (n = 94)

and 12 (n = 65). Each of the five remaining samples (n = 670-890) underwent the following delayed feeding treatments: daily feeding from day 0, feeding from days 3 to 10, preceded by non-feeding periods (progressively prolonging the latter by one day), and no feeding until all larvae had died (days 9-13). The number of dead larvae was counted twice a day, at 08:00 and 17:00 hrs.

Starvation tolerance of the larvae was expressed as irreversible starvation period (ISP; duration in days to a point in time at which the survival rate of larvae, which experienced delayed feeding for certain periods, had decreased to 50% of that of the control (fed from the day of capture), on the day by which all the unfed larvae die; based on Lasker et al., 1970) and median survival period (MSP, duration in days to a point of time in which the mortality of larvae, either starved or having undergone delayed feeding, reaches 50%; called point of no return [PNR] in Oozeki et al., 1989, but not PNR sensu Blaxter and Hempel, 1963).

Results

Abundance and gut contents of wild larvae

During the period from 10 May to 28 July 1989, the abundance of larvae collected from the surf zone fluctuated greatly, with several more or less distinct (Fig. 2). Some of the former peaks appeared to coincide with the new or full moon, but the existence of a lunar periodicity in abundance could not be confirmed due to the lack of continuous daily data.

Of the 993 larvae examined, 72 contained some gut contents, the feeding incidence rate being 7.3%. Even so, majority of the latter showed low gut fullness indices; 63 and 7 specimens scored indices 1 and 2, respectively. Higher indices (3 and 5) were seen in only 2 specimens. In all of the specimens, contents were observed only in the hind gut.

The gut contents consisted of diatoms (Coscinodiscus spp. and Triceratium sp.), copepods (eggs, nauplii and copepodids) and other organic matter in 45 specimens, the remaining 27 larvae appearing to contain inorganic matter only (Table 2).

These gut content data suggest that most of the larvae collected were either not feeding or feeding poorly, although it was unclear from the data alone if such paucity of gut contents was due to a scarcity of plankton or difficulty in preying upon plankton in

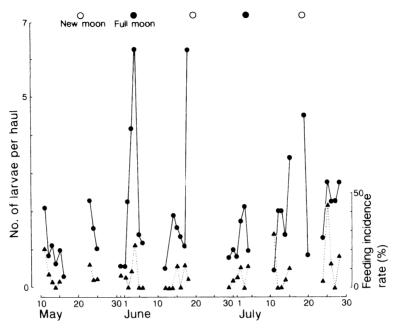


Fig. 2. Changes in abundance (solid circles and lines, expressed as the number of larvae per haul) and feeding incidence rate (solid triangles and dotted lines, expressed as percentage of larvae containing food organisms and other substances in the gut) of *Chanos chanos* larvae collected from the surf zone at Tigbauan from May 10 to July 28, 1989.

turbulent water.

Although not prominent, the feeding incidence rates also fluctuated, the peaks more or less coinciding with the larval abundance peaks (Fig. 2).

Total length and otolith increments of wild larvae

The total lengths of 2,386 larvae collected from Tigbauan and Villa ranged from 6.45 to 16.05 mm, with 96.1% falling between 12 and 15 mm TL (Fig. 3). The sagittae were somewhat oval (Fig. 4), with the otolith increment counts showing little convergence. Of the 2,386 larvae, 78% had increment counts from 15 to 20, although the number varied overall from 5 to 29 (Figs. 4, 5).

The relationships between TL and number of otolith increments in the 2,386 larvae are shown in Figure 5. Except for 14 specimens collected from Tigbauan the day after a typhoon hit the area (28 September 1987), all larvae were more than 10.90 mm in TL and had 11 or more otolith increments. The remaining 14 larvae were smaller (6.45–12.75 mm TL) and had fewer increments (5–10), which suggested that they represented an accidental occurrence of unusually early-stage larvae transported by storm waves. Their TL and otolith increment counts showed a positive relationship (Fig. 5A), whereas no such relationship was seen in other specimens. In the latter TL fell within a narrow range but the increment counts varied greatly (Fig. 5B-D).

