

Hatching Period and Early-Stage Growth Rate of the Gold Estuarine Anchovy *Stolephorus insularis* in Taiwan as Inferred from Otolith Daily Growth Increments

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Wann-Nian Tzeng, Han Chu, Kang-Ning Shen, and Yu-Tzu Wang (2008) Hatching period and early-stage growth rate of the gold estuarine anchovy *Stolephorus insularis* in Taiwan as inferred from otolith daily growth increments. *Zoological Studies* 47(5): 544-554. To understand the reproductive strategies and recruitment dynamics of the gold estuarine anchovy *Stolephorus insularis* in a subtropical area, their seasonal abundance was investigated, and their hatching period and growth rate were estimated from otolith daily growth increments. Specimens were collected from the Tatu River estuary on the west-central coast of Taiwan during 1997-1998. Juvenile fish dominated the catch composition, suggesting that the estuary is a nursery for newly recruited juveniles of *S. insularis*. The distribution of hatching dates for anchovy in subtropical Taiwan was similar to that of temperate zone fish, with a major spawning season in spring and a minor spawning season in autumn. This spawning strategy coincided with a new production cycle that was higher in spring than in autumn. Mean standard lengths and ages of the anchovy at recruitment were significantly larger for the autumn than for the spring and summer cohorts (all $p < 0.001$), while the somatic and otolith growth rates were higher in spring than in summer and autumn (all $p < 0.001$). Larval anchovy grew faster and reached their maximum growth rate (inflection point of the growth curve) earlier during summer than during either spring or autumn. The growth rate after the inflection point was lower in autumn than in either spring or summer. The reproductive and growth rate variability indicated that the spring cohort is the major component of the stock and that the autumn cohort is a minor supplement to overall recruitment. <http://zoolstud.sinica.edu.tw/Journals/47.5/544.pdf>

Key words: *Stolephorus insularis*, Otolith, Spawning season, Growth rate, Production cycle.

The gold estuarine anchovy *Stolephorus insularis* (Hardenberg 1933) is a small pelagic fish with a short lifespan that feeds mainly on crustaceans, particularly copepods (Milton et al. 1990). It is widely distributed in tropical coastal waters of the Indo-Pacific to western Pacific Oceans between 27°N and 8°S. This anchovy is generally caught as bait for commercial fisheries. It is also abundant in the coastal waters of Taiwan and around the Penghu Archipelago (the Pescadores) in the Taiwan Strait, where it is a target species of small-fish fisheries in Taiwan

(Tzeng and Wang 1992, Wang and Tzeng 1997, Tzeng et al. 2002, Chen and Chiu 2003). It also constitutes the dominant component of the larval and juvenile communities in estuaries.

The life cycle of this species is poorly known. It may spawn offshore, with the post-larvae and juveniles migrating to and staying in estuaries until the young stage. The seasonal recruitment of larvae and juveniles in estuaries depends on its spawning regime, which has evolved to adapt to seasonal changes in productivity. Tropical fish are generally characterized by a protracted spawning

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season, an adaptation to the continually low productivity in tropical waters, whereas temperate-zone fish usually spawn in 2 seasonal peaks that typically follow the cycle of seasonal production, with a peak of new production in spring and a minor peak of recycled production in autumn (Cushing 1975). The Tropic of Cancer (23°30'N), a boundary between temperate and tropical zones, passes through central Taiwan, and it is not clear whether *S. insularis* in the estuaries of Taiwan follows a temperate or tropical spawning pattern. Larvae and juveniles of *S. insularis* are abundantly recruited to the estuaries of Taiwan with a major peak in abundance in spring and a minor peak in autumn (Tzeng et al. 2002). This implies that *S. insularis* in Taiwan is a temperate-, rather than a tropical-type, spawner. However, this has not been validated by further scientific study. The link between the spawning season and production cycle can accelerate larval growth and reduce the risk of predation thereby increasing the survival rate (match and mismatch hypothesis) (Cushing 1975 1982, Sinclair and Tremblay 1984). The match or mismatch between the timing of production and spawning is a key factor determining the growth rate of the fish in early life and subsequently the year-class strength of the fish stock (Hjort 1914, Cushing 1975, Smith 1985). Understanding the spawning period and growth patterns of the early stages of fish development is very important for analyzing fish recruitment and population dynamics.

Since Pannella (1971) discovered the daily growth increment in otoliths, it has been widely used to determine larval ages and to back-calculate birthdates and spawning regimes of fish (e.g., Townsend and Graham 1981, Methot 1983, Tzeng 1990, Secor et al. 1992, Wang and Tzeng 1999, Wang and Tzeng 2000). Larval growth rate variability among different spawning seasons can also be elucidated by comparing the otolith daily growth rates and lengths-at-age among seasonal cohorts (Crecco and Savoy 1985, Al-Hossaini et al. 1989, Thorrold and Williams 1989, Rutherford and Houde 1995, Wang and Tzeng 2000).

In this study, we attempted to elucidate the hatching period and growth strategies of *S. insularis* in subtropical Taiwan. The hatching date and early-stage growth rate of the fish were determined from the daily growth increment pattern of otoliths of fish collected in an estuary on the west-central coast of Taiwan during different seasons. The link between seasonal spawning timing and production cycles was also addressed.

