

The Reproductive Biology of the Gizzard Shad, *Nematalosa come* (Richardson, 1846), in the Kaohsiung River and Its Harbor Area, Southern Taiwan

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Meng-Hsien Chen and Ju-Shiou Hsiao (1996) The reproductive biology of the gizzard shad, *Nematalosa come* (Richardson, 1846), in the Kaohsiung River and its harbor area, southern Taiwan. *Zoological Studies* 35(4): 261-271. The gonadal development of the gizzard shad, *Nematalosa come*, is described. Gonadosomatic indices and frequency of advanced maturity stages demonstrated that spawning activity reached a peak from February to April. Histological examination of the gonads showed that spawning is asynchronous. The sex ratio was M:F = 1.2:1. Minimum fork length and body weight of males and females at sexual maturity were 12 cm and 13 cm, and 39 g and 45 g, respectively. Average batch fecundity was $89\,289 \pm 23\,670$. The relationships between the fecundity (F) and body weight (BW), fork length (FL) and gonad weight (GW) were $\log F = 3.516 + 0.673 \log BW$ ($r = 0.540$), $\log F = 3.147 + 1.413 \log FL$ ($r = 0.433$), and $\log F = 4.184 + 0.822 \log GW$ ($r = 0.755$), respectively. There was no evidence that spawning is related to flooding but *N. come* may undertake an upstream spawning migration. Storm sewage discharges in the Kaohsiung River system may have an important influence on recruitment and population abundance of the shad.

Key words: Maturity, Asynchrony, Fecundity, Spawning migration, Estuarine fishes.

Five of the 12 Indo-Pacific species of gizzard shads (Dorosomatinae) (Nelson and Rothman 1973) occur in Taiwan (Shen 1994). Since the 1980s, gizzard shads, mainly *Nematalosa come*, have replaced the moonfish, *Mene maculata* (Bloch and Schneider, 1801), as bait in an important long-line tuna fishery in southern Taiwan. As a consequence, efforts to catch shad have dramatically increased (You 1988).

The reproduction of other species of gizzard shads has been described elsewhere, including (1) measurements of fecundity, oocyte diameter, and gonadosomatic indices of *Dorosoma cepedianum* (Kilambi and Baglin 1969a, Jester and Jensen 1972) and *Dorosoma petenense* (Kilambi and Baglin 1969b, Johnson 1971) in the USA. Similar studies have been made of *Anodontostoma chacunda* (Jacob 1948, Rao 1965) in India; of *Nematalosa vlaminghi* (Chubb and Potter 1984) and *N. erebi* (Puckridge and Walker 1990) in Australia; of

Konosirus punctatus (Takita 1978a) in Japan; and of *N. japonica* (You 1988) in Taiwan. (2) Descriptions have been made of macro- and microscopic development of the ovaries of *Dorosoma cepedianum* (Bodola 1966, Shelton 1978); of *Konosirus punctatus* (Takita 1978b); and of *Nematalosa vlaminghi* (Chubb and Potter 1984). (3) Furthermore observations have been reported of spawning behavior and spawning sites of *Dorosoma cepedianum* (Jester and Jensen 1972). However data bearing on the reproduction of *N. come* are lacking.

The Kaohsiung River (Jenai River) is 12 km long. It originates at the Chawkon Reservoir and flows through the center of Kaohsiung City, before entering Kaohsiung Harbor. In 1987, a sewage interceptor (Chiping Bridge Barrier) was built in the middle section of the river which, with 11 interceptors on the lower reaches, has greatly improved the water quality of the estuary. The estuary now supports several fish species, including *Liza*

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macrolepis, *Megalops cyprinoides*, *Chanos chanos*, *Leiognathus equula*, *L. nuchalis*, *Gerres filamentosus*, and the gizzard shad, *N. come*, which is predominant, comprising up to 60% of gill net catches (Chen 1995).

The purpose of this study was to characterize various features of the reproduction of *N. come* in the Kaohsiung River and its harbor area, including its spawning season, minimum size at sexual maturity, spawning pattern, sex ratio, and fecundity. The results will contribute to the knowledge of the ecology of *N. come*, and will provide valuable information for the estimation of its potential recruitment and population abundance. Attempts were also made to investigate the factors causing varia-

tions in population abundance by comparing these populations with environmental factors and with the situation of other gizzard shads elsewhere in the world.

MATERIALS AND METHODS

From November 1993 to December 1994, monthly fish samples were collected by use of gill nets (30 m long, 1.8 m deep, mesh sizes of 2.5 and 4 cm) at 3 sites in the lower reaches of the Kaohsiung River (sites A, B, and C), one at the river mouth (site D) and one along a dock in Kaohsiung Harbor (site E) (Fig. 1).