In larvae collected daily from July 24 to 29, 1989

Table 2. Gut contents of 993 Chanos chanos larvae collected in the surf zone at Tigbauan from May 10 to July 28, 1989

Items found in gut	No. of larvae with each item	% of larvae with each item	
Diatoms			
Coscinodiscus spp.	10	13.9	
Triceratium sp.	1	1.4	
Copepods			
Calanoida spp.	2*	2.8	
Cyclopoida spp.	1	1.4	
Unidentified	2	2.8	
Eggs	4	5.6	
Other			
Organic matter	27 37.5		
Sand grains	27	37.5	
•	<u>- :</u>	•	

^{*} Two larvae containing copepods had ingested other organic matter.

at Villa, the mode of otolith increment counts was 16 on July 24 and 25, and increased thereafter at a rate of about 0.5 increment/day, attaining a count of 18 on July 27 and thereafter (Fig. 6A). An increase in modal increment counts was also observed in larvae collected at irregular, essentially 3-day intervals from July 3 to 13, 1989 at Villa (samples collected on and before June 27 were precluded because of their different TL compositions). In these larvae, the mode increased continuously from 17 to 23, at a rate of about 0.6/day (Fig. 6B). During the period of increment increase in both cases, the TL showed no

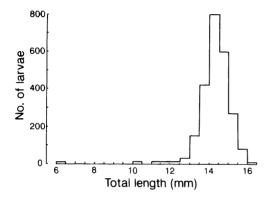


Fig. 3. Frequency distribution of total length for 2,386 *Chanos chanos* larvae collected from the surf zone at Tigbauan and Villa during 1987 and 1989.

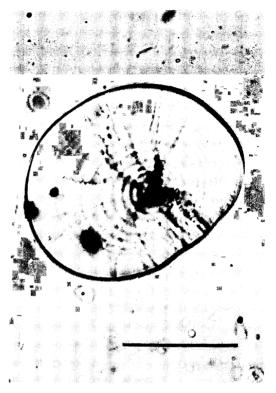


Fig. 4. Sagittal otolith removed from wild-caught Chanos chanos larvae (14.02 mm TL) at Villa, 1988. Sixteen otolith increments counted. Scale indicates 0.1 mm.

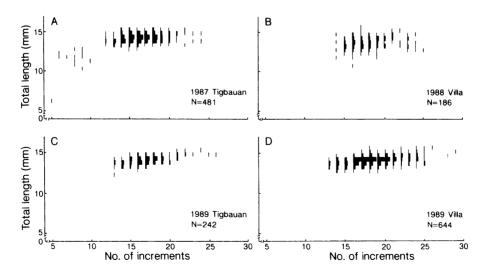
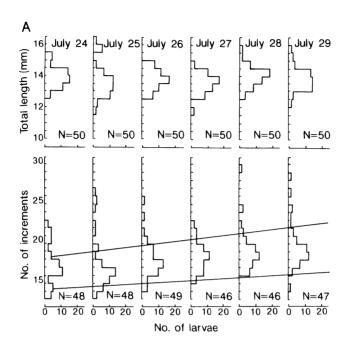


Fig. 5. Relationships between total length and otolith increment counts in *Chanos chanos* larvae collected from the surf zone at Tigbauan in 1987 (A) and 1989 (C) and at Villa in 1988 (B) and 1989 (D), shown as histograms of the number of larvae.



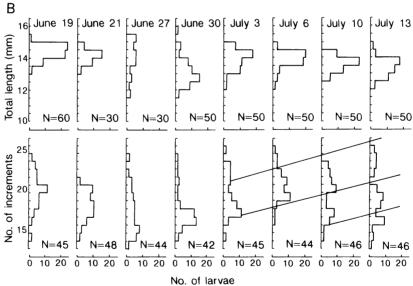


Fig. 6. Temporal transition of total length and otolith increment count compositions in *Chanos chanos* larvae collected from the surf zone at Villa in 1989. A) larvae collected daily from July 24 to 29; B) larvae collected at irregular intervals from June 19 to July 13. Lines indicate modal changes of otolith increment counts.

noticeable increase (Fig. 6A, B).