MATERIALS AND METHODS

Specimens of *S. insularis* were collected using an anchored bag-net from the Tatu River estuary on the west-central coast of Taiwan (Fig. 1). The net was set against the tidal current during the nocturnal flood of the spring tide during the new moon from Nov. 1997 to Dec. 1998. The sampling location, procedures, and fishing gear were similar to those described in a study by Tzeng et al. (2002). Surface water temperature and salinity were measured with a microprocessor conductivity meter during sampling. Species were identified following Leis and Rennis (1983), Ozawa (1986), Wang (1987), Okiyama (1988), and Leis and Trnski (1989). In total, 1518 larval and juvenile *S. insularis* were collected. The development of the fish was classified into 4 stages following Leis and Rennis (1983) and Wang (1987): flexion larva (FI), postflexion larva (Po), juvenile (Ju), and young (Yo). Standard length (SL) was measured to the nearest 0.1 mm.

Sagittal otoliths, the largest of 3 pairs of otoliths, were removed from a fish's head with a sharpened needle, rinsed with distilled water, air-dried, and stored in plastic bottles. Right otoliths were embedded in epofix resin, ground, and polished along the sagittal plane until the primordia were exposed. The polished otoliths were then etched with 10% ethylenediaminetetraacetic acid (EDTA) to enhance the daily growth increments (DGIs). DGIs were counted with the aid of an image processing system, and the radii and DGI width of the otoliths were measured from primordium to rostrum with the aid of SigmaScan Pro 5 software (SPSS science, Chicago, USA) to calculate the otolith growth rate of the fish. Daily ages of fish were directly estimated from DGI counts without adjusting for yolk sac duration, because DGIs were assumed to be deposited daily after hatching (Gjoesaeter et al. 1984, Thorrold and Williams 1989, Hoedt 2002). One study indicated a 1 d delay in the appearance of the 1st increment after hatching in other clupeoids (Hayashi et al. 1989). The hatching (birth) date of the fish was back-calculated from DGIs and the date of capture. Specimens were classified into spring (Mar.-May), summer (June-Aug.), and autumn (Sept.-Nov.) cohorts based on the back-calculated hatching dates.

The relationship between standard length and otolith diameter was fitted by an allometric growth equation, $y = ax^b$, and the somatic growth equation of the fish was fitted with length-at-age data by the

exponential equation, $y = ae^{b \cdot \text{age}}$. The significance of differences in growth equations among cohorts was tested by analysis of covariance (ANCOVA) after logarithmic transformation to fit the normal distribution hypothesis. The difference in increment widths of otoliths among cohorts was tested with repeated-measures analysis of variance (ANOVA). Differences in the transition rate of development between stages among cohorts were tested by a non-parametric ANOVA.

RESULTS

Water temperature and salinity

The water surface temperature in the Tatu River estuary on the west-central coast of Taiwan changes seasonally, with a minimum of approximately 15°C in Feb. when the north-eastern monsoon prevails, and a maximum of approximately 30°C in Aug. when the southwestern monsoon prevails. It increased from 15°C in

Feb. to 29.5°C in May, and remained at a high level until early Oct. when it decreased (Fig. 2). The difference in water temperature between the coldest and warmest months was approximately 15°C. The seasonal temperature regime indicated that the study area has a more-temperate than tropical climate.

Seasonal changes in surface salinity in the estuary were irregular, ranging from 1.0 ppt in June to 34.9 ppt in Jan. (Fig. 2).

Developmental stage composition and seasonal abundances

Juvenile *S. insularis* dominated the composition of specimens collected in the Tatu River estuary and accounted for approximately 60% of the total catch, followed by postflexion larvae and young stages, which accounted for approximately 20% each. Flexion larvae accounted for approximately 2% (Fig. 3).

The seasonal abundance by stage indicated that *S. insularis* was recruited to the estuary mainly

