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THE REPRODUCTIVE BIOLOGY OF THE JAPANESE LITTLENECK, *TAPES PHILIPPINARUM* (A. ADAMS AND REEVE, 1850) (BIVALVIA: VENERIDAE)

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ABSTRACT A study was undertaken of natural populations of Manila clams (Japanese littleneck clams), *Tapes philippinarum*, from five bays and inlets in the northwestern part of the Sea of Japan. Seasonal gonadal changes were observed histologically in samples of Manila clams collected from Vostok Bay between January and December 1985. Five stages of gonadal development were identified. The first stage was the Active Stage of growth and maturation. At the beginning of this stage the gonad was poorly developed. In April, gametogenic activity increased and a spreading system of follicles was observed in the gonad. Along with developing gametes in the follicles there were blood cells and reserve tissue. This stage ended in June. In the Ripe Stage, the gametes matured. The female gonad was filled with mature oocytes that measured 64 μm in diameter. The male follicles were filled with spermatozoa that formed strands. Spawning usually began in mid to late June when water temperatures reached 15–16°C. Most individuals spawned in July and August during which time the Partially Spent Stage of the gonad was observed. Spawning was nearly completed by October when water temperatures declined to 15°C. The Spent Stage was characterized by spent follicles that sometimes contained residual gametes. Individuals in this stage were seen until October. The final stage was the Resting Stage which was seen in November and December. During this stage resorption of residual gametes occurred.

Manila clams became sexually mature during the first year of life at a minimum shell length of 7–8 mm, however, this varied among populations. The sex ratio of most populations sampled was close to 1:1. Hermaphroditism and parasitic castration are described.

KEY WORDS: clams, *Tapes philipinarum*, development, populations, hermaphroditism, Sea of Japan, South Primorye

INTRODUCTION

The Manila clam (Japanese littleneck), *Tapes philippinarum* (Adams and Reeve, 1850) is a subtropical to low boreal species of the western Pacific. It is of commercial importance in Canada, China, France, Japan, Korea, and U.S.A. (Mann 1979a, Doumenge 1984, Shi et al. 1984, Bourne 1989, Chew 1989, Manzi & Castagna 1989). The reproductive biology of this species in the Far East of Russia has not been thoroughly studied (Kulikova 1979; Rakov 1986, 1988). In this paper we present data on the sex ratio of Manila clam populations and on the seasonal changes in gonads of *T. philippinarum* in the northwestern part of the Sea of Japan.

REVIEW OF THE LITERATURE

Synonymy

There are difficulties in studying the biology of *T. philippinarum* because of the many scientific names for this species in the literature: *Amygdala ducalis, A. semidecussata, A. philippinarum, Paphia bifurcata, P. philippinarum, P.* (*Venerupis*) *philippinarum, Protothaca philippinarum, Tapes decussatta, T. decussatus, T. denticulata, T. indica, T. japonica, T. philippinarum, T. semidecussata, T. variegata, T. violascens, T.* (*Amygdala*) *japonica, T.* (*Amygdala*) *philippinarum, Venerupis japonica, V. philippinarum, V. semidecussata, V.* (*Amygdala*) *philippinarum, V.* (*Ruditapes*) *philippinarum, Venus decussata, V. japonica, V. philippinarum, V. tesselata, V.* (*Tapes*) *decussata, Ruditapes philippinarum* (Partridge 1977, Scarlato 1981, Cesari & Pellizzato 1985, Chew 1989, Malouf & Briceli 1989).

A revision of species belonging to the subfamily Tapetinae and their synonymy has been given by Fischer-Piette and Métivier (1971).

Distribution

Natural populations of Manila clams occur in the Philippines, the South China and East China Seas, Yellow Sea, Sea of Japan, the Sea of Okhotsk and in shallow waters around the South Kurile Islands (Scarlato 1981) (Fig. 1).

Since the beginning of the 20th century Manila clams have been introduced to various parts of the world (Fig. 1). Manila clams were imported into the Hawaiian Islands from Japan (Bryan 1919, Thaanum 1921, Brock 1960) where populations exist at present (Yap 1977). In the 1930's the species was accidentally introduced to the Pacific coast of North America from Japan along with importations of Pacific oyster, *Crassostrea gigas*, seed (Quayle 1938, 1941) and it spread quickly along the west coast of the U.S.A. and Canada as far north as northern British Columbia (Nosho & Chew 1972, Bourne 1982).

During the late 1960's, Manila clams were imported into France where they are cultivated at present on both the Mediterranean and Atlantic coasts (Chevallier et al. 1975, 1976, Doumenge 1984, Rakov 1986, 1988). In the late 1970's, Manila clams along with Pacific oysters were introduced into the United Kingdom from Oregon and artificially propogated at Menai Bridge, North Wales. From the United Kingdom, Manila clam seed was exported to Ireland. Juvenile Manila clams from both English and French hatcheries were imported into Spain (Mann 1983). During the same years the species was introduced to Tahiti (French Polynesia) (Coeroli et al. 1984). Since 1983, Manila

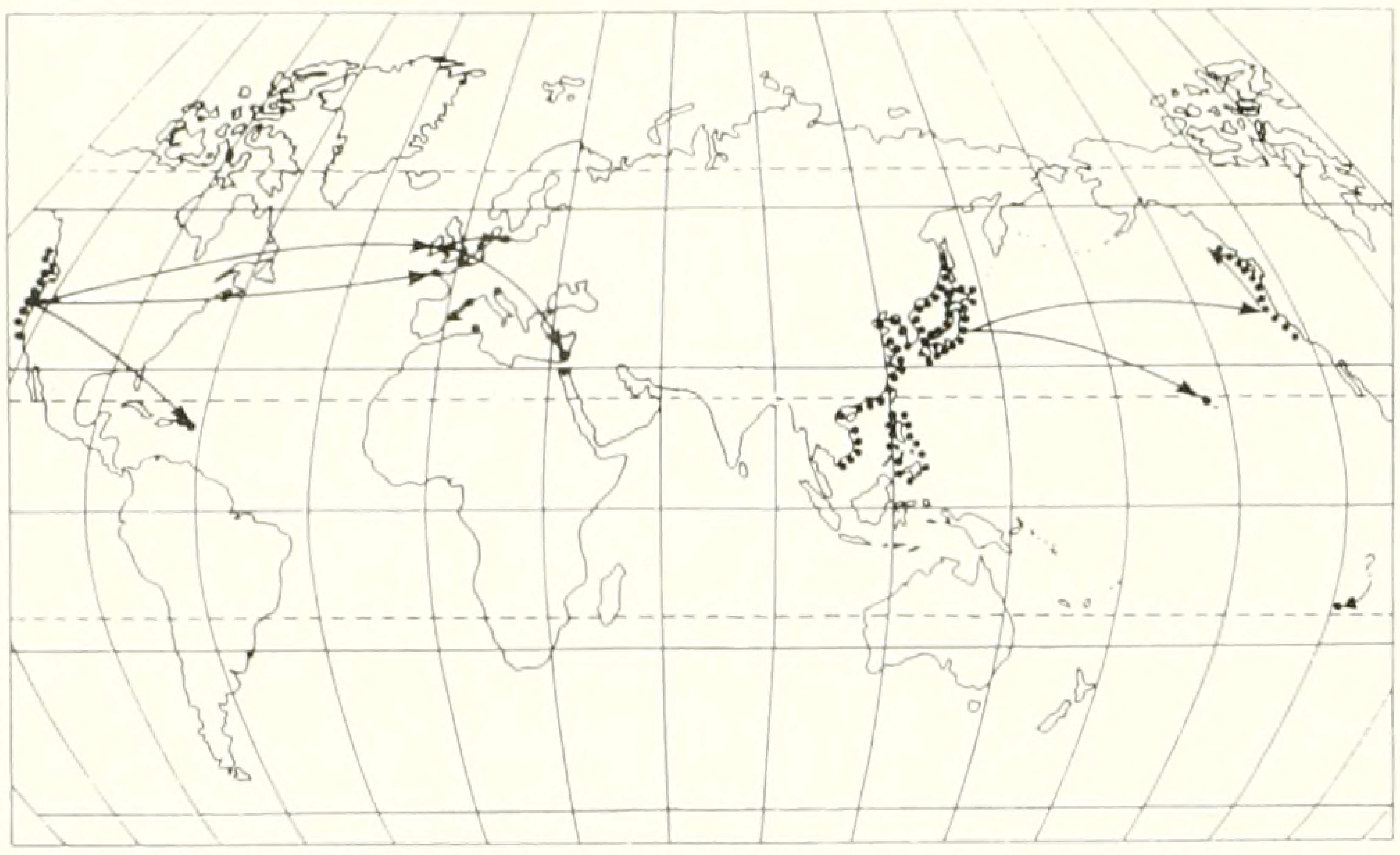


Figure 1. Map showing the distribution of Manila clams, *Tapes philippinarum*, throughout the world. Arrows indicate the source of importations. ? indicates the source of the imports is unknown.