Otolith increment formation and growth of larvae in captivity

Laboratory-hatched larvae. —In larvae fed with rotifers, the first otolith increment was observed on day 1 after hatching, the increment count thereafter increasing daily. The number of increments (N) corresponded almost exactly to that of days after hatching (D) (Fig. 7A), the relationship between N and D being expressed by the following equation:

$$N = 0.201 + 0.969D$$
 $(r = 0.999)$.

The means and standard deviations of TL were 4.81 ± 0.19 mm (n=20), 5.66 ± 0.23 mm (n=11), 6.32 ± 0.18 mm (n=10), 7.45 ± 0.44 mm (n=15) and 13.15 ± 1.40 mm (n=14) on days 0, 5, 7, 15 and 30, respectively. The relationship between TL (L) and N was:

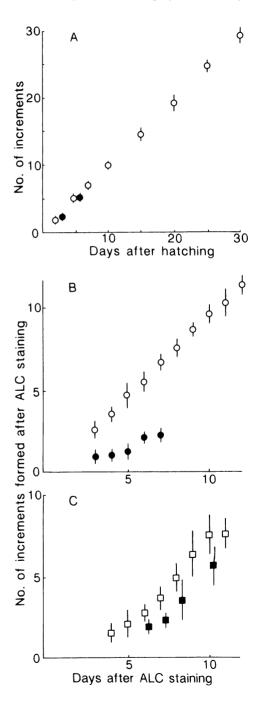
$$L = 4.283 + 0.275N$$
 $(r = 0.982)$.

In unfed larvae, the number of otolith increments also coincided with age, on days 3 and 5 (Fig. 7A). The TL of unfed larvae was 5.47 ± 0.25 mm (n=10) on day 3 and 5.45 ± 0.16 mm (n=10) on day 5. Wild-caught larvae.—Otoliths of larvae collected from the surf zone at Tigbauan were marked with Alizarin-complexone (ALC) on the day of their capture (day 0). In larvae fed Artemia nauplii continuously from day 1, the relationship between the number of otolith increments formed outside the ALC zone (AN) and days after marking (AD = days after capture) (Fig. 7B) was expressed as:

$$AN = -0.253 + 0.979AD$$
 $(r = 0.999)$.

Fig. 7. Formation of otolith increments in *Chanos chanos* larvae. A) number of otolith increments in laboratory-hatched larvae under feeding (○) and non-feeding (●) conditions; B) number of increments formed after ALC staining in wild-caught larvae under feeding (○) and non-feeding (●) conditions; C) number of increments after ALC staining in wild-caught larvae, following delayed feeding for 3 (□) or 5 days (■) from ALC staining. Vertical bars indicate standard deviation.

As in laboratory-hatched larvae, otolith increments were found to be formed at a rate of 1 increment/day. However, the number of increments counted on day 3 (mean = 2.5) was fewer than the number of days after marking by 0.5, this disparity



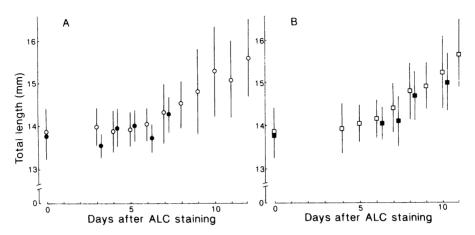


Fig. 8. Changes in total length of wild-caught *Chanos chanos* larvae after ALC staining. A) changes under feeding (○) and non-feeding (●) conditions; B) changes after 3-day (□) or 5-day (■) delayed feeding treatments. Vertical bars indicate standard deviation.