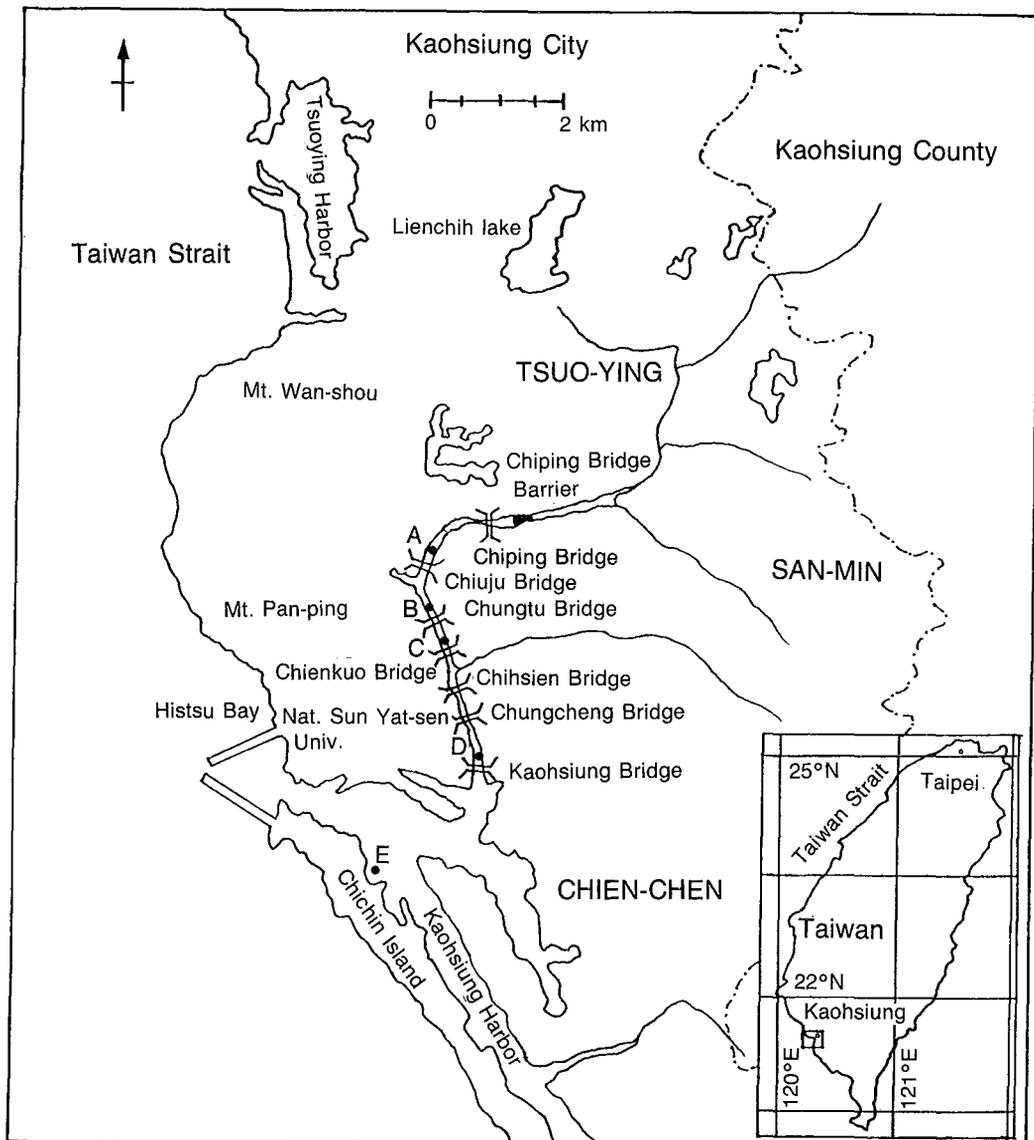


Fig. 1. Sampling sites at the lower reaches of the Kaohsiung River and its harbor area, southern Taiwan.

Mean monthly water temperatures varied between 17 to 20 °C in winter and 29 to 30 °C in summer. Salinities ranged between 1.8‰ to 2.4‰ at sites A and B and 2.8‰ to 3.4‰ at the other sites. Ammonia-nitrogen ranged between 1.3 to 8.0 mg l⁻¹ in the wet season (July to September) and between 0.7 to 6.5 mg l⁻¹ in the rest of the year. DO, BOD₅, suspended solids, Secchi depth, and pH ranged from 0 to 15 mg l⁻¹, 0.1 to 22.7 mg l⁻¹, 3 to 159 mg l⁻¹, 12 to > 30 cm, and 7.3 to 8.5, respectively. The water quality in the study area is usually classed as "poor" in the rainy season (June to August) by the Environmental Protection Bureau, Kaohsiung City Council, due to sewage storm discharges.

The total length (TL), fork length (FL), and wet body weight (BW) of the gizzard shad were recorded to the nearest 1 mm and 0.1 g, respectively. When the sample size from any site was large, a sub-sample of 100 to 200 fish was randomly selected. Sex was determined by gonad inspection. The gonads were removed and weighed, and the maturity stages of gamete maturation were determined by visual observation according to the criteria (Table 1) adopted from Johnson

(1971), Holden and Raitt (1974), and Chubb and Potter (1984). Gonadosomatic indices (GSI) were calculated as (gonad weight/body weight) x 100 (Holden and Raitt 1974, West 1990).

Each month 10 to 15 freshly caught fish were randomly selected and gonadal tissues were prepared for histological examination (Baker et al. 1966, Wallace and Selman 1981, Devlaming et al. 1982).

Ovaries at advanced maturational stages (stage III and higher) were prepared following the method of Lowerre-Barbieri and Barbieri (1993) to estimate fecundity and to measure egg diameters. Ovarian development in different portions of the ovary was evaluated, and it was found that there were no significant differences (Two-way ANOVA, $p > 0.05$). Thereafter, a piece of the left-middle portion of the ovary was sampled for fecundity count.