clams have been cultured in a lagoon near Venice, Italy (Cesari & Pellizzato 1985). Together with Pacific oyster seed, Manila clam seed was introduced into Flensburg Fjord in Kiel Bay, Germany from Scotland (Neudecker 1984). In recent years, experimental culture of this species has been carried out in artificial upwelling systems in St. Croix (U.S. Virgin Islands) (Rodde et al. 1976), in suspended culture in Tunisia (Gimazane & Medhioub 1979), in Belgian hatcheries (Claus et al. 1983), and in the effluent of marine fish culture ponds in Israel (Shpigel & Fridman 1990).

Along the far eastern coast of Russia, Manila clams occur in Primorye (Maritime Territory), near the western coast of Sakhalin Island, in Aniva Bay, Busse Lagoon and in the shallow waters of the South Kurile Islands (Kunashir and Shikotan Islands) (Golikov & Scarlato 1967, Scarlato 1981). In Primorye this species is distributed from Possjet Bay to the Amur estuary (Bazikalova 1931, Rasin 1934).

Reproduction

Tapes philippinarum is a dioecious animal (Bardach et al. 1972, Chew 1989, Eversole 1989, Devauchelle 1990). Only two instances of hermaphroditism (0.1% of the population) were reported in Manila clam populations from Big Beef Harbour and Misery Point in the Hood Canal, Washington (Holland & Chew 1974).

In natural populations, *T. philippinarum* becomes sexually mature in the first to the third year of age. In Akkeshi Lake (the northeast coast of Hokkaido Island) males mature at an age of two years and shell length of 22–27 mm, females at an age of 3 years and shell length of 30–35 mm (Yamamoto & Iwata 1956). Ko (1957 cit. in Holland & Chew 1974) observed earlier maturation of this species in Sasebo Bay, Japan. According to this author, mature gonads developed in Manila clams at a shell length of 12 mm and at shell length about 15 mm many individuals spawned. In ponds where juvenile Manila clams are raised in China (Dong Shi, Jinjiang District) 70% of Manila clams attained sexual maturity at the age of 1 year at which time they ranged in size from 12–15 mm (Qi & Yang 1988).

In Hood Canal (State of Washington, U.S.A.), Manila clams developed mature gametes at a shell length of 5–10 mm. However, they did not spawn at this size. A small proportion of the population spawned at a shell length of 15–20 mm and all individuals over 20 mm spawned which was in their first year (Holland & Chew 1974).

In Hawaii, the minimum size of male and female Manila clams with mature gametes was 15.1 mm and 15.3 mm, respectively. However, the major contribution to reproduction was made by individuals over 20 mm (about 1 year old), because the gonad was poorly developed in smaller individuals (Yap 1977). In French waters, Manila clams attained sexual maturity at an age of one year and a shell length of 15–20 mm (Devauchelle 1990).

In south Primorye, in Possjet and Slavyansky Bays, Manila clams began spawning at an age of 2 years, although the largest 1 year olds also had ripe gametes (Rakov 1986). In Vostok Bay, Manila clams became sexually mature at an age of 1 to 2 years (Denisenko 1978).

Spawning of *T. philippinarum*, can occur either once or twice each year depending on location and environmental conditions such as temperature (Table 1). In northern populations, spawning occurred once each year and was usually limited to one or two months that varied from April to October at various localities. Further south, spawning in some population extended for the duration of this period such as in Hood Canal, Washington, U.S.A. (Holland & Chew 1974). In other populations, such as those in the central and southern parts of Japan, Manila clams spawned twice each year, in late spring to early summer and again throughout the autumn (Obha 1959, Bardach et al. 1972, Kikuchi 1984). Populations located close to the equator spawn year round with peak spawning periods during December and January in Hawaii (Yap 1977) and again in May to July in Israel (Shpigel & Fridman 1990).

The fecundity of *T. philippinarum* as reported in the literature ranges from 4.32×10^5 eggs in individuals that are 20 mm in shell length to 2.35×10^6 eggs in individuals that are 40 mm in shell length (Yap 1977). Lower values of fecundity were reported in work from China, 1.88×10^5 and 1.503×10^6 eggs for Manila clams with shell lengths of 19 and 42 mm respectively (Shi et al. 1984). The diameter of ripe eggs has been reported as 63–66 Ùm (Miyazaki 1934), 60–75 Ùm (Loosanoff & Davis 1963) and 71–80 Ùm (Qi 1987).

MATERIALS AND METHODS

In the present study, *T. philippinarum* were sampled from the upper subtidal zone in five bays and inlets in the northwestern part of the Sea of Japan during 1984 to 1988 (Figs. 2 and 3). A square metal frame ($1/16$ m^2 in area) was used to collect clams randomly. All substrate was removed to a depth of 10 cm and then sifted through a 1 mm mesh screen and all adult clams removed. The clams were measured anteroposteriorly (shell length) to the nearest 0.1 mm. Age of clams was estimated by counting the number of annual growth rings (Zolotarev 1976, Silina & Popov 1989). A description of the sampling sites is given in Table 2.

For histological analysis of the gonads, 15 adult clams with a shell length over 20 mm were sampled monthly in Vostok Bay during 1985. Sections of gonads were fixed in Bouin's solution and embedded in paraffin. Histological sections 5–7 Ùm in thickness were stained with haematoxylin after the method of Heiden-

TABLE 1.

Spawning periods of the Japanese littleneck clam, *Ruditapes philippinarum*.

Location	J F M A M J J A S O N D	Temperature (°C)	Authority
Sakhalin Is.			
Busse Lagoon		18–20	Kulikova, 1979
South Primorye			
Vostok Bay, Litovka estuary		18–20	Denisenko, 1978
Vostok Bay, Srednyaya Bay		17–19	Denisenko, 1978
Vostok Bay, Tikhaya Zavod		15–24	This study
Slavyansky and Possjet Bays		18–22	Rakov, 1986
Japan			
Hokkaido is.		20–23	Cahn, 1951, cit. after Yap, 1977
Hokkaido is.			Yamamoto & Iwata, 1956
Tokyo Bay			Naito, 1931 cit. in Ohba, 1959
Tokyo Bay			Kikuchi, 1984
Hiroshima Bay			Hiroshima Fish. Exp. St., 1952 cit. in Ohba, 1959
Ariake Bay			Tanaka, 1954, cit. in Ohba, 1959
Kasaoka Bay			Yasuda et al., 1954, cit. in Ohba, 1959
Mucasa-shoal, the Bisan Seto Channel, the Inland Sea		14–21, 25–18	Ohba, 1959
Ariakenuomi			Kikuchi, 1984
Korea			
Inchon Bay			Choi, 1965
China			
Fujian Prov.		18–27	Qui et al., 1983
Fujian Prov.		18–27	Shi et al., 1984
Jinjiang Distr.		23–19	Qi & Yang, 1988
USA			
Oahu, Hawaiian Islands		21–28*	Yap, 1977
St. Croix, Virgin Islands		22–29	Rodde et al., 1976
St. Croix		22–26	Rodde et al., 1976
St. Croix		24–29**	Rodde et al., 1976
Big Beef Harbor, Hood Canal, Washington			Nosho & Chew, 1972
Big Beef Harbor, Hood Canal		13–20	Holland & Chew, 1974
Misery Point, Hood Canal		13–26	Holland & Chew, 1974
Canada			
Str. of Georgia, British Columbia		≥15	Bourne, 1982
France			
Thau Lagoon (Hérault)		20–25	Maitre-Allain, 1985
Normandy			Medhioub & Lubet, 1988
Israel			
Eilat		27–31	Shpigel & Fridman, 1990

Remarks: Thick line shows the period of intensive spawning, break—the spawning is obscure.
* Vermeij, 1978.
** Clams were induced to spawn by heat shock and addition of gonad suspension.

hain. The state of sexual maturation in the populations during the prespawning periods was done using smear preparations of the gonads. Statistical analysis was done according to the method of Urbakh (1984).