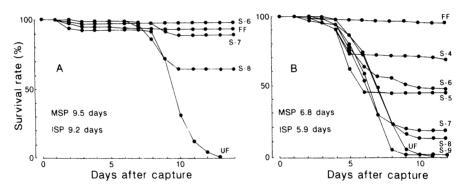


Fig. 9. Survivorship patterns of wild-caught Chanos chanos larvae in capitivity. A) larvae collected from Villa on June 21, 1989; B) larvae collected from Villa on June 6, 1989. FF—feeding from day 0 (day of capture); UF—larvae not fed; S-4 to S-9—delayed feeding for 4 to 9 days. MSP—mean survival period; ISP—irreversible starvation period.

remaining thereafter, indicating that the rate of increment formation from day 0 to day 3 was lower than 1 increment/day, despite the larvae being fed a sufficient amount of *Artemia* nauplii.

In larvae reared unfed throughout the experiment, otolith increments were formed at a rate of about 0.4/day (Fig. 7B), with the following relationship between AN and AD:

$$AN = -0.417 + 0.397AD$$
 $(r = 0.962)$.

In larvae fed only from day 4 to day 11, inclusive, the rate of increment formation decreased to about 0.6/day by day 6, but recovered thereafter to about 1/day (Fig. 7C), the relationships between AN and AD being:

$$AN = -0.884 + 0.592AD$$
 ($r = 0.998$) (days 4-6).
 $AN = -3.559 + 1.061AD$ ($r = 0.983$) (days 7-11).

Larvae fed only from day 6 to day 10, inclusive, showed a greatly reduced increment formation rate of about 0.25/day from day 6 to 7. However, the rate increased thereafter to nearly 1/day (Fig. 7C), with the following AN-AD relationship:

$$AN = -4.003 + 0.947AD$$
 (r=0.983) (days 7-10).

Increase in TL of wild-caught larvae was much slower during the period from capture (day 0) to day 6 than during the subsequent period, even though they were fed *Artemia* from day 0. The growth rate was similar to that of unfed larvae (Fig. 8A). In

larvae fed after 3 or 5 days of starvation, the growth rate was as low as in the above-mentioned fed and unfed larvae until day 6 or 7. Thereafter the rate increased as in larvae fed from day 1 (Fig. 8B).

Starvation tolerance of wild-caught larvae

Seven replicates of delayed-feeding experiments, each with 10 different feeding treatments, were conducted using seven samples collected from Villa. Figure 9 shows examples of survival patterns under different, delayed-feeding treatments. All of the samples showed similar survivorship patterns in that the survival rates were maintained at high levels for an initial period, before declining rapidly. However, the duration from capture to the onset of such declines differed considerably between the samples (Fig. 10 shows patterns for larvae starved throughout the experiment), resulting in a wide range of median survival periods (MSP) (4.6 to 9.9 days) and irreversible starvation periods (ISP) (5.2 to 9.2 days).

The MSPs were similar to their corresponding ISPs, and appeared to oscillate, although accurate fluctuation patterns could not be drawn due to insufficient data (Fig. 11).

Table 3 shows MSP, mean number of otolith increments (MN) and mean total length of larvae at capture (ML) for each sample, along with mean water temperature during rearing (T). The relationships between these parameters were expressed by the following equation:

$$MSP = -0.33MN + 5.13ML - 2.10T - 2.16$$
,

in which partial correlation coefficients were -0.59, 0.92 and -0.74, respectively (p < 0.01), and the multiple correlation coefficient was 0.96 (p < 0.01). This equation indicates that the MSP increased both with increased larval total lengths at capture and with lowered larval otolith increment counts at capture and lower water temperatures during rearing.

Discussion

Otolith increment formation and trophic conditions

Under sufficient feeding conditions, otolith increments were formed at a rate of about 1/day in both laboratory, early-stage larvae and more developed,

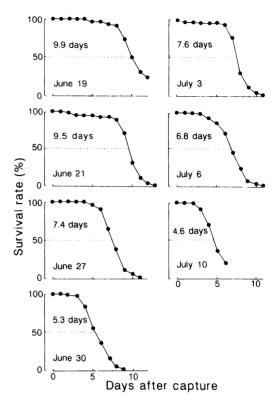


Fig. 10. Survivorship patterns of wild-caught Chanos chanos larvae under non-feeding conditions in captivity. Larvae collected from Villa. Numer of days shown equals mean survival period.