RESULTS

Among a total of 1 056 gizzard shad sampled, 469 males and 373 females were dissected for reproductive analyses. Most fish were caught at

Table 1. Macroscopic description of the maturity stages of the gonads of *Nematalosa come*. Stages adopted from Johnson (1971), Holden and Raitt (1974), and Chubb and Potter (1984)

Maturity stage	Ovary	Testis
I.	Immature Two small, pale pinkish, translucent, thread-like gonads lying close under the vertebral column. Ova are not visible to naked eye, but small transparent oocytes can be seen microscopically.	Spermatogonial proliferation Like stage I female gonads, but colorless or whitish. Length less than 1/10 of the body cavity.
II.	Maturing virgin & recovering spent Pinkish-gray, translucent, occupying about 1/6 of the body cavity. Size increased in diameter. Single eggs not visible to naked eye, but the recovering spent ovary contains some unshed eggs.	Early spermatogenesis Pale pinkish, elongated shape, occupying about 1/8 of the body cavity.
III.	Ripening Opaque and pinkish-yellow with blood capillaries. Eggs visible to naked eye as whitish granules. Occupying more than 1/5 body cavity.	Late spermatogenesis Opaque and whitish to creamy with oval cross section shape, and occupying more than 1/4 of body cavity.
IV	Ripe Opaque and yellow. Ova discernible to naked eye. The ovary occupies 1/2-2/3 of body cavity, and is roughly triangular in cross section.	Functional maturation Opaque and whitish; as female in III, occupies 1/2-2/3 of body cavity. Roughly triangular in cross section, and milt appears on pressure to the abdomen.
V	Spent Swollen, filling, pinkish-yellow, occupying 1/2-2/3 of body cavity. Eggs opaque or translucent, clearly visible with a very thin wall and easily extruded on pressure.	

site D, whereas in the reach above site D shad were caught from February to April and November (Table 2).

The linear regression between the total length (TL) and fork length (FL) was $TL = 0.4144 + 1.1491 FL$ ($r = 0.9762$).

The relationships between lengths and weights of males and females did not differ significantly (ANCOVA, $p \leq 0.05$). The equations were $\log BW = -1.7542 + 3.0510 \log FL$ ($r = 0.9611$) for males, and $\log BW = -1.6844 + 2.9906 \log FL$ ($r = 0.9635$) for females. The combined relationship was $\log BW = -1.8285 + 3.1154 \log FL$ ($r = 0.9567$).

The sex ratios for gizzard shad (M:F = 1.2:1) were significantly different from 1:1 (χ^2 , $p \leq 0.05$).

The characteristics of egg development of the shad were similar to those described by Chubb and Potter (1984). Details of the microscopic characteristics in each maturity stage are given in Table 3. Several egg developmental stages were

noted in the ovarian sections. The ovaries in maturity stages IV and V presented empty follicles; those in maturity stages II and V contained atretic oocytes. Thus the macroscopic determination of maturity stages matched fairly well with the histological results so that macroscopic examination was sufficient to indicate the maturational level of the shad.

The mean monthly GSIs for both males and females rose sharply from February to reach their highest values in March and, in general, subsequently declined rapidly after April (Fig. 5). The maximum monthly mean GSI in this period ranged from 1.6 to 16.2 in males and from 1.8 to 26.0 in females. For the rest of the year, values were less than 1.0 for both male and female fish.

To determine the length and weight at maturation the gonadosomatic indices were plotted against fork length and body weight as shown in Fig. 6. The minimum sizes at 1st maturity were defined as the smallest sizes exhibiting a rise of GSI.

Table 2. List of *Nematalosa come* caught in the Kaohsiung River and its adjacent harbor area from November 1993 to December 1994

Sampling site	A		B		C		D		E		Total	
	Month	No	FL	No	FL	No	FL	No	FL	No	FL	
1993 Nov	—	—	—	—	—	—	17	9.8 ± 1.1 (8.5–13.1)	—	—	17	9.9 ± 1.1 (8.5–13.1)
Dec	—	—	—	—	—	—	51	14.1 ± 1.1 (12.5–17.5)	—	—	51	14.1 ± 1.1 (12.5–17.5)
1994 Jan	—	—	—	—	7	14.2 ± 0.7 (13.5–15.4)	66	13.7 ± 1.5 (8.9–17.5)	—	—	73	14.0 ± 1.0 (8.9–17.5)
Feb	—	—	66	13.8 ± 1.4 (9.9–17.5)	8	13.8 ± 0.8 (12.5–15.2)	58	13.3 ± 1.0 (11.5–16.7)	—	—	132	13.6 ± 1.2 (9.9–16.7)
Mar	34	14.9 ± 0.8 (13.5–16.8)	67	14.0 ± 0.9 (12.0–16.7)	16	13.3 ± 0.7 (12.0–14.2)	1	14.0	—	—	118	14.2 ± 1.0 (12.0–16.8)
Apr	0	0	5	16.5 ± 0.3 (16.0–16.8)	0	0	7	12.9 ± 3.0 (10.5–18.8)	—	—	12	14.4 ± 2.9 (10.5–18.8)
May	0	0	0	0	0	0	1	10.8	—	—	1	10.8
Jun	0	0	0	0	0	0	0	0	0	0	0	0
Jul	0	0	0	0	0	0	0	0	60	13.7 ± 1.0 (12.4–19.3)	60	13.7 ± 1.0 (12.4–19.3)
Aug	0	0	0	0	0	0	0	0	94	14.1 ± 0.7 (12.5–16.4)	94	14.1 ± 0.7 (12.5–16.4)
Sep	0	0	0	0	0	0	256	14.3 ± 0.8 (12.8–17.5)	0	0	256	14.3 ± 0.8 (12.8–17.5)
Oct	0	0	0	0	0	0	0	0	6	13.9 ± 0.6 (13.4–14.8)	6	13.9 ± 0.6 (13.4–14.8)
Nov	28	14.5 ± 0.8 (12.9–16.2)	3	14.0 ± 0.6 (13.5–14.6)	0	0	25	14.4 ± 0.8 (12.9–16.5)	6	14.2 ± 0.4 (13.5–14.7)	62	14.4 ± 0.8 (12.9–16.5)
Dec	0	0	0	0	0	0	152	14.4 ± 0.1 (10.2–16.4)	22	14.1 ± 1.4 (8.7–15.9)	174	14.3 ± 0.8 (8.7–16.4)

FL = Fork length (cm); mean ± S.D. and range in parentheses; "—" means no samples collected.