RESULTS AND DISCUSSION

Sexual Characteristics

The age at which Manila clams become sexually mature in the northwestern part of the Sea of Japan varied with geographic distribution (Fig. 4). In Possjet Bay and most sampling stations in Vostok Bay from about 3 to 60% of Manila clams were sexually mature in their first year. In most cases, the majority of clams that matured during their first year were males. In the second year over 80% of the clams from these two Bays were sexually mature. At this time in Melkovodnaya, Vladimir, and Olga Bays, less than 30% of Manila clams were sexually mature. In the third year, from 60 to 80% of the clams in Vladimir and Olga Bays were mature. At all locations, most of Manila clams over three years of age were sexually mature, and in most locations numbers of males and

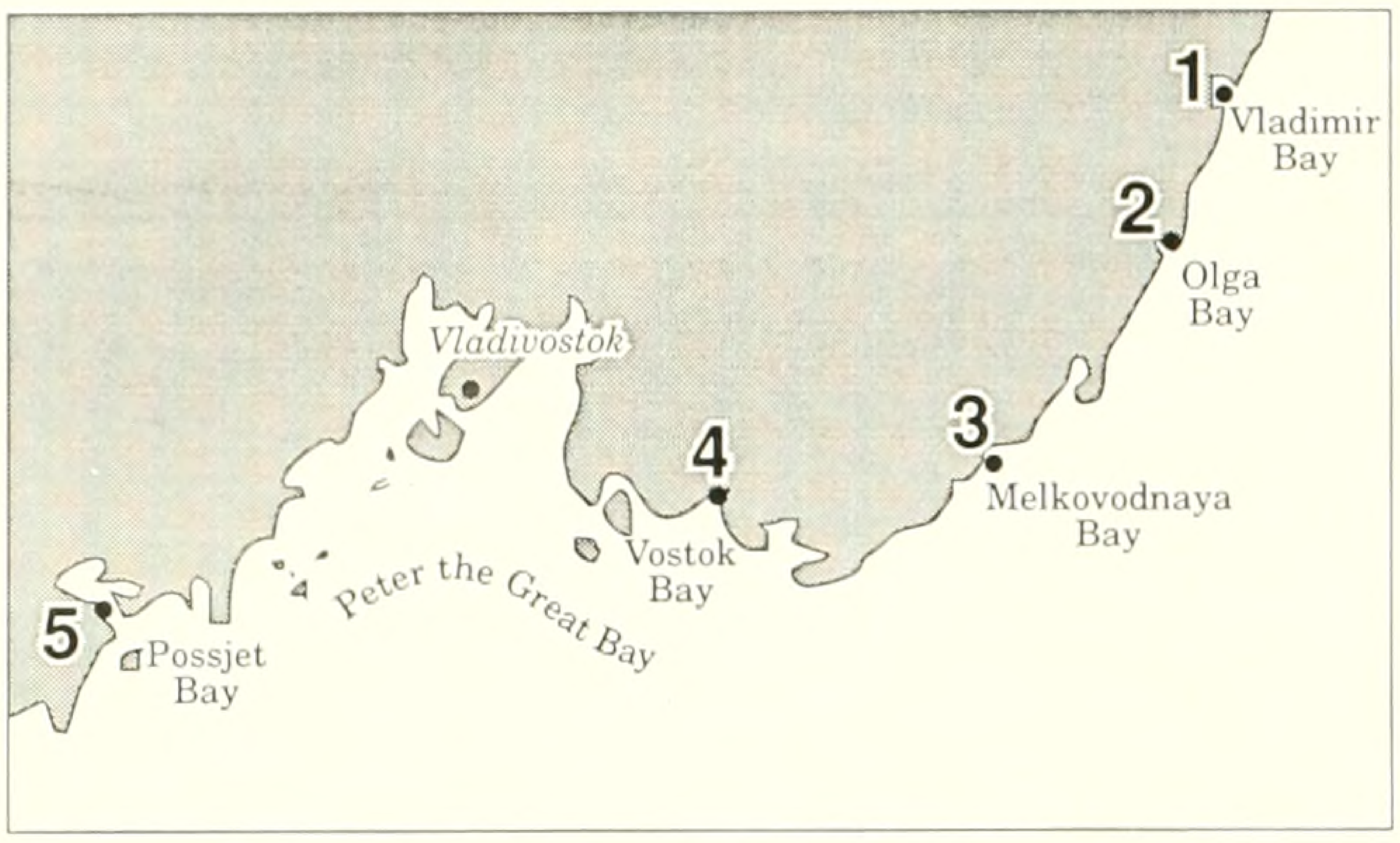


Figure 2. Map of the northwestern part of the Sea of Japan showing the location of Peter the Great Bay and the location of study areas. 1. Vladimir Bay; 2. Olga Bay; 3. Melkovodnaya Bay; 4. Vostok Bay; 5. Possjet Bay.