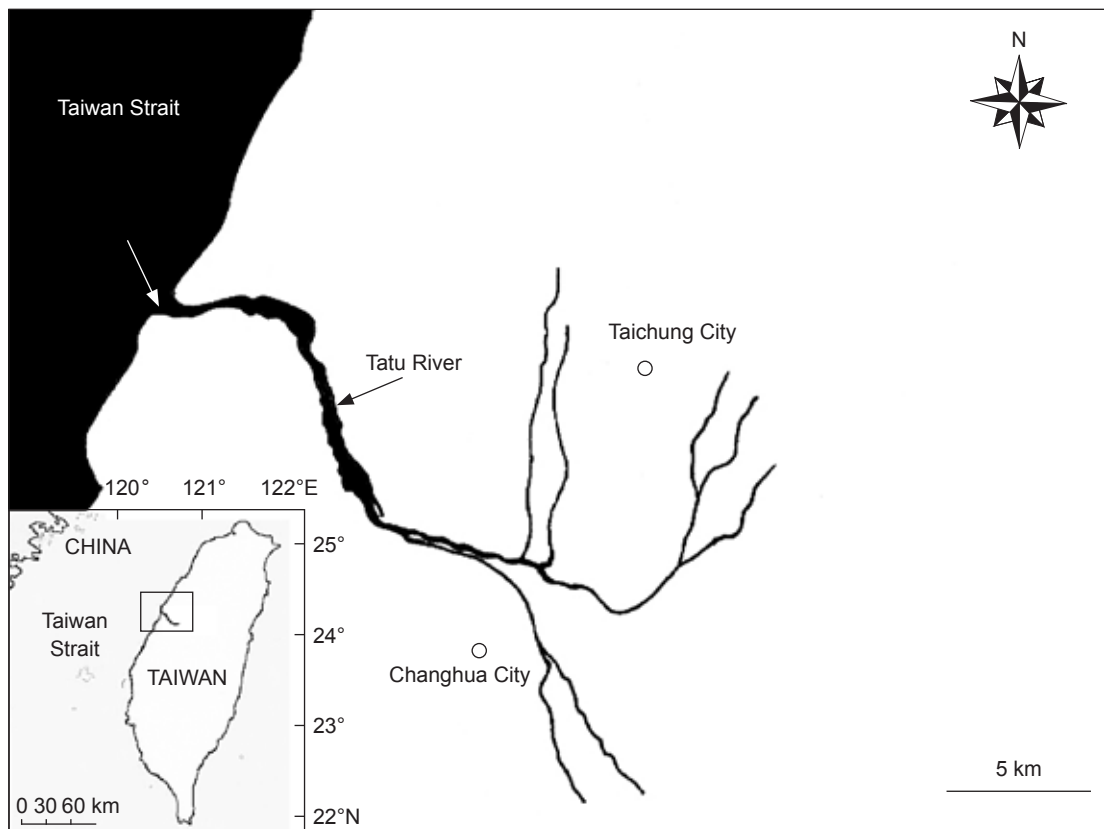


Fig. 1. Location of the sampling site in the Tatu River estuary (white arrow).

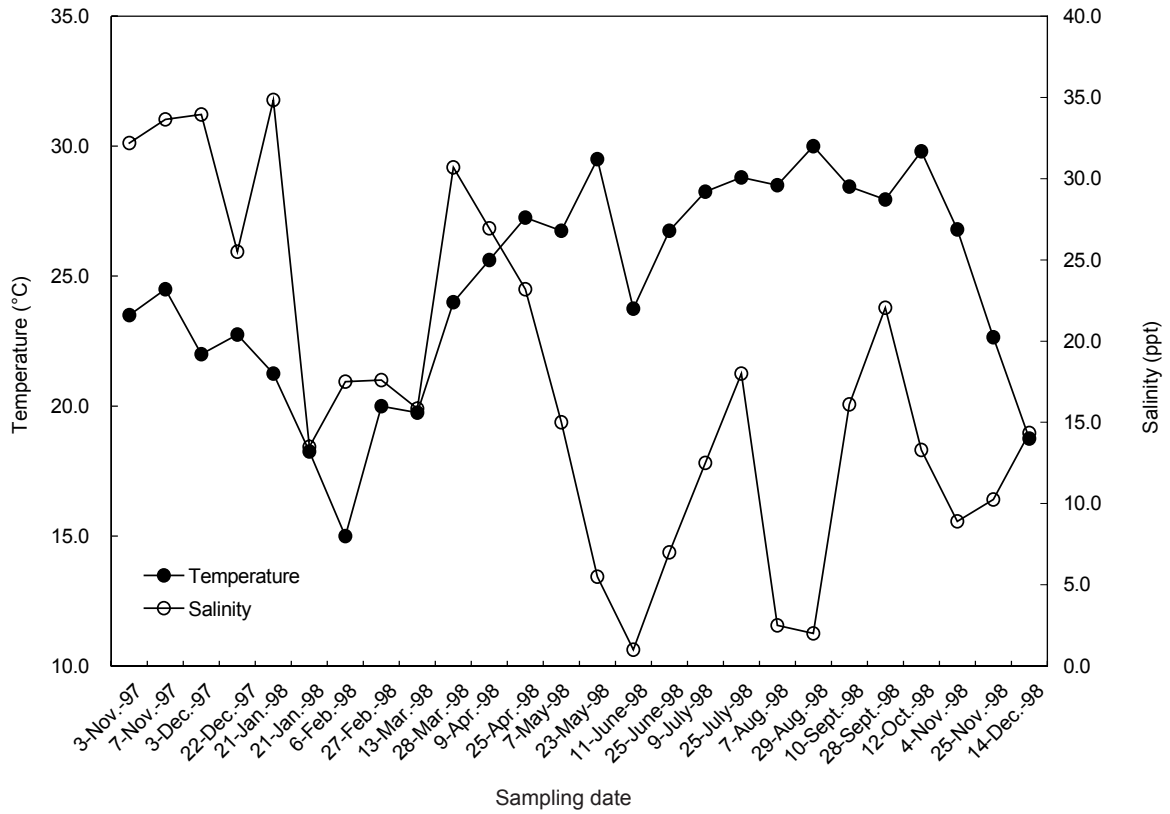


Fig. 2. Seasonal changes in surface water temperature and salinity in the Tatu River estuary.