Table 3. Macroscopic description of the maturity stages of the gonads of *Nematalosa come*. The histological characteristics of egg and sperm development are based on the criteria developed by Chubb and Potter (1984), Devlaming (1972), and Wallance and Selman (1981)

Maturity stage	Ovary	Testis
I.	Immature (Fig. 2 a) Germ cells, oogonia, and primary oocytes abundant. Range of cell diameters is 25-80 μm , with GSI ranging 0.11-0.94.	Spermatogonial proliferation (Fig. 4 a) Mostly spermatogonia, a few spermatocytes, and spermatids, present. GSI ranges 0.08-0.81.
II.	Maturing virgin & recovering spent (Fig. 2 b) Oogonia, early perinuclear, and reserve-fund oocytes abundant. Some oocytes with vacuolated cytoplasm (stage 5) present up to 5%-10%. Reabsorption of yolked oocytes can be seen. Dominant oocyte diameters between 100 and 250 μm . GSI ranges 0.24-3.66.	Early spermatogenesis (Fig. 4 b) With a few spermatogonia, and equal numbers of spermatocytes and spermatids (up to 20%). GSI ranges 0.19-5.13.
III.	Ripening (Fig. 2 c) Stage 5 oocytes abundant. Oocytes begin to be packed with yolk granules in the cytoplasm. Many oocytes larger than 200 μm in diameter. GSI ranges 1.39-7.62.	Late spermatogenesis (Fig. 4 b) Spermatozoa (30%-40%) more numerous than spermatids with about 20%. GSI ranges 1.34-7.54.
IV.	Ripe (Fig. 3 a, b) Yolk granule oocytes predominate with oocyte diameters ranging between 351 and 520 μm . GSI ranges 4.51-14.90.	Functional maturation (Fig. 4 c) Testes containing more than 60% basophilic spermatozoa. GSI ranges 3.85-6.89.
V.	Spent (Fig. 3 c) Post-ovulatory follicles, advanced yolked oocytes, and atretic oocytes present simultaneously. This is evidence for asynchrony of maturation. GSI ranges 0.37-7.01.	

These were 12.0 cm and 13.0 cm FL, and 39.0 g and 45.0 g BW for male and female gizzard shad, respectively. Estimated total lengths were 14.2 cm and 15.6 cm for males and females, respectively.

At least 6 groups of different egg diameters were found in the shad's ovaries with respective modes of 0.075, 0.125, 0.250, 0.375, 0.500, and 0.625 mm (Fig. 7). As maturity advanced the numbers of larger eggs increased. At stage IV, the ovaries contained more than 80% of ova with diameters exceeding 0.500 mm.

The mean number of large yolked oocytes (egg diam. \geq 0.500 mm) in 18 females was $89\ 289 \pm 23\ 670$, with values ranging from 51 407 to 142 209 in the size range of 15.5 cm to 21.0 cm (FL). The relationships between the fecundity (F) and body weight (BW), fork length (FL) and gonad weight (GW) were $\log F = 3.516 + 0.673 \log BW$ ($r = 0.540$), $\log F = 3.147 + 1.413 \log FL$ ($r = 0.433$), and $\log F = 4.184 + 0.822 \log GW$ ($r = 0.755$), respectively.

Climatological data showed that the peak precipitation and maximum monthly days of rain in the Kaohsiung area occurred in May-July, and in June and August, respectively (Fig. 8). Moreover, measurements of chlorophyll *a* represented the relative abundance of phytoplankton. Chlorophyll

a concentrations measured in the inner and outer harbor revealed that the levels in the former site were greater than those in the latter site and peaked in May (Fig. 9).

DISCUSSION

No significant differences between male and female length-weight relationships were found in *N. come*. Similar results were also reported for other Dorosomatinae, such as *Dorosoma cepedianum* (Bodola 1966, Jester and Jensen 1972).

The sex ratio for *N. come* of 1.2:1 in favor of males conforms with ratios recorded for other species, e.g., *D. cepedianum* in New Mexico, USA (Jester and Jensen 1972) and *N. japonica* in Tung-kang, Taiwan (You 1988). Jester and Jensen (1972) suggested that hyper-activity of spawning males may bias their apparent capture numbers.

The spawning season of various gizzard shads varies with latitude. *Nematalosa come* in this study spawned in February-April at water temperatures of 20 to 24 °C, 1 month earlier than *N. japonica* in Tung-kang, further south in Taiwan (You 1988). The shads, *N. vlaminghi* and *N. erebi*, in Australia showed a spawning season from December to

January (Chubb and Potter 1984, Puckridge and Walker 1990). However, different spawning periods were reported for American shads, such as that of *D. cepedianum* in Elephant Butte Lake, New

Mexico, which was in May (Jester and Jensen 1972), whereas that of *D. pentenense* in Salt River Reservoirs, Arizona, from April to mid-June (Johnson 1971). Other reports on spawning season include