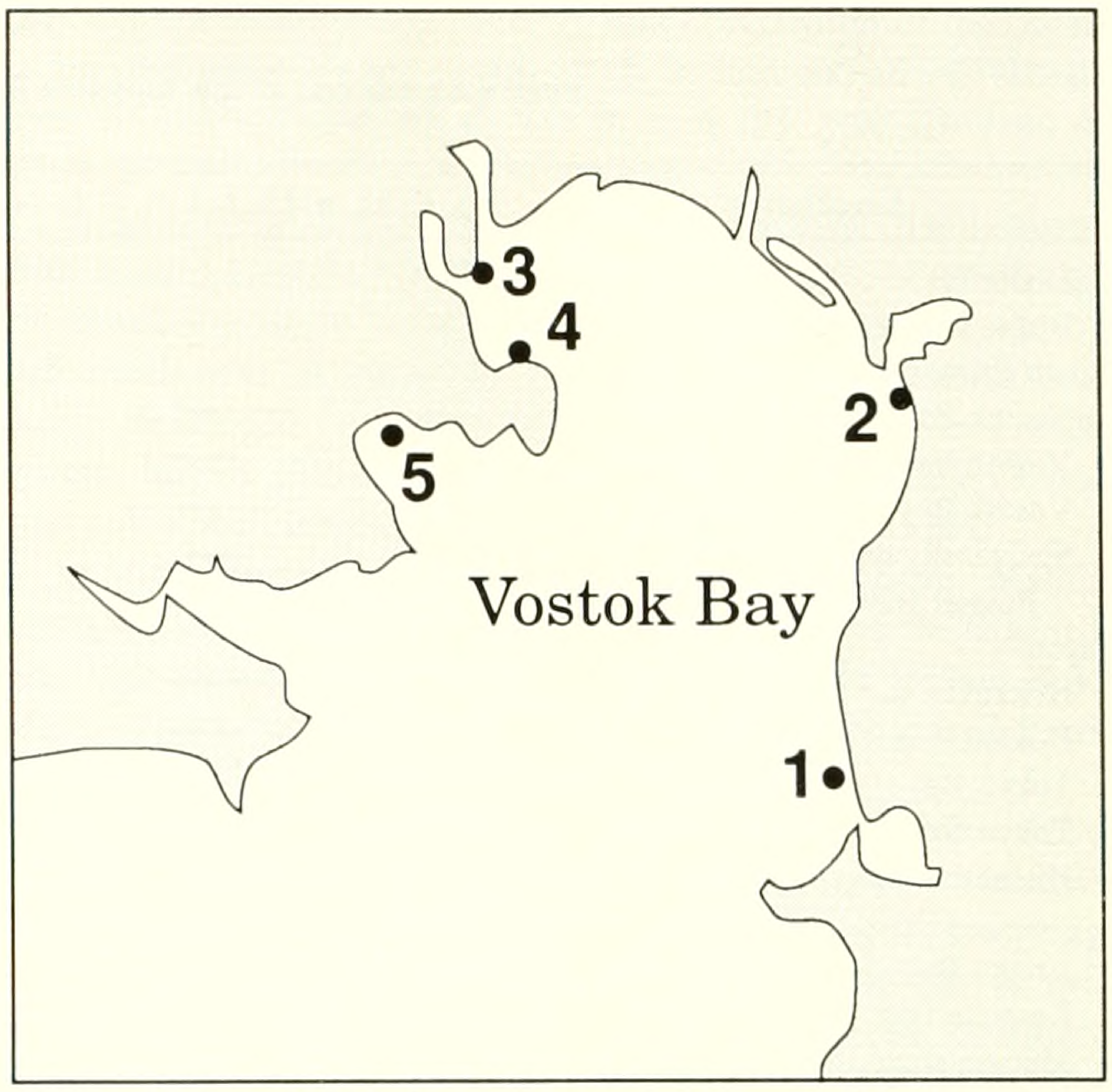


Figure 3. Map of Vostok Bay showing the location of sampling sites.

females were equal. The majority of the oldest clams were females.

Attainment of sexual maturity also depended on habitat. In Possjet Bay and in some localities of Vostok Bay (Stns. 2B and 3), all Manila clams were sexually mature in the second year and in most populations in Vostok and Melkovodnaya bays all were sexually mature at age three. In Olga Bay, sexual maturation of Manila clams was completed only in the fourth year and in Vladimir Bay in the fifth year.

The size (shell length) at which Manila clams become sexually mature varied among populations. In Possjet Bay and in most populations in Vostok Bay (Fig. 4) males matured at a shell length of 10–15 mm and females at 15–20 mm. In other populations that were sampled, sexual maturity occurred at a larger size. Most Manila clams in Vostok Bay became mature at a shell length of 20–30 mm. In Melkovodnaya and Olga Bays all Manila clams attained sexual maturity when their shell lengths were 30–35 mm while in Vladimir Bay some individuals as large as 40–45 mm did not have ripe gametes (Fig. 4). It should be noted that in many Manila clam populations there were individuals in the oldest (largest) age (size) groups whose sex was unidentifiable (Table 3). Occasionally smaller individuals were sexually mature. For example, in 1985, the minimum shell length of males in two populations in Vostok Bay (Stns. 2B and 4) was 8.0 mm and 8.6 mm respectively. At Station 2B, the minimum shell length of a sexually mature females was 7.5 mm.

Despite differences in minimum size at which sexual maturity is attained in males and females, a significant prevalence of males was observed only in some size groups (Fig. 4). Generally a sex ratio close to 1:1 was characteristic for most populations in the northwestern part of the Sea of Japan. An exception was the population in Vostok Bay where the number of females was higher than males, 1.5:1 (Stns. 2A and B) and 1.2:1 (Stn. 4, 1985) (Table 3).

Hermaphrodites were found in populations in Vostok and Vladimir bays but they did not exceed 2% of the population (Fig. 4, Table 3). Parasitic castration was observed in all populations except those in Possjet Bay (Table 3). The percentage of Manila clams infested with parasitic trematodes in Vostok Bay ranged from 0.3% (Stn. 4, 1984) to 4.1% (Stn. 2A). In the

TABLE 2.

The main characteristics of sampling sites in the northwestern part of the Sea of Japan.

Sampling Sites	Depth, m	Sediment	Degree of wave activity
Vladimir Bay	0.5–2.0	Boulder, coarse pebble with sand and shell	I–II
Olga Bay	1.0–1.5	Sand	II–III
Melkovodnaya Bay	0–0.5	Gravel, pebble	II–III
Vostok Bay			
St. 1	0.5–1.0	Boulder	II
St. 2A	0–0.5	Fine and medium sand	III
St. 2B	1.0–1.5	Gravel, fine sand	III
St. 3	0.5–1.0	Silty sand	I
St. 4	0–1.0	Gravel, pebble	I
St. 5A	0–0.5	Gravel, pebble	II
St. 5B	2.0	Medium sand	II
Possjet Bay	0.5–1.0	Sand	I–II

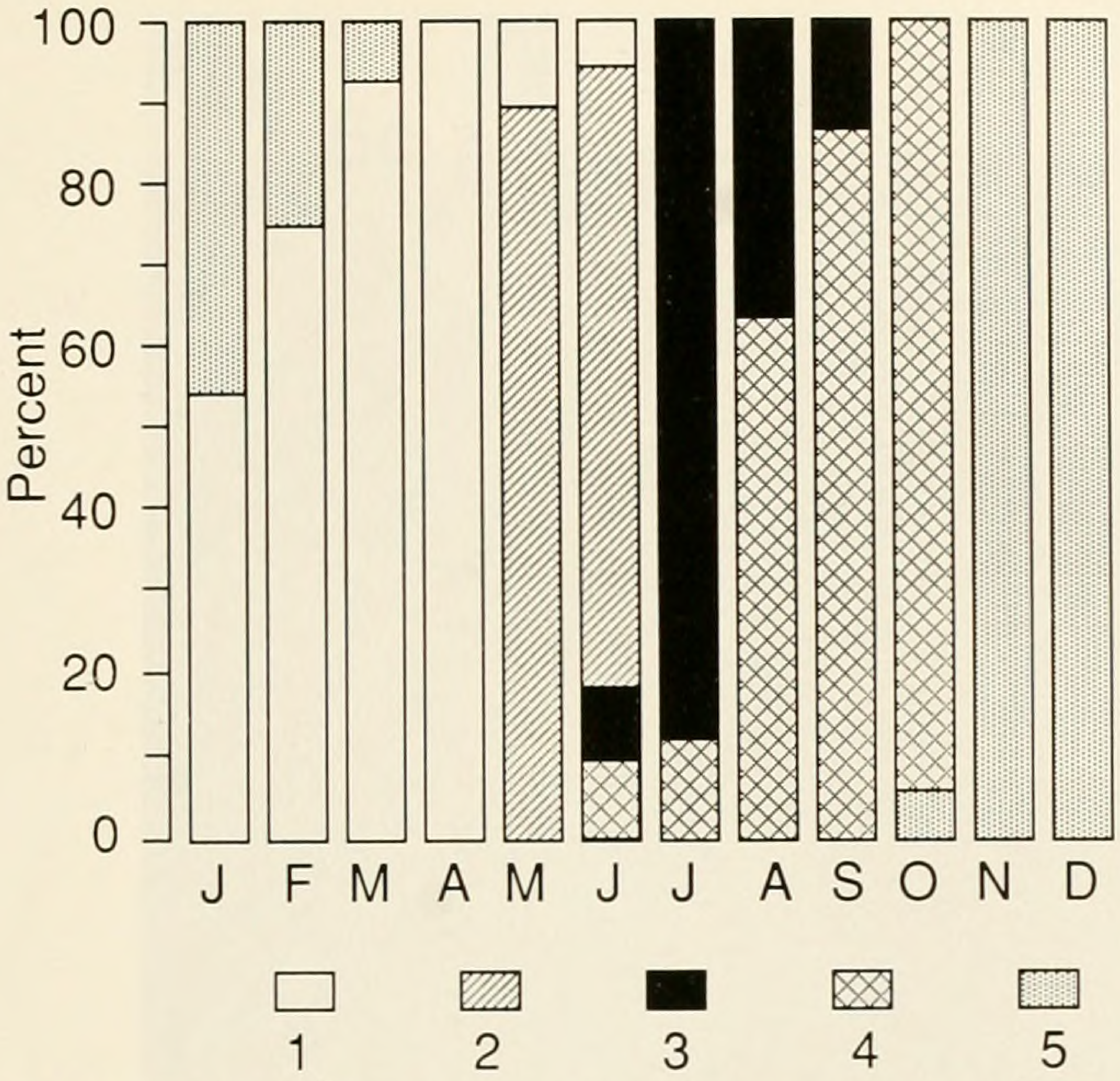


Figure 4. Distribution of male and female, hermaphrodite and castrated Manila clams, *Tapes philippinarum*, at sampling locations in the northwest part of the Sea of Japan in relation to age (A) and size (B). 1. sex unidentifiable; 2. male; 3. female; 4. hermaphrodites; 5. castrated animals.

other bays, the percentage of castrated Manila clams did not exceed 1.1%.