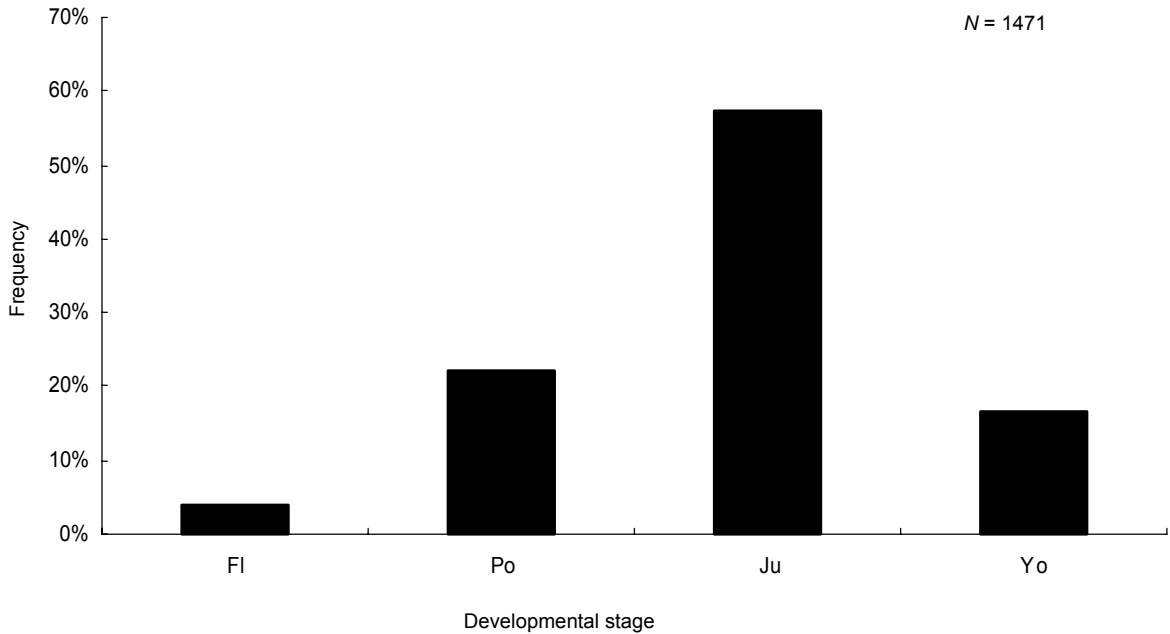


Fig. 3. Stage composition of larvae and juveniles of *Stolephorus insularis* collected in the Tatu River estuary. FI: flexion larva; Po: postflexion larva; Ju: juvenile; Yo: young.

as juveniles, with peak abundances in spring (Apr.) and early summer (June) and a minor peak in autumn (Nov.). A peak in abundance was found in Nov. 1997 but not in Nov. 1998 (Fig. 4).

Flexion and postflexion larvae occurred mainly in Nov., Mar.-Apr., and June-Aug. These timings indicate that the fish has protracted spawning behavior with a major spawning season from spring to early summer, a minor season in autumn, and no spawning in winter.

Comparison of mean age and length among cohorts

The standard-length frequency distributions of *S. insularis* at recruitment to the estuary are shown by stage and cohort in figure 5. Post hoc tests indicated that the size of the autumn cohort was significantly larger than the spring and summer cohorts, irrespective of the stage (postflexion, larval, juvenile, and young fish, all $p < 0.001$). Lengths did not significantly differ between spring and summer cohorts ($p = 0.98, 0.20$) except at the juvenile stage where the spring cohort was longer than the summer cohort ($p < 0.001$).

Similarly, the mean ages at recruitment were also significantly older in the autumn than in the spring and summer cohorts ($p < 0.001-0.002$), but did not significantly differ between the spring and summer cohorts ($p = 0.47-0.96$), irrespective of the

developmental stage (Table 1). The mean (\pm S.D.) ages of juveniles at recruitment to the estuary were 36.6 ± 4.6 d in spring and 35.1 ± 7.6 d in summer, but increased to 54.0 ± 9.4 d in autumn. This indicated that the age at recruitment to the estuary was delayed by approximately 18 d for the autumn cohort.

Relationship between otolith radius and standard length

Relationships between maximum otolith radius (R, μm) and standard length (L, mm) of *S. insularis* were fitted by the allometric growth equations by season as follows:

Autumn $R = 2.4365L^{1.7296}$ ($R^2 = 0.89$),
 Spring $R = 0.8274L^{2.0648}$ ($R^2 = 0.98$), and
 Summer $R = 0.5511L^{2.1895}$ ($R^2 = 0.96$).

ANCOVA indicated that there were no significant differences in either slope or adjusted mean among the equations ($p = 0.7528$). Accordingly, the relationship between otolith radius and standard length of *S. insularis* was calculated from pooled data as follows (Fig. 6):

$R = 0.8416L^{2.0567}$ ($R^2 = 0.97$).

Comparison of somatic growth among cohorts

Growth curves of *S. insularis* were fitted by exponential equations as follows (Fig. 7):

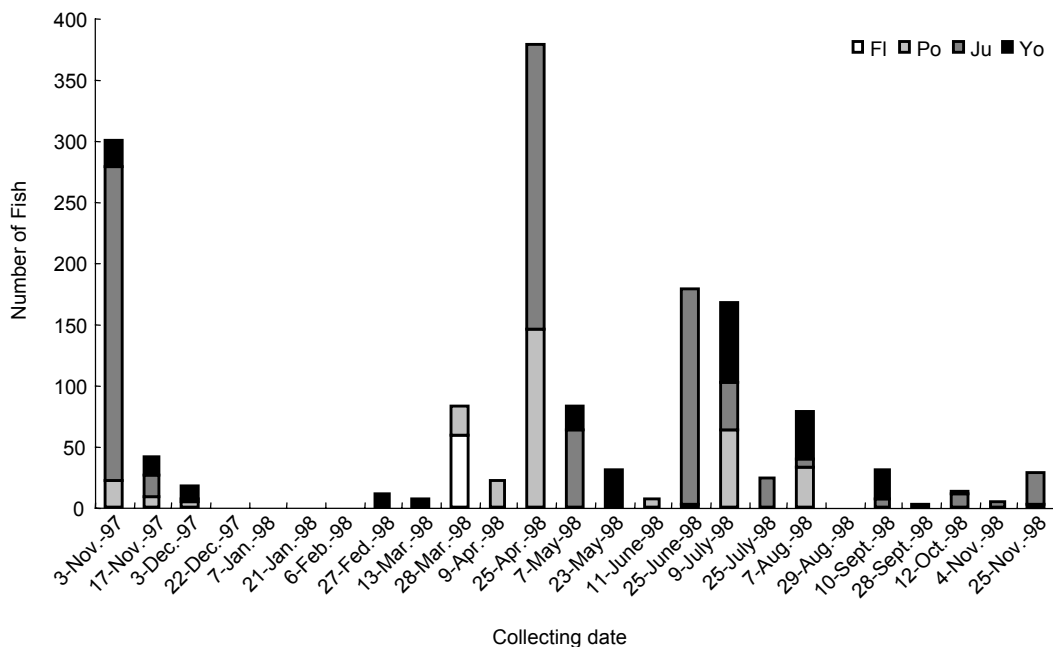


Fig. 4. Monthly changes, by stage, of abundance in numbers of *Stolephorus insularis*.