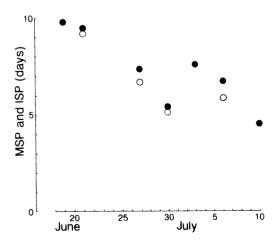


Fig. 11. Mean survival period (MSP, ●) and irreversible starvation period (ISP, ○) for Chanos chanos larvae collected from Villa, plotted against the date of their capture.

wild-caught larvae (Fig. 7A, B). In the former, the relationship between the number of increments (N) and that of days after hatching (D) was approximated as N=D. Tzeng and Yu (1988) reported that the first otolith increment in Chanos chanos larvae appeared at the time of completion of yolk absorption, i.e., about 2 days after hatching, suggesting the relationship N = D - 1. However, the results of the present study showed that the first increment was formed by the time larvae reached 1 day old, probably between day 0 and day 1. Furthermore, the volk of C. chanos larvae has been observed to persist for much longer periods, e.g., for 3 days (Liao et al., 1979), 120 hours (Bagarinao, 1986) and 110-125 hours (Kohno et al., 1990). The "first incremental zone" of Tzeng and Yu (1988) was "a thick amorphous structure," containing a few crests, in their digitized image diagram. This broad zone may have contained two increments, although these are not distinguishable in the figure.

When newly-hatched larvae were reared unfed throughout the experimental periods, otolith increments were formed at a rate similar to that for fed larvae, at least till day 5 (Fig. 7A). This unretarded increment formation is considered to have been supported by the endogenous nutrition of the larvae, since the yolk of *C. chanos* larvae may persist until about day 5 after hatching, as stated above.

In wild-caught larvae, the increment formation rate declined to about 0.4/day under non-feeding conditions (Fig. 7B). In the delayed feeding experiments, in which wild-caught larvae were fed after 4 or 6 days of starvation, the increment formation rate was low during the starvation periods (about 0.6/day for larvae starved for 4 days), but increased to about

Table 3. Median survival periods (MSP, days), mean numbers of otolith increments (MN), mean total lengths (ML, mm) of Chanos chanos larvae at capture and water temperatures (T) during 7 delayed-feeding experiments

Date*	MSP	ML	MN	Т
June 19	9.9	14.55	19.96	26.4
21	9.5	14.33	17.94	26.5
27	7.4	14.31	17.48	27.1
30	5.3	13.70	17.17	26.9
July 3	7.6	14.10	19.02	27.0
6	6.8	14.12	20.54	26.5
10	4.6	13.87	19.20	27.3

^{*} Date indicates the start of each experiment.

1/day, with 2- to 3-day time lags from the resumption of feeding (Fig. 7C).

These results indicated that the otolith increments of C. chanos larvae are first formed by day 1 after hatching, increasing in number at a rate of 1 increment/day under normal trophic conditions, and that nutrition deficiency causes considerable retardation of increment formation. Long-term starvation usually causes stagnation of otolith increment formation (Tanaka, 1984). Thus, Tzeng and Yu (1992) reported that starvation caused a reduction in increment formation rate to 0.65/day in C. chanos larvae, and Umezawa and Tsukamoto (1991) reported retardation of increment formation in unfed Anguilla japonica elvers. On the other hand, Mugiya and Muramatsu (1982) found that a 7-day starvation period did not influence increment formation in gold fish. Increment formation may not be affected by food deprivation provided that energy reserves are sufficient for maintaining limited skeletal growth (Marshall and Parker, 1982; Volk et al., 1984). Hence, wild-caught C. chanos larvae reared unfed are considered to have insufficient energy reserves for normal daily increment formation.

Starvation of larvae may result in the formation of a "check ring" (Liew, 1974) or narrower increments (Tanaka, 1984). However, such structures were not observed in the present study, or by Tzeng and Yu (1992). Higher resolution studies using SEM are necessary for their disclosure, if present at all.

Growth and trophic conditions

Under laboratory conditions, *C. chanos* larvae grow in length continuously from hatching to the juvenile stage (Vanstone et al., 1977; Liao et al., 1979; Taki et al., 1987). Although not verified experimentally in this study, there is no reason to doubt continuous, positive TL growth under normal trophic conditions in *C. chanos* larvae, since the species does not undergo obvious morphological transformation during early development.