Reproductive Cycle

Seasonal changes in the gonads of Manila clams can be divided into several developmental stages.

Active Stage

This is the longest developmental stage and includes much of the basic gametogenic processes. At the beginning of this stage, the gonad was weakly developed. Small acini were loosely scattered in the visceral mass of the molluscs. In the female, oogonia and small developing oocytes occurred along the acinus walls. Gametogenic activity and enlargement of the system of acini was observed in April. The gonad was composed of small, near-wall oocytes (Fig. 5a). In the male, this stage was characterized by the presence of a fairly pronounced spermatogenous layer. Spermatogonia were visible along the wall of the acini. They had a lightly-coloured, oval-shaped nucleus, often with two nucleoli (Fig. 6a). Proliferation of spermatogonia proceeded in some regions of the acini. Rarely mitoses of spermatogonia was observed (Fig. 6b). Some individuals had numerous spermatocytes 1 and II in the gonad. There were few spermatozoa located in the centre of the lumen of the acini (Fig. 6c).

In both males and females, there were hemocytes (blood cells) and cells of reserve tissue along with developing gametes (Medhioub & Lubet 1988).

This stage ended during June in the study area.

Ripe Stage

In this stage, gametes located along the wall of the acini became fully mature. The amount of connective tissue and reserve cells in the acini decreased considerably and the acinus attained maximum size.

The female gonad was mainly composed of ripe oocytes measuring 64 Ùm in diameter (nonfixed cells). Many of the oocytes occurred near the wall of the acinus (Fig. 5b). In males a narrow spermatogenic layer was still present along the wall of the acinus. However, most of the gonad was occupied by spermatozoa arranged in strands (Fig. 6a). The head of *T. philippinarum* spermatozoa is shaped like a thickened comma.

Partially Spent Stage

In Vostok Bay, Manila clams began to spawn in the second half of June when water temperatures reached 15–16°C but most

TABLE 3.

Population sex structure of the Japanese littleneck clam, *Ruditapes philippinarum*, in the north-western part of the Sea of Japan.

Sampling Location	Year	No. of Animals	Male, %	Female, %	Juvenile, %	Hermaphrodites, %	Castrated %	Sex Unidentifiable, %
Vladimir Bay	1988	355	20.3	18.0	17.7	1.1	1.1	41.8
Olga Bay	1988	93	14.0	12.9	65.6	0	1.1	6.4
Melkovodnaya Bay	1985	97	30.9	42.3	25.8	0	1.0	0
Vostok Bay								
St. 1	1986	97	18.6	19.6	59.8	0	2.0	0
St. 2B	1985	390	14.1	21.5	63.3	0.3	0.8	0
St. 2A	1986	343	35.6	54.2	5.0	1.2	4.0	0
St. 3	1985	283	40.4	48.8	5.6	0.9	3.3	1.0
St. 4	1984	742	12.8	12.5	72.1	2.0	0.3	0.3
St. 4	1985	551	35.0	43.2	18.7	0.9	1.1	1.1
St. 5A	1985	349	16.0	19.5	57.3	0	0.6	6.6
St. 5B	1984	276	25.0	22.1	52.2	0	0.7	0
Possjet Bay	1988	148	14.2	12.2	73.6	0	0	0

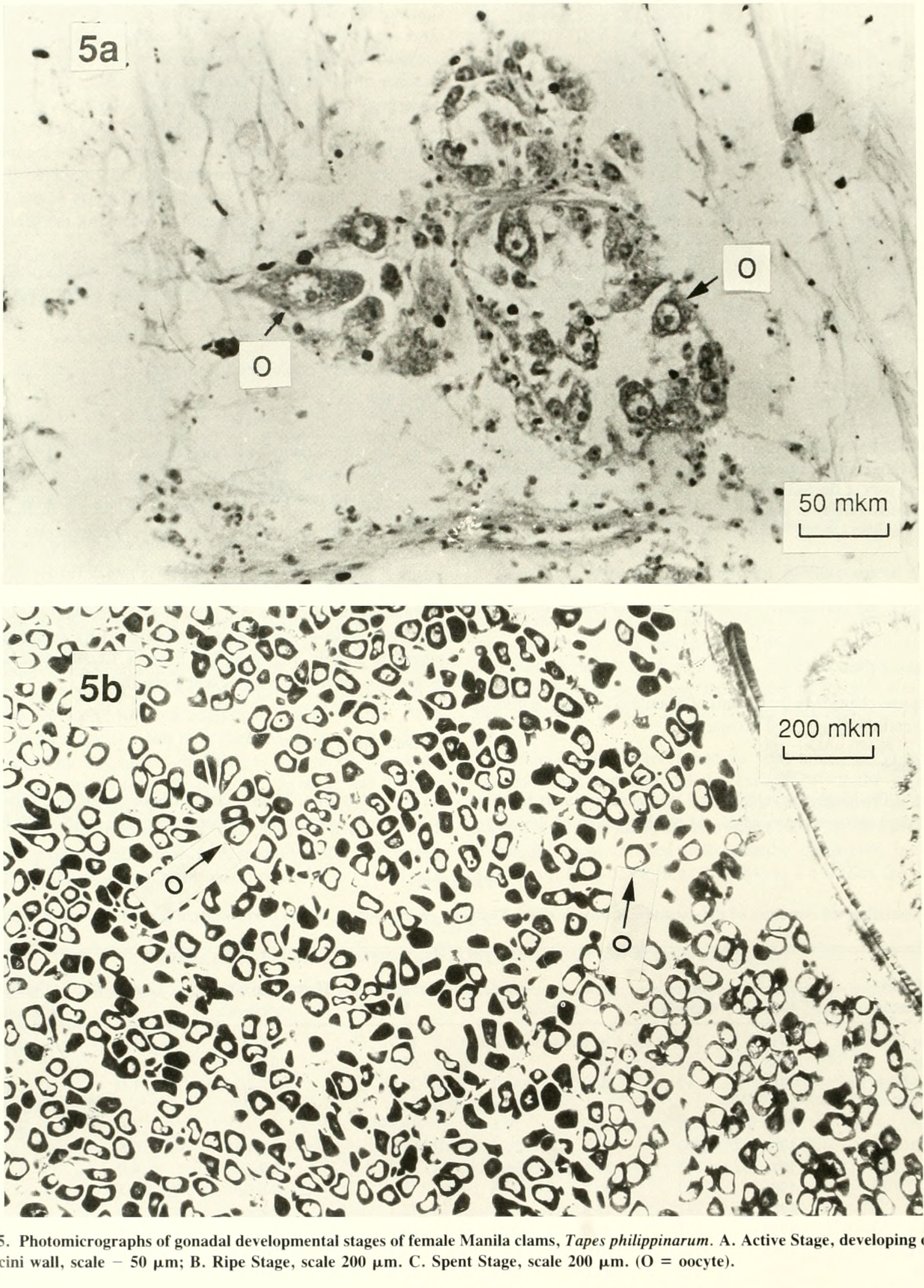


Figure 5. Photomicrographs of gonadal developmental stages of female Manila clams, *Tapes philippinarum*. A. Active Stage, developing oocytes along acini wall, scale – 50 μm; B. Ripe Stage, scale 200 μm. C. Spent Stage, scale 200 μm. (O = oocyte).