Spring $R = 7.8094e^{0.0247D}$ ($R^2 = 0.87$),
 Summer $R = 10.305e^{0.020D}$ ($R^2 = 0.90$), and
 Autumn $R = 12.237e^{0.0136D}$ ($R^2 = 0.66$);
 where R and D are otolith radius (μm) and
 age (d), respectively.

ANCOVA indicated that the slope (growth
 rate) of the equation significantly differed among
 cohorts ($p < 0.0001$). Post hoc tests further

indicated that growth rates in decreasing order
 were spring > summer > autumn (all $p < 0.001$).

**Differences in otolith daily growth patterns
 among cohorts**

Patterns of daily growth increments in otoliths
 were compared among 3 selected young S.

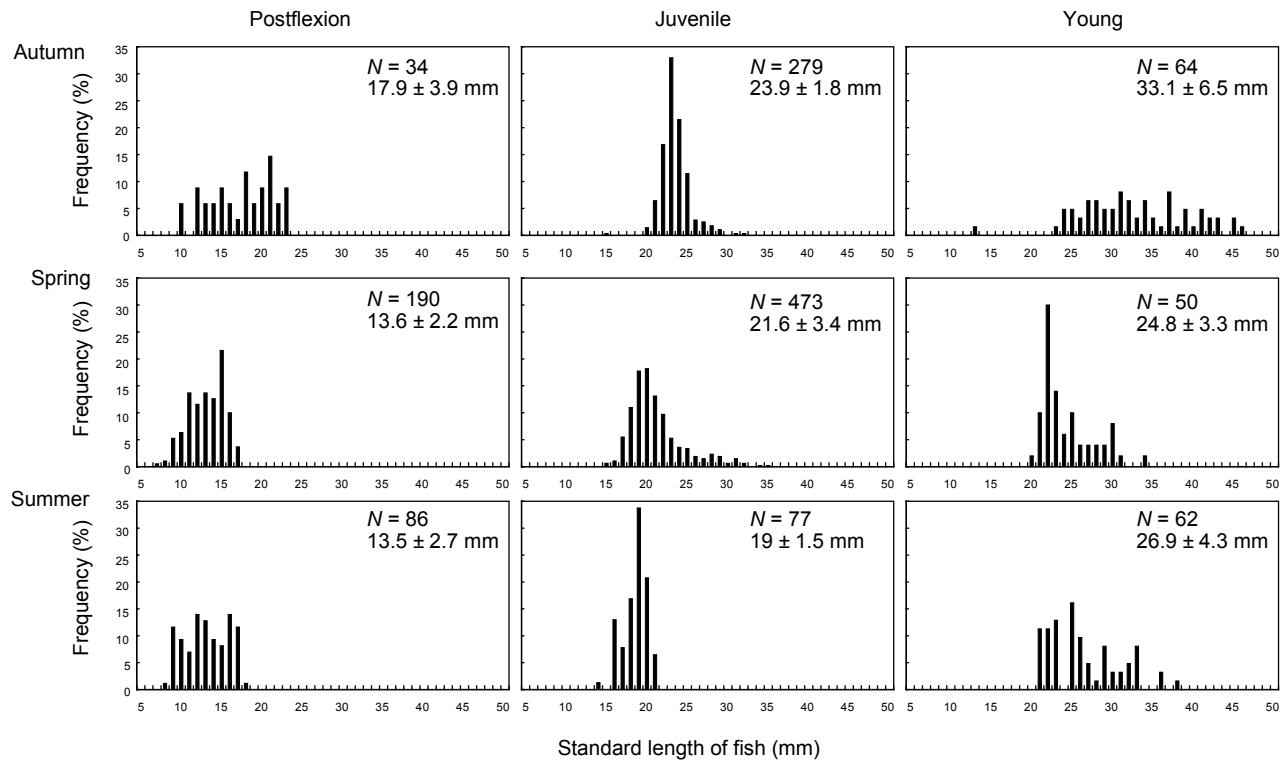


Fig. 5. Standard-length frequency distributions of larval *Stolephorus insularis* by stage and cohort. Spring cohort, Mar.-May; summer cohort, June-Aug.; autumn cohort, Sept.- Nov.