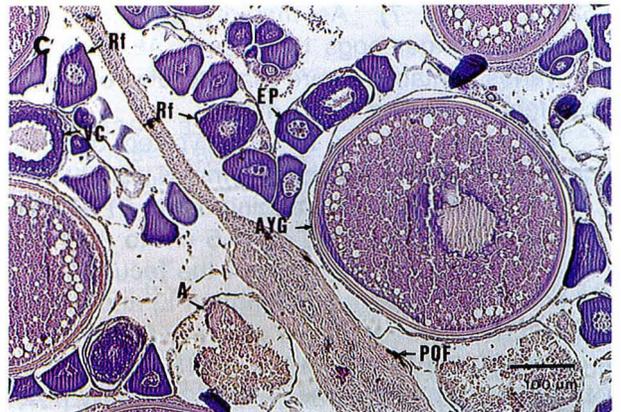
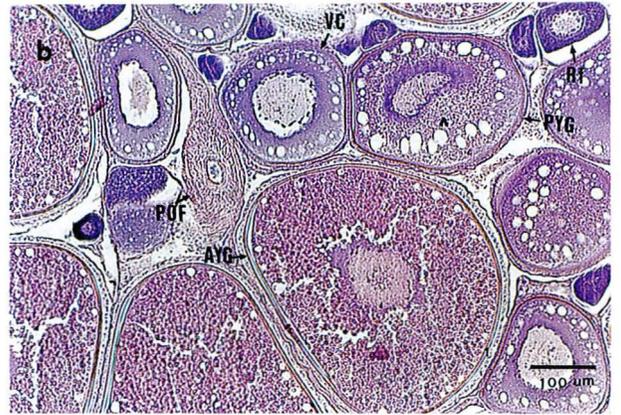
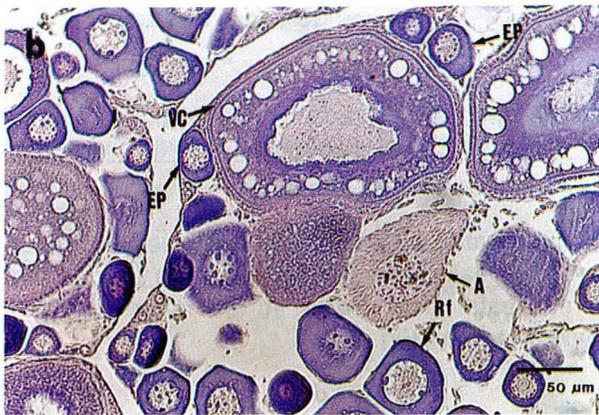
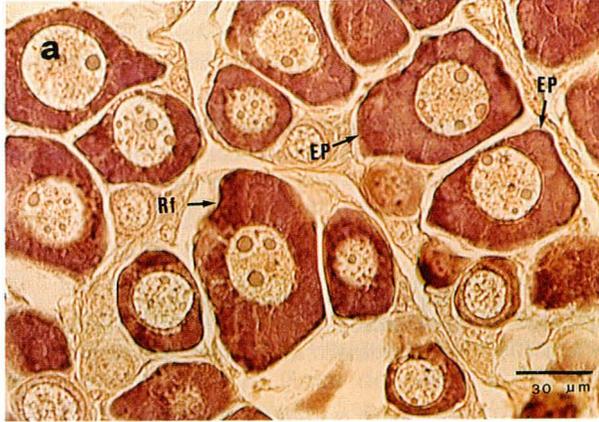


Fig. 2. Oocytes of *Nematalosa come* in various maturity stages. (a) Ovary in maturity stage I containing various primary oocytes, including early perinuclear (EP) oocytes, and reserve fund (Rf) oocytes (x 400). (b) Ovary in maturity stage II containing a variety of type of oocytes, such as oocytes with vacuolated cytoplasm (VC), atretic (A) oocytes, and Rf oocytes (x 200). (c) Ovary in maturity stage III dominated by primary yolk granule (PYG) oocytes and VC oocytes (x 100).

Fig. 3. Oocytes of *Nematalosa come* in various maturity stages. (a) A secondary yolk granule (SYG) oocyte fully packed with yolk granules (x 200). (b) Ovary in maturity stage IV containing a variety of types of oocytes, i.e., VC, PYG, SYG and advanced yolk granule (AYG) oocytes (x 100). (c) Spent ovary containing both post-ovulatory follicles (Pof), and AYG and A oocytes (x 100).

those of Rao (1965) who found that *A. chacunda* in India spawned from November to February, and Takita (1978b) who reported that *K. punctatus* in Ariake Sound, west Kyushu, Japan, spawned from April to May.

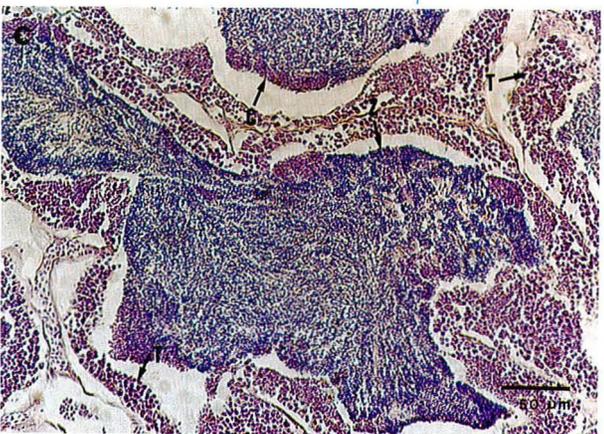
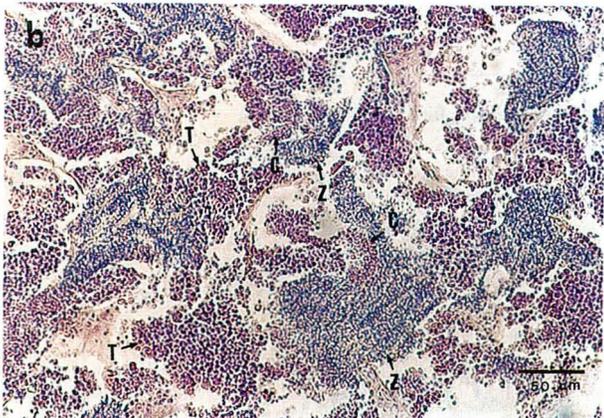
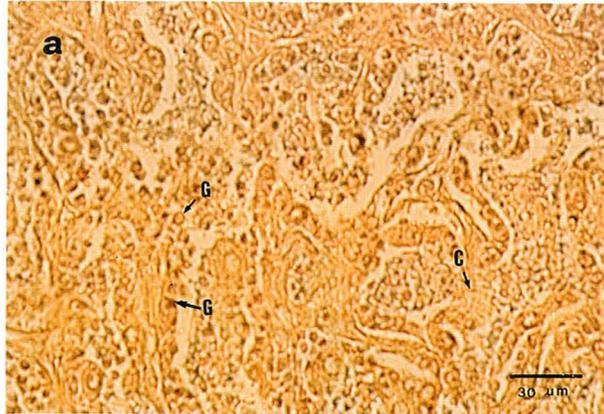