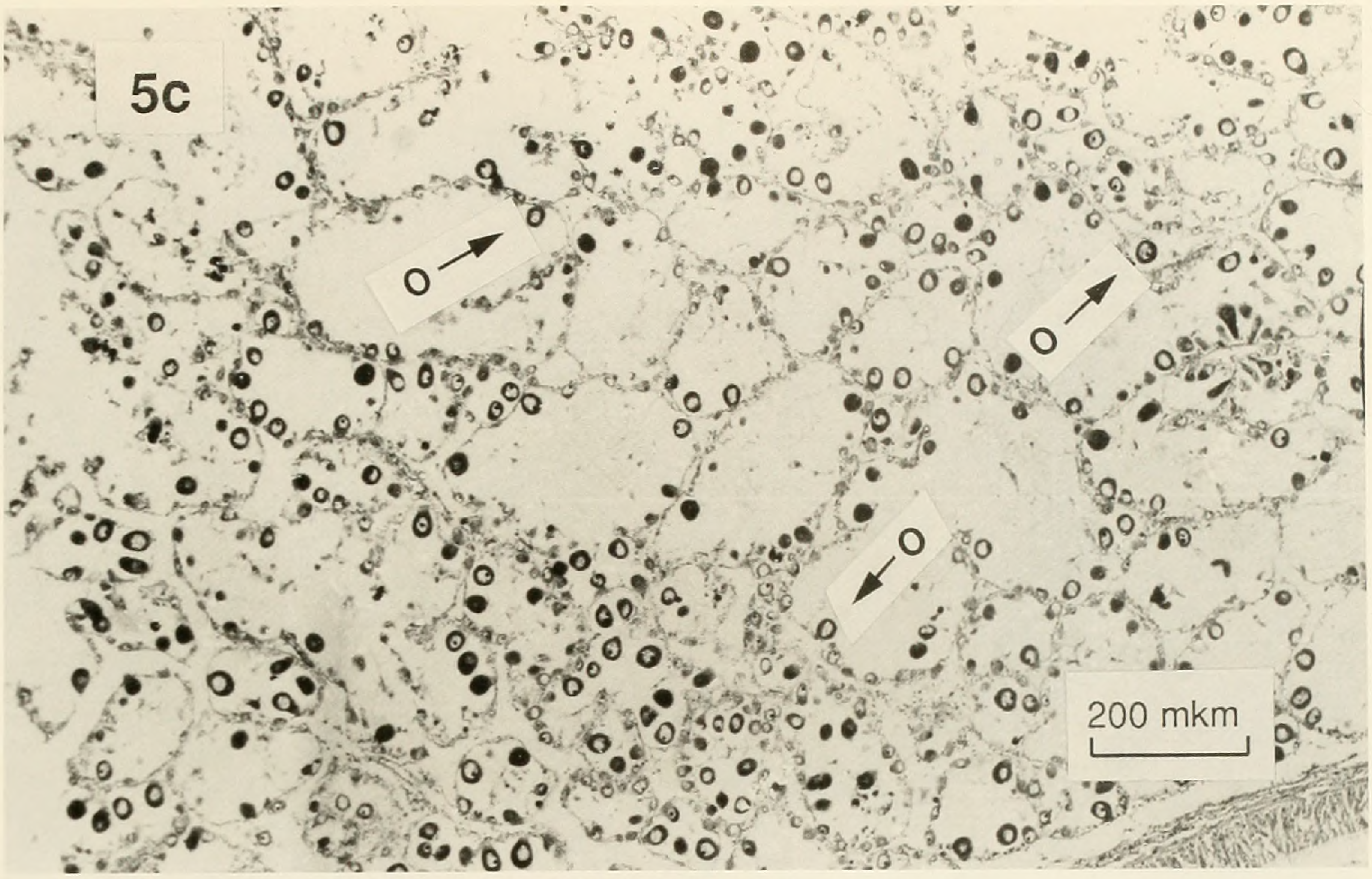


Figure 5. Continued.

individuals spawned in July and August (Fig. 7). There was one gametogenic cycle each year. In Vostok Bay, spawning was continuous during the reproductive period. However, there were peaks and lows in spawning activity. Spawning ceased at the end of September when water temperatures declined below 15°C.

Spent Stage

This stage was characterized by empty, shrunken acini. Residual gametes were present in some regions of the gonad (Figs. 5c and 6e). This stage lasted until November.

In October, resorption of residual gametes was completed. The connective tissue grew between the acini and their number and size decreased. Growth of reserve connective tissue inside the acini was characteristic for Manila clams in this stage (Fig. 6f).

Inactive Stage

In this stage it was difficult to determine the sex of animals even by histological examination of the gonad. Reduction of the gonad was most pronounced in November and December.

From January to March some gametogenic activity occured in gonads of some individuals which allowed sex identification. However, generally the gonad was undeveloped.

The percentage of each gonadal development stage in a population by month is shown in Figure 8.

The reproductive cycle of Manila clams in Vostok Bay was similar to findings for this species in other temperate waters. Spawning temperature and the single spawning per year indicated that spawning is primarily induced by water temperature, which is peculiar to this particular region, along with other, but none the less important and interrelated, environmental factors. Under experimental conditions, maturation of the gonad in *T. philippinarum* occurred at a temperature of 12°C and spawning occurred when water temperatures exceeded 15°C (Mann 1979b). As indicated above, in southern regions of Manila clam distribution, spawning is arrested at high water temperatures (Obha 1959, Maitre-Allain 1985). As with mussels in Primorye (Yakovlev 1986) low autumn temperatures arrest gametogenic activity and gonad maturation and prevent a second spawning.

Reproductive cycles in the same species can vary significantly with geographic location. This involves the timing of the gonadal cycle, the timing and duration of spawning and the number of spawnings per year. The phenomenon of a molluscan species spawning twice a year in the southern part of its range and only once in the northern part of its range has been reported for different species of mollusc (Ropes & Stickney 1968, Lubet 1984, Maximovich 1985, Yakovlev 1986).

A comparison of data on size and age at sexual maturity of Manila clams suggest that some individuals in populations at south Primorye became sexually mature at a smaller size than those in other parts of the world (Yamamoto & Iwata 1956, Yap 1977, Qi & Yang 1988). The situation observed in our study in south Primorye is similar to that in Manila clams in the State of Washington (U.S.A.) where males and females were sexually mature in the first year of their life at a shell length of 5–10 mm (Holland & Chew 1974). In most other areas the minimum size and age of sexual maturity is approximately the same, about 1 year of age and