The increase in TL of wild-caught larvae under delayed feeding treatments was slow during the starvation period and subsequent 1 or 2 days, and then increased (Fig. 8B). Growth retardation was also seen in those fed from the day of capture (Fig. 8A). Such growth retardation seems to have been caused by either nutrition deficiency or the effects of handling, or both.

Feeding of larvae in the surf zone

In the 2,386 surf zone larvae examined for TL and otolith increments, increases in TL with increased otolith increments were seen only for 14 small larvae (Fig. 6), which were considered to have been unusually early-stage larvae transported by storm waves. The steep increase in TL of these small larvae in relation to the number of otolith increments indicated that they had grown normally in off-shore waters, under sufficient feeding conditions.

On the other hand, the gut contents of C. chanos larvae occurring in the surf zone showed very low values, the feeding incidence rate being 7.3\% in the present study, 11.2% in Banno (1980), 12.1% in Kinoshita (1981) and 5.3% in Taki et al. (1990). The higher feeding incidence rates usually seen in larvae of other species, e.g., 50% or more for Clupea harengus (Blaxter, 1963), 20% or more for Engraulis mordax and Sardinops sagax (Arthur, 1976), about 70% for Thunnus thynnus (Uotani et al., 1990), point to the possibility of food defecation in the C. chanos larvae due to rough handling and formalin fixation. However, the lack of food substances in the mid-gut of the specimens examined strongly indicates a lack of gut contents overall, since mid-gut contents remain despite larval defecation and food discharge caused by rough handling and fixation. On the basis of these observations, milkfish larvae in the surf zone are considered to be under deficient feeding conditions. In addition, daily decreases of the RNA-DNA ratio, which declines in starved fish (Buckly, 1980; Clemmesen, 1987), were observed in C. chanos larvae collected daily from the surf zone (Morioka, unpublished data), indicating that larvae were not feeding well in that habitat.

In previous papers dealing with the otoliths of surf-zone larvae of *C. chanos*, the number of increments was taken as directly reflecting the age (number of days) of the larvae (Kawamura and Washiyama, 1984; Tzeng and Yu, 1990). However, trophic conditions should be taken into account in determining the age of such larvae.

Recruitment and stay of larvae in the surf zone

In view of the fluctuations in abundance of wild larvae (Fig. 2), some periodicity may exist in the recruitment of *C. chanos* larvae to the surf zone, assuming that larvae occurring in peak periods represent new arrivals. The comparatively high feeding

incidence rates, corresponding in many cases to the abundance peaks (Fig. 2), and the probable oscillation of MSP and ISP (Fig. 11) support this, provided that the new arrivals had fed sufficiently on their way to the surf zone.

However, the data obtained in this study were not sufficient to confirm the existence of recruitment periodicity, much less the existence of relationships between recruitment and the lunar cycle. Kuronuma and Yamashita (1962) in Vietnamese waters and Kumagai (1984) in Philippine waters noticed lunar periodicity in the occurrence of milkfish larvae in inshore waters, but Senta and Hirai (1981) did not observe periodic occurrence of larvae at Tanegashima, southern Japan.

The otolith increment counts of larvae at the time of their arrival in the surf zone under normal oceanic conditions are considered to be around 15, on the basis of the increment counts of 15 or more in the majority of surf-zone larvae (Fig. 5) and the increase in the modal number of increments starting from 16 or more (Fig. 6).

In wild larvae collected daily from the surf zone, an increase in TL was not observed (Fig. 6), although otolith increments sometimes increased in number, though at a low rate (0.5–0.6/day, Fig. 6). Two interpretations for these are possible: (1) an influx of larvae to the surf zone stays for a period, during which their increase in TL is negligible but otolith increments increase at a low rate due to deficient feeding conditions; and (2) replacement of larval groups occurs, that is, recruitment of young larvae and disappearance of older larvae occurs concurrently.