Fig. 4. Testis of *Nematalosa come* in various maturity stages. (a) Testis in maturity stage I containing mostly spermatogonia (G), and spermatocytes (C) (x 400). (b) Testis in maturity stage II and III containing spermatids (T) and spermatozoa (Z) (x 200). (c) Testis in maturity stage IV full of spermatozoa (x 200).

Spawning in some freshwater and estuarine teleosts has been shown to be related to flooding, photoperiod, water temperature and food availability (Potts and Wootton 1984). We found that the spawning of *N. come* in the Kaohsiung River system was independent of flooding (see Figs. 5, 8) as did Puckridge and Walker (1990) for *N. erebi*. Shads appear to spawn from early spring to summer when plankton peaks, providing food for their young (Fig. 9).

Multiple modes of egg diameters reveal that *N. come* is a partial spawner, similar to other Dorosomatinae (Takita 1978b, Chubb and Potter 1984, Puckridge and Walker 1990). Several post-ovulatory follicles were found in fish at advanced maturity stages suggesting that the fish is asynchronous, spawning more than once each season. However, no evidence was found that the smallest oocytes (diam. < 0.125 mm) in mature females would reach maturity during the current spawning season.

The minimum body size at maturity of female *N. come* was similar to that reported by Chubb and Potter (1984) for female *N. vlaminghi* which matured at the age of 2 yr with a total length of

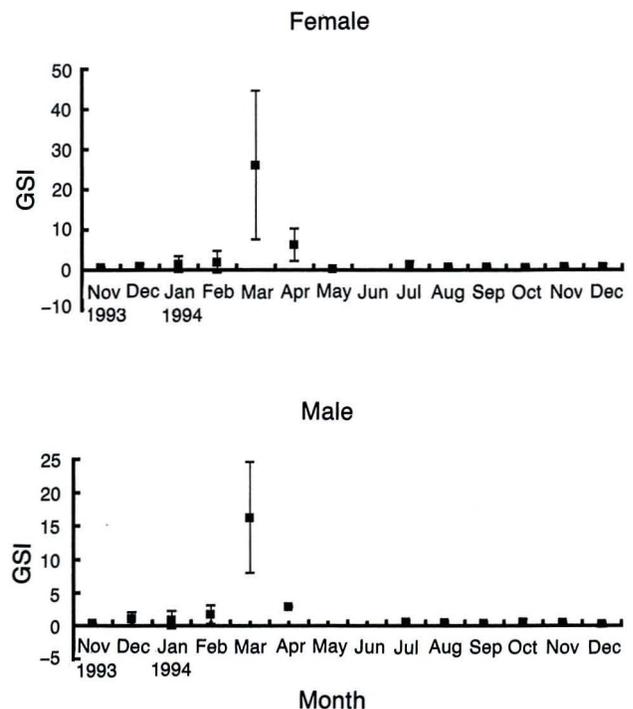


Fig. 5. Mean monthly gonadosomatic indices (GSI, Mean \pm S.D.) for female and male *Nematalosa come* in the lower reaches of the Kaohsiung River.