Table 1. Comparison, among cohorts, of mean age by stage for *Stolephorus insularis*. Fl: flexion larva, Po: postflexion larva, Ju: juvenile, Yo: young

Cohorts	Mean (\pm S.D.) (sample size) and range of age (d) by stages			
	Fl	Po	Ju	Yo
Autumn (Au)		39.9 \pm 6.5 (9) 31 - 50	54.0 \pm 9.4 (10) 38 - 64	70.3 \pm 9.0 (8) 53 - 84
Spring (Sp)	7.9 \pm 2.2 (9) 7 - 11	21.2 \pm 5.0 (9) 14 - 28	36.6 \pm 4.6 (13) 30 - 43	51.1 \pm 10.3 (9) 43 - 70
Summer (Su)		19.9 \pm 5.2 (12) 12 - 30	35.1 \pm 7.6 (7) 26 - 46	53.0 \pm 6.3 (9) 45 - 67
Comparison		Au > Sp = Su	Au > Sp = Su	Au > Sp = Su

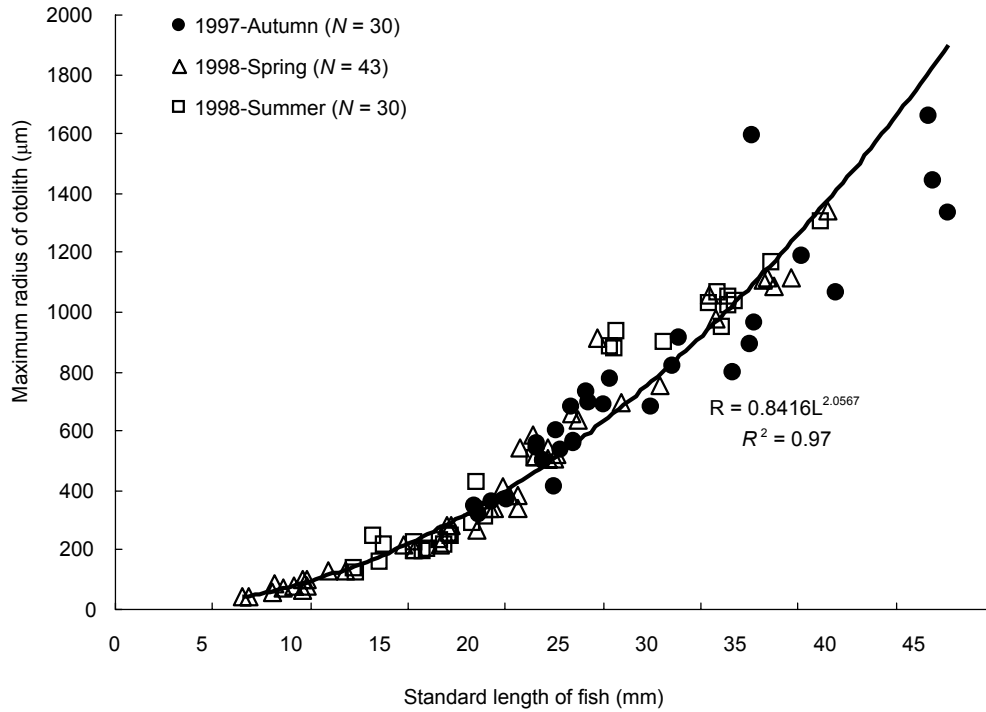


Fig. 6. Relationship between maximum otolith radius and standard length of *Stolephorus insularis*.

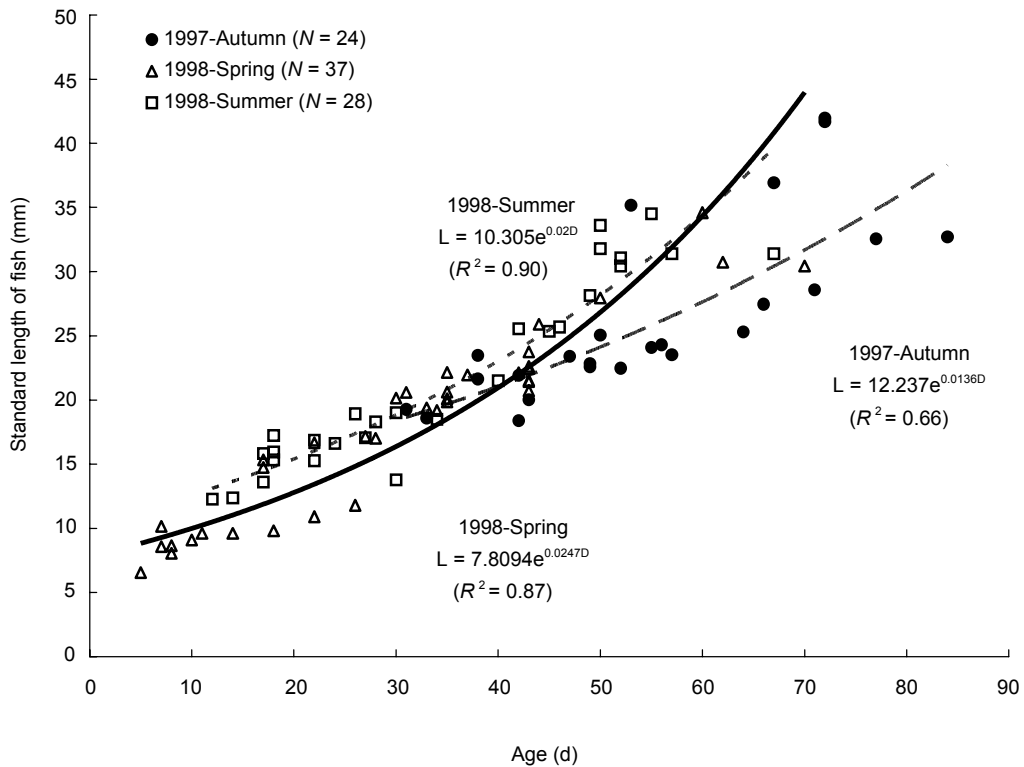


Fig. 7. Somatic growth equations, by cohort, of *Stolephorus insularis*.