The second interpretation is considered applicable in the case where neither TL nor otolith increments increase. Daily increases of otolith increments and RNA-DNA ratios (Morioka, unpublished data) indicated that the trophic conditions of milkfish larvae became worse during their stay in the surf zone, supporting case (1).

If the larvae have been well-fed before reaching the surf zone, their otolith increment numbers therefore equaling their ages, their actual age at arrival should be about 15 days. On the other hand, their hypothetical maximum age can be calculated as [(15-5)/0.5]+5=25 days, assuming that increments are formed at a rate of 1/day until day 5, even under non-feeding conditions (Fig. 7A), and increments are produced at 0.5/day after they arrive in the surf zone (based on the formation rate of 0.4 in unfed,

wild-caught larvae [Fig. 7B] and rates of 0.5 and 0.6 estimated from the transition of increment frequency distribution for wild larvae [Fig. 6A, B]). However, the latter assumption, premised on starvation throughout the period from the onset of feeding to arrival in the surf zone, seems implausible.

Assuming that larvae are recruited to the surf zone at the 15 otolith increments stage, after spending well-fed offshore lives, and remain in the surf zone under deficient feeding conditions until the 20 increments stage (based on the frequency of increment counts for wild larvae, Fig. 4), the maximum duration of their stay in the surf zone is (20-15)/0.5 = 10 days. This figure is consistent with the maximum MSP value of 9.9 days (Fig. 10).

However, the above calculation does not necessarily indicate that larvae remain in the surf zone for the entire period. In fact, the abrupt decreases seen in larval abundance (Fig. 2) may reflect larvae leaving the surf zone shortly after their initial arrival, for unknown destinations.

Conclusive Remarks

Generally, a surf zone is rich in zooplankton biomass, apparently much more so than deeper water beyond the zone (Brown and McLachlan, 1990). Although the surf zone surveyed in the present study was no exception (Morioka, unpublished data), all of the data obtained in this study pointed to a food deficiency in the surf-zone larvae of Chanos chanos. Although it was unclear whether or not the food deficiency was due to difficulty in preying up on floating particulate food organisms in turbulent water, the surf zone did not appear to be suitable for long sojourns of C. chanos larvae. Based on the present study, such larvae may have to depart the surf zone within 10 days for better nursery grounds. On the other hand, larval routes to juvenile nursery grounds may bypass the surf zone altogether. However, early juveniles have been found only occasionally in coastal wetlands, the alleged nursery grounds for milkfish juveniles. Further investigations are required to determine if the complete disappearance from the surf zone of milkfish larvae results from their movement to other habitats, either in inland or offshore waters, or from their eventual death.

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砕波帯におけるサバヒー仔魚の加入と生残

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フィリピン、パナイ島のイロイロ周辺での仔魚の採集と人工 生産仔魚・天然仔魚の飼育実験に基づいて、沿岸砕波帯でのサバヒー仔魚の加入・滞留の状況を検討した。砕波帯に出現する 仔魚の全長は、その多く(2,386 個体の 96%)が 12.0-15.0 mmの 狭い範囲に入り、耳石輪紋数は 15-20 本の間に多く分布した (2,386 個体の 78%)、天然仔魚では輪紋数が 0.5-0.6 本/日の割 合で増加する経日変化が観察される場合があったが、この間の全長分布には経日的な増大は認められなかった。 給餌飼育下では、人工、天然仔魚ともに輪紋は1本/日の割合で増加したが、天然仔魚を無給餌飼育すると、増加率は0.4本/日に低下した。飼育下での天然仔魚の飢餓耐性は輪紋数の少ない個体ほど、つまり加入後間もない個体ほど強く、50% 致死日数は最長で9.9日であった。また、天然仔魚の摂餌個体率は7.3%ときわめて低い値を示した。これらの結果から、仔魚は冲合いでは良好な栄養条件下にあるが、砕波帯では摂餌条件は劣悪化すると考えられた。砕波帯への加入時の日令を15日前後と推定し、砕波帯では低い栄養状態により体成長が停滞し輪紋形成率が低下すると仮定すると、滞留可能期間は約10日と推定された。

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