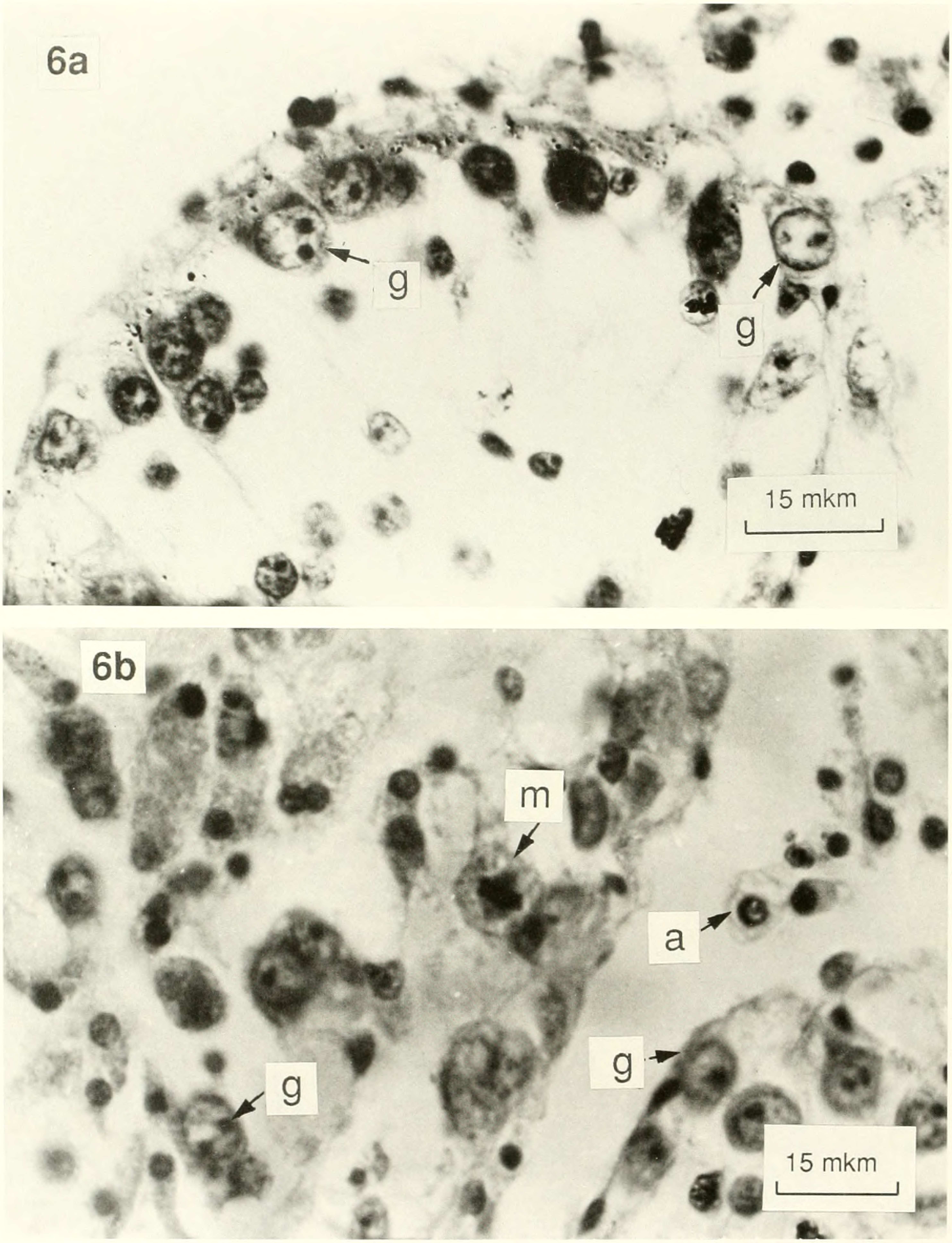
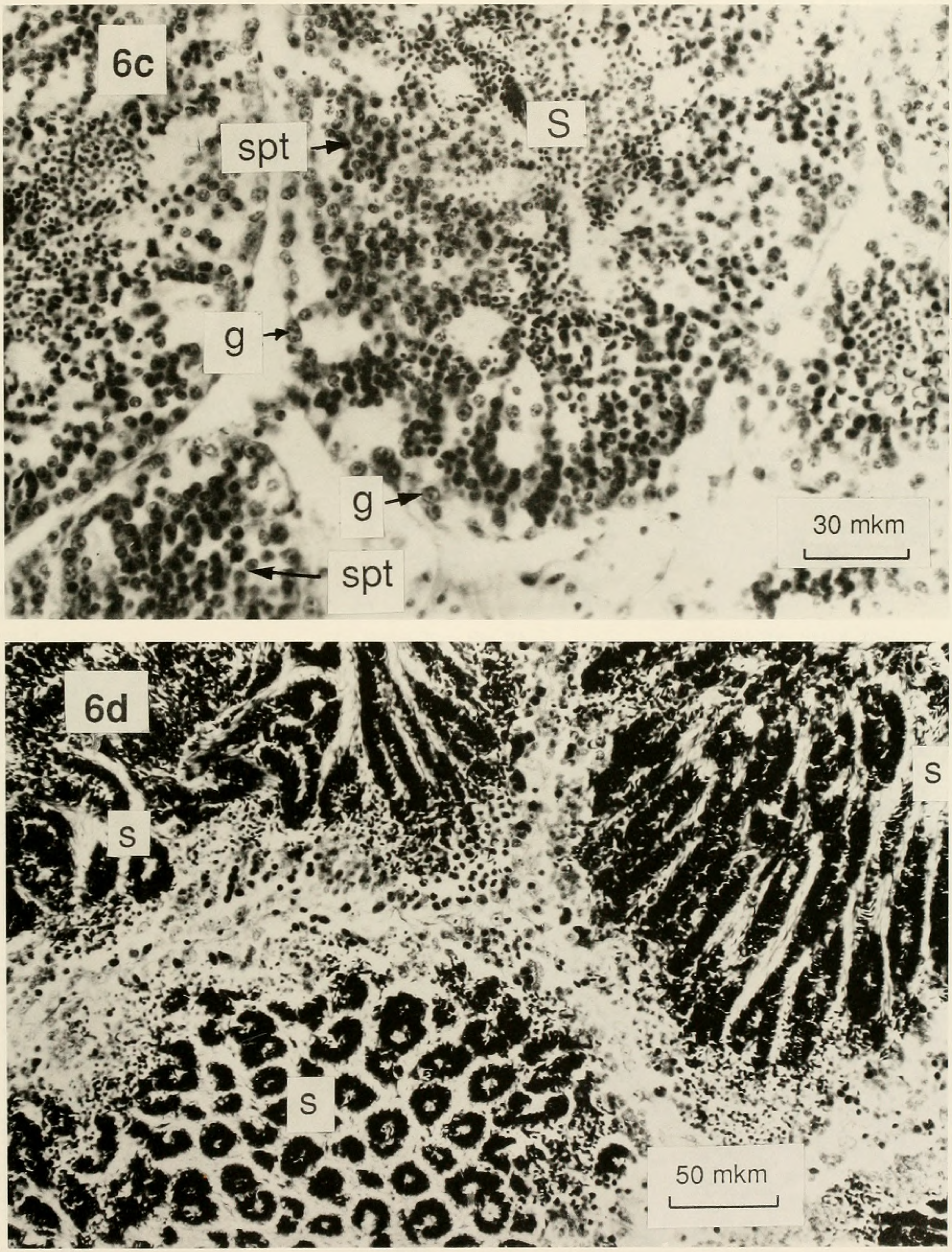


Figure 6. Photomicrographs of gonadal developmental stages of male Manila clams, *Tapes philippinarum*. A. Active Stage: spermatogonia with two nucleoli, scale 15 μm; B. mitosis of spermatogonia, scale 15 μm; C. developing male, scale 30 μm; D. Ripe Stage, scale 50 μm; E. Spent Stage, scale 30 μm; F. Resting Stage, residual spermatozoans and connective tissues in the lumen of acini, scale 50 μm. (a = amebocyte, g = spermatogonia, m = mitosis, s = spermatozoa; spt = spermatocyte; t = connective tissue).