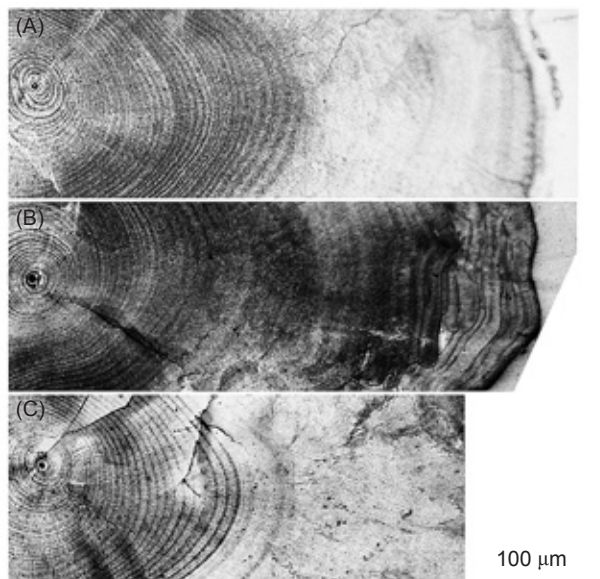


Fig. 8. Patterns of daily growth increments in otoliths of 3 young *Stolephorus insularis*. (A) Autumn cohort, 28.93 mm standard length (SL) collected on 3 Nov. 1997; (B) spring cohort, 34.59 mm SL, 23 May 1998; (C) summer cohort, 30.44 mm SL, 7 Aug. 1998.

insularis which represented each of the cohorts (Fig. 8). Results indicated that the increment width (otolith daily growth rate) and the timing at the transition of the otolith growth rate differed among cohorts. The increment width was narrower in the core than outer layer of the otolith in each of the 3 cohorts, while the timing of the growth transition from slower to faster was earlier in the summer (at approximately 28 d old) than in the spring (35 d old) and autumn cohorts (43 d old).

Repeated-measures ANOVA indicated that the otolith mean daily growth rates significantly differed among cohorts ($p < 0.001$). Non-parametric ANOVA further indicated that the timing at inflexion from positive to negative growth acceleration occurred fastest for the summer cohort (on average at approximately 35 d old), followed by the spring (44 d old) and autumn (50 d old) cohorts (Fig. 9).

DISCUSSION

The gold estuarine anchovy *S. insularis* is mainly recruited in the Tatu River estuary at the juvenile stage during the period from spring

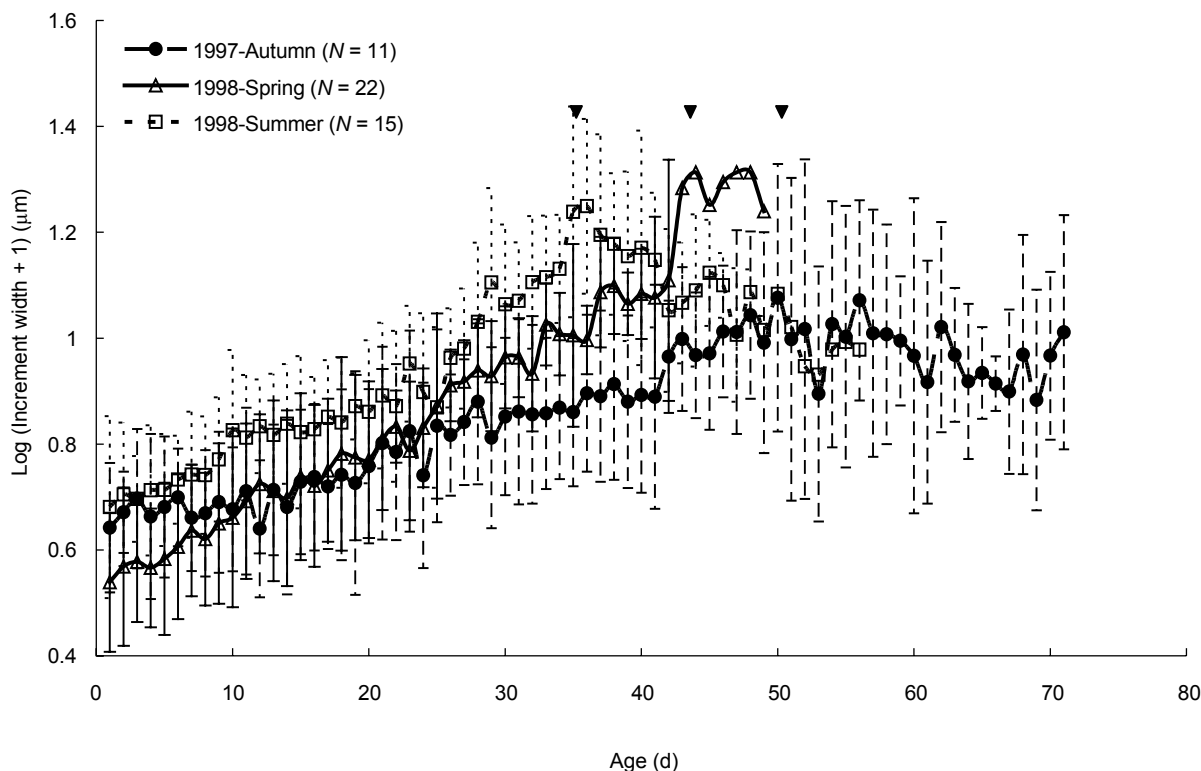


Fig. 9. Comparison of temporal changes, among cohorts, in mean (\pm S.D.) otolith increment widths of *Stolephorus insularis*. Arrows indicate the timing at the transition of the growth rate.