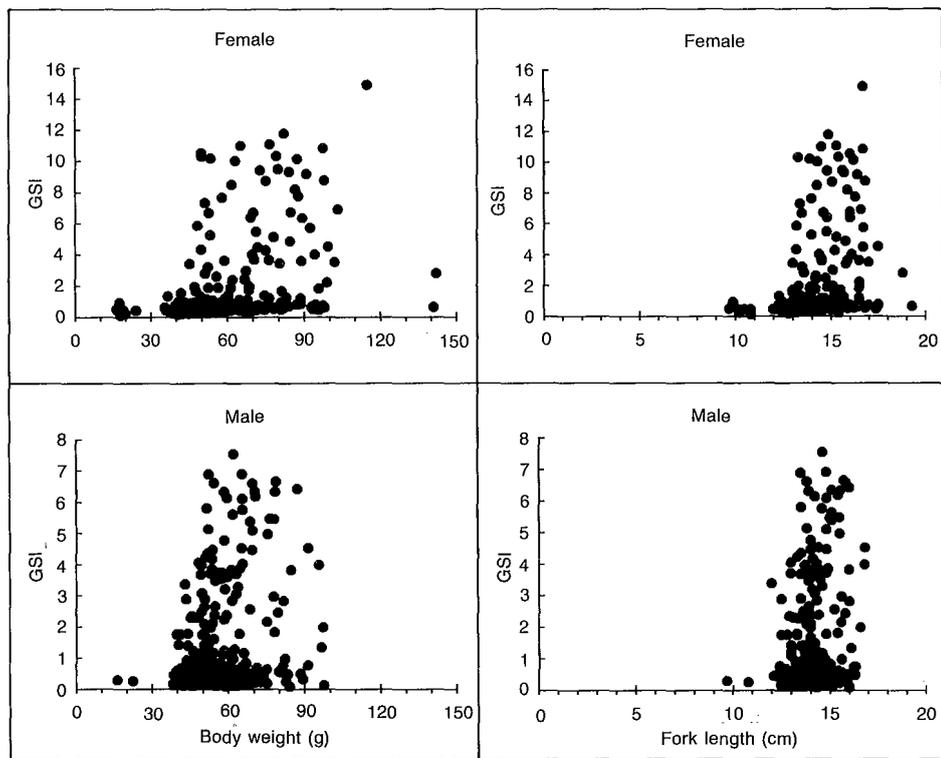


Fig. 6. Gonadosomatic index (GSI) versus fork length and body weight in male and female gizzard shads.

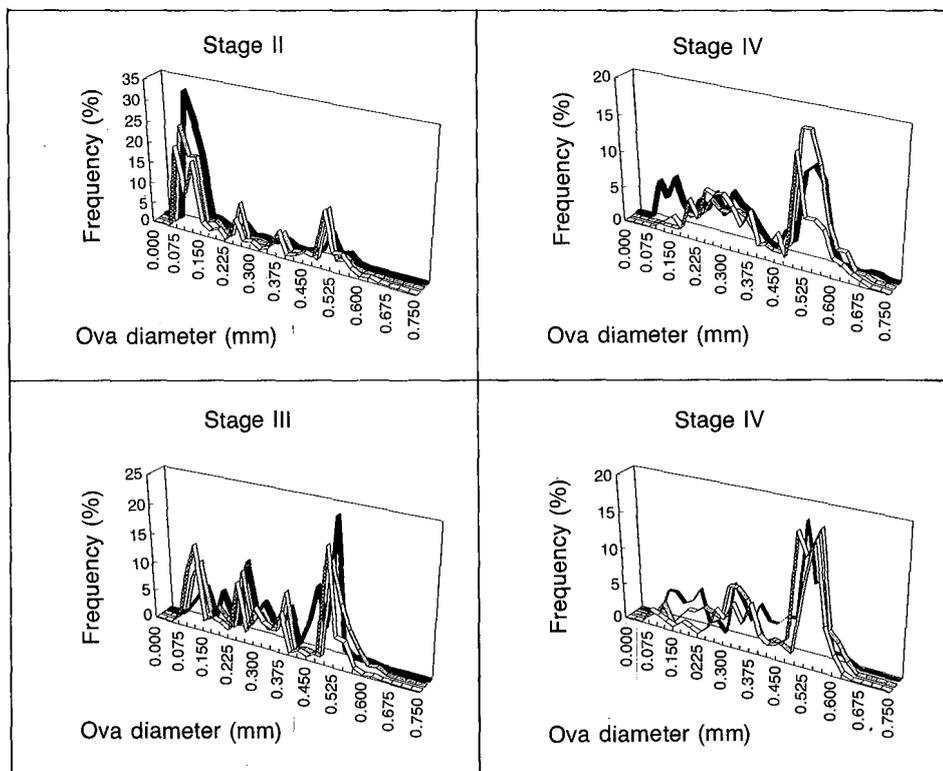


Fig. 7. The distribution of egg sizes in maturity stages II to IV of anterior (open), middle (dotted), and posterior (solid) parts of gizzard shad ovaries.

15.9 cm and a body weight of 40.4 g. However, the median lengths at maturity of *N. erebi*, 15.9 cm and 19.9 cm for males and females, respectively (Puckridge and Walker 1990), are larger than those of *N. come*. Chubb and Potter (1986) reported that the mean total body length of *N. vlaminghi* at the end of their 1st year of life is

about 10 cm (TL). Although the minimum age at maturity of *N. vlaminghi* was 2 yr, they also stated that most fish did not reach maturity until the end of their 3rd year. Accordingly, *N. come* demonstrates a similar minimum size at maturity with *N. vlaminghi*. We propose that the sexually mature age for *N. come* may be the same as *N. vlaminghi*, at an age of 2⁺ to 3⁺ yr. However, the differences in the maturity size between male and female *N. come* is not fully understood, and might result from a slower growth rate of males.

The capture of a number of mature fish at the uppermost sampling sites of the Kaohsiung River implies that *N. come* may undertake an upstream spawning migration (see Table 2). Chubb and Potter (1984) reported that *N. vlaminghi* was a semi-anadromous fish spawning in the upper region of estuaries. The fact that no fish were caught upstream in May and June may be due to either a post-spawning migration out to sea, or to poor water quality in the wet season, forcing fish to leave.