to early summer (Apr.-July) and autumn (Nov.) (Figs. 3, 4), at a mean age of 1 mo for the spring and summer cohorts and 1.5 mo for the autumn cohort (Table 1). Anchovy ages at recruitment and seasonal occurrences and abundances indicated that spawning occurred mainly from spring to early summer, with a minor spawning peak in autumn and no spawning in winter. On the other hand, the back-calculated hatching date distribution demonstrated that larger juveniles which appeared in early spring had spawned the previous autumn. These overwintering juveniles are the first ones discovered in Taiwan. The abundance of the juvenile stage relative to other stages (flexion and postflexion larvae and young) indicated that these fish were spawned offshore and not in the estuary. After hatching, the larvae passively disperse and are completely recruited to the estuary at the juvenile stage, and then leave the estuary at the young stage. The estuary obviously plays an important role as a nursery for juvenile anchovy, similar to other species (Raynie and Shaw 1994, MacGregor and Houde 1996).

Although the Tropic of Cancer passes through central Taiwan, the seasonal temperature variation in the Tatu River estuary in west-central Taiwan is more temperate than tropical (Fig. 2). The spawning behavior of *S. insularis* in the estuary followed Cushing's match-mismatch theory (Cushing 1975), and coincides with the spring and autumn phytoplankton blooms in temperate areas (Lalli and Parsons 1993). Although primary productivity data in the study area are unavailable to validate the relationship between seasonal productivity and spawning behavior of the anchovy, seasonal changes in phytoplankton and zooplankton in the nearby Tanshui River estuary of northern Taiwan seem to reflect this phenomenon (Chern and Tzeng 1993). Water temperatures in shallow waters of the continental shelf of the Taiwan Strait dramatically change with the seasonal monsoon. The Tanshui and Tatu Rivers respectively on the north and west-central coasts of Taiwan are both influenced by the prevailing northeast monsoon in winter and southwest winds in summer, which produce seasonal changes in both temperature and coastal currents (Chu 1963, Tzeng et al. 2002). Such physical oceanographic processes may influence biological processes such as the seasonal spawning activity of *S. insularis*, plankton production that provides food for fish larvae, and the transport and retention of larvae in estuaries as well. Navaluna and Pauly (1986) found a relationship between monsoon

winds and the seasonal recruitment of stolephorid anchovies in the Philippines. Dalzell (1987) also found that the spawning of stolephorid anchovies followed seasonal changes in the hydrological environment driven by the seasonal monsoons, which subsequently influenced spring planktonic production.

Growth curves of both length-at-age and otolith daily growth increment width indicated that *S. insularis* grew faster in spring/summer than in autumn, and the mean fish ages indicated that the duration of vulnerability to predation mortality might be longer in autumn than in spring/summer (Table 1, Figs. 7-9). Differences in growth strategies among cohorts during the early life stages were evident. The bigger-is-better hypothesis states that juvenile fish that grow slowly are exposed to predation over a longer period and therefore have lower survival rates than faster-growing fish (Houde 1987, Miller et al. 1988, Rice et al. 1993, Cushing and Horwood 1994, Ottersen and Loeng 2000). Based on the otolith increment width, the summer cohort grew faster and reached the growth rate inflexion point earlier than did the spring and autumn cohorts. In addition, the growth rate after the inflexion point was lower in autumn than in the spring and summer cohorts. Also, somatic growth was slower and the durations of larval and juvenile stages were longer in autumn than in the spring and summer cohorts; thus, autumn-hatched larvae are expected to have lower survival rates. Small annual differences in growth or mortality rates in early stages can lead to large annual fluctuations in recruitment (Leggett et al. 1984, Houde 1987, Frank 1991, Fey 2001).

A peak recruitment occurred in Nov. 1997 but the recruitment failed in autumn 1998 (Fig. 4). This may have been due to interactions of physical and biological processes (Boehlert and Mundy 1988). The spring and summer cohorts of the fish experienced higher temperatures than the autumn cohorts (Fig. 2) and subsequently had higher growth rates (Figs. 7, 9), because higher temperatures can cause high production of prey items leading to higher growth and survival rates through the vulnerable larval and juvenile stages (Ottersen and Loeng 2000). Anderson (1988) also proposed that the survival of a cohort was directly related to the growth rate during the pre-recruitment period. The seasonal growth period of phytoplankton is shorter and the magnitude of productivity is lower in autumn than in spring and early summer (Chern and Tzeng 1993). This suggests that the autumn cohort is more

susceptible to recruitment failure, due to its mismatch with the production cycle, than is the spring or summer cohort. Alternatively, Nov.-Dec. salinities were lower in 1998 than in 1997 which may indicate that environmental conditions for the transport or retention of larvae and juveniles in the estuary were unfavorable in autumn 1998. The drastic decrease in salinity observed from Apr. to June was probably due to high river discharge as a result of typhoon-associated rains. The higher freshwater discharge in autumn 1998 might have prevented the fish from entering the estuary, either due to strong currents, or the inability of the fish to tolerate fresh water. Factors causing the recruitment failure observed in Nov. 1998 (Fig. 4) are presently unclear. That failure was probably due to simple biological processes during migration from the spawning ground to the nursery ground (member-vagrant hypothesis, Sinclair 1988), or due to a negative effect of unstable oceanographic conditions on larval growth and survival during the pre-recruitment period (ocean stability hypothesis, Lasker 1975 1978, Blaber and Blaber 1980, Anderson 1988, Ottersen and Loeng 2000). Dalzell (1987) also found 2 stolephorid anchovy species that have extreme variability in reproductive success and recruitment, with almost no spawning in some years. These uncertainties underline the need for more research on a long-term basis.

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