Although the shad spawned independently of the rainy season, the regulation of flooding in this period played an important role in the abundance of the *N. come* population. Normally the rainy season commences from May to August (see Fig. 8). At the same time the sewage storm discharges are operated. Soon after, the water quality downstream of the Chiping Bridge Barrier declines sharply, according to the Water Quality Monitoring Program of Kaohsiung River, Environmental Protection Bureau, Kaohsiung City Council (pers. comm.). Consequently, nursery grounds for the juvenile shads might be destroyed. Moreover, given a heavy flood or typhoon, juveniles would be washed into the outer harbor where food is

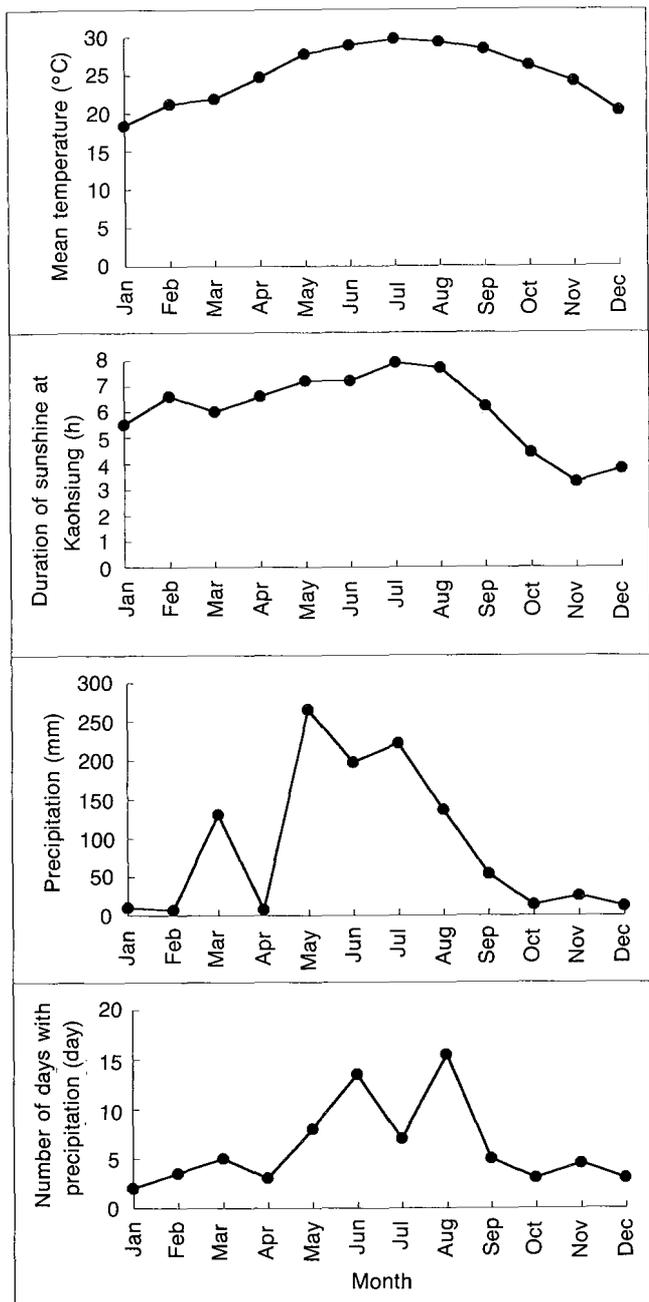


Fig. 8. Monthly means of temperature, duration of sunshine, precipitation, and the numbers of days with precipitation in the Kaohsiung area. (data from Central Weather Bureau 1993)

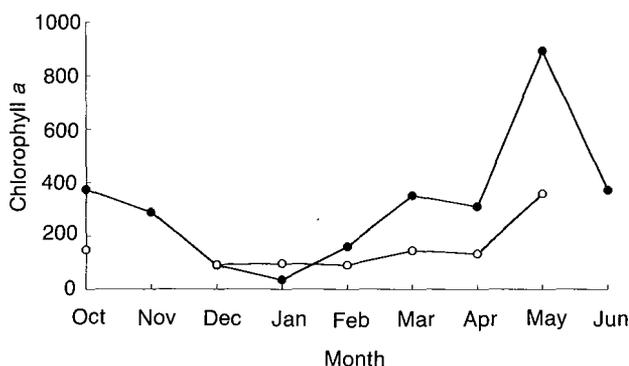


Fig. 9. Monthly values for chlorophyll a ($\mu\text{g l}^{-1}$) in Kaohsiung Harbor (solid circles) and the offshore waters (open circles).

less abundant and thus survival rates would fall. More importantly, if the rains started early in March, the fresh water would attract shad to spawn in the upper reaches just below the barrier. Then the vulnerable fry would encounter an unfavorable environment. Hence, we suggest that the greatest abundance of the population occurs in conjunction with the rains each year. The fact that the population dramatically declines in this area is due to the intense fishing pressures on one hand and the natural cyclicality of the rainy season on the other hand.

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高雄市仁愛河及高雄第一港口產環球海鯨 (*Nematalosa come*) 之生殖生物學研究

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1993年11月至1994年12月在高雄市仁愛河及高雄第一港口的五個採樣點，每月以流刺網採集環球海鯨 (*Nematalosa come*)，進行其生殖生物學的研究。由生殖腺指數及卵巢成熟期之月別變化得知其生殖高峰為2月到4月。生殖腺組織切片的結果顯示，此魚種的產卵形式為分批不同步。研究中最小成熟個體，雌魚和雄魚分別為尾叉長13和12公分，體重為45和39公克。雌雄性比為1:1.2。每批次的平均孕卵數為 89289 ± 23670 ，孕卵數 (F) 與體重 (BW)，尾叉長 (FL) 及生殖腺 (GW) 的關係式分別為 $\log FL = 3.516 + 0.673 \log BW$ ($r=0.540$)， $\log F = 3.147 + 1.1413 \log FL$ ($r=0.433$)，以及 $\log F = 4.184 + 0.822 \log GW$ ($r=0.755$)。

我們的研究雖然沒有直接證據顯示環球海鯨的生殖與洪水有關，但因其可能有溯河產卵的習性，所以我們推測仁愛河整治過後所設立之截流站的開啟與關閉，將對此族群的盛衰有直接的影響。

關鍵詞：成熟期，分批不同步，孕卵數，產卵洄游，河口魚類。

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