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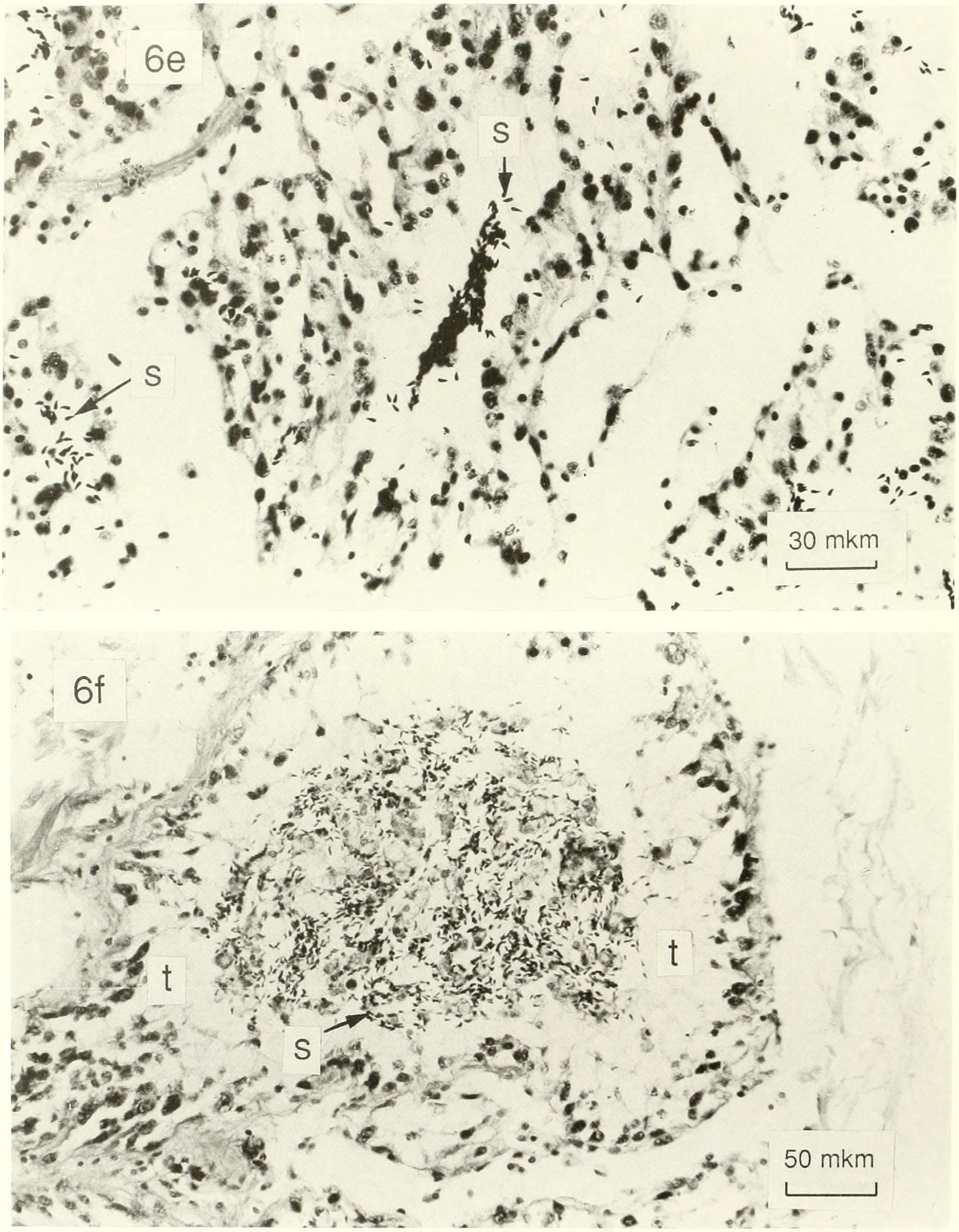

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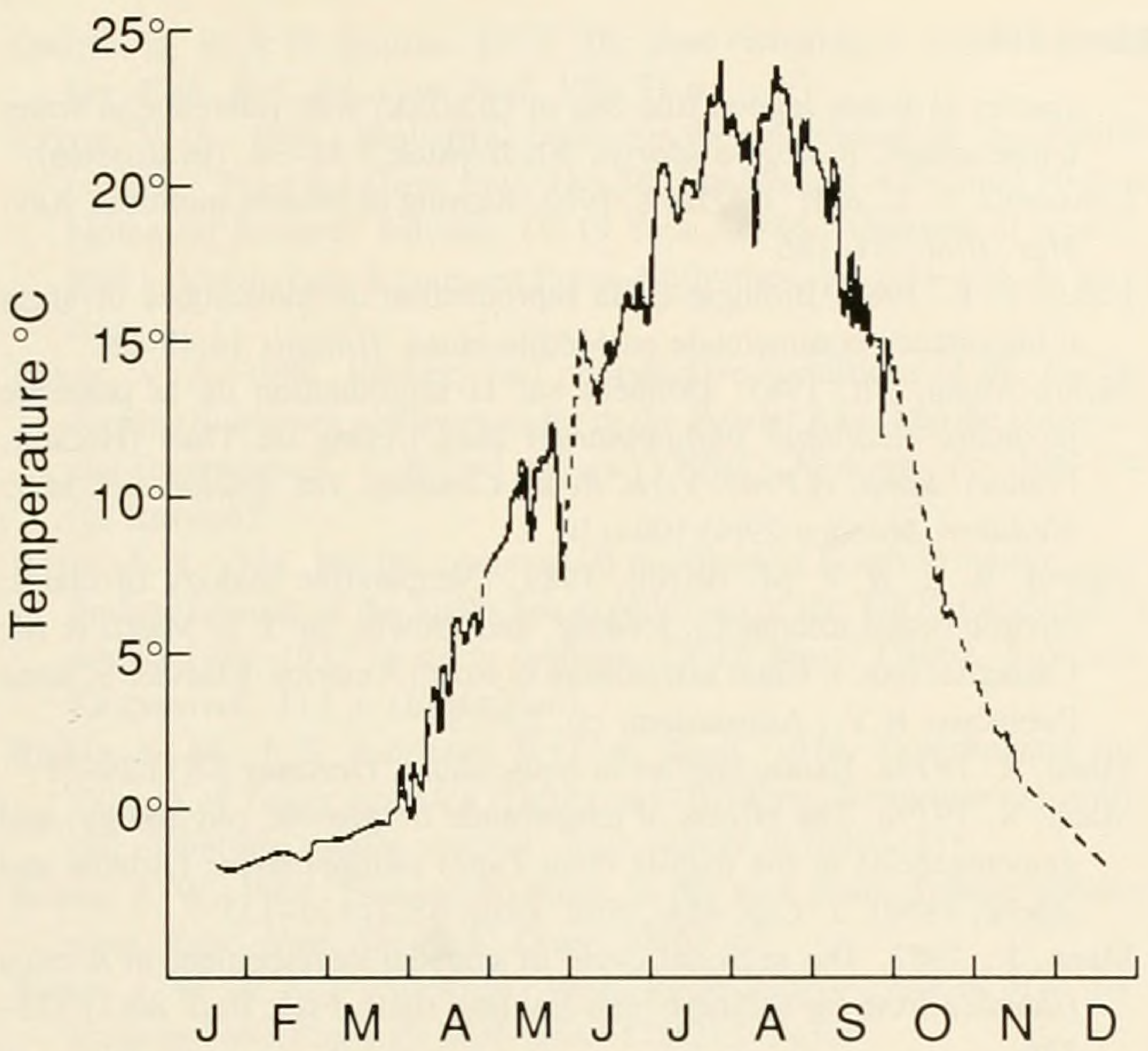

Figure 7. Seasonal changes in surface water temperatures (depth 0–0.5 m) in Vostok Bay during 1985.

a shell length of 10–15 mm (Ko 1957 cit. in Holland & Chew 1974, Yap 1977, Qi & Yang 1988).

Previous studies of the reproductive biology of *T. philippinarum* have shown that this species is dioecious (Bardach et al. 1972, Chew 1989, Eversole 1989, Devauchelle 1990). The number of hermaphrodites found in the present study and by other workers (Holland & Chew 1974) shows that this is an unusual phenomenon. Such unusual phenomena have been reported in other dioecious molluscan species (Ropes 1968, Naidu 1970, Bredge 1981, Mann 1982). However, Manila clams in some localities in the Sea of Japan show peculiar reproductive strategies. In Vostok (Stns. 3 and 4) and Possjet Bays all small (less than 15 mm shell length) individuals produced sperm during their first breeding season but in succeeding spawnings the number of males and females were equal but there was an excess of females in older (6–8 years) clams in some populations (Vladimir Bay and Stn. 4 samples in 1985 and Stn. 5A in Vostok Bay). Based on these statistically significant results we can assume that *T. philippinarum* is an alternative hermaphrodite in this region, according to Coe's classification (Coe 1943). The phenomenon of sex reversal may be connected with adaptation of this species to low boreal conditions in south Primorye.

Castration of Manila clams that is caused by the parasitic trematodes *Cercaria tapidis* and *C. pectinata* has been reported elsewhere in the literature (Rybakow 1983a and b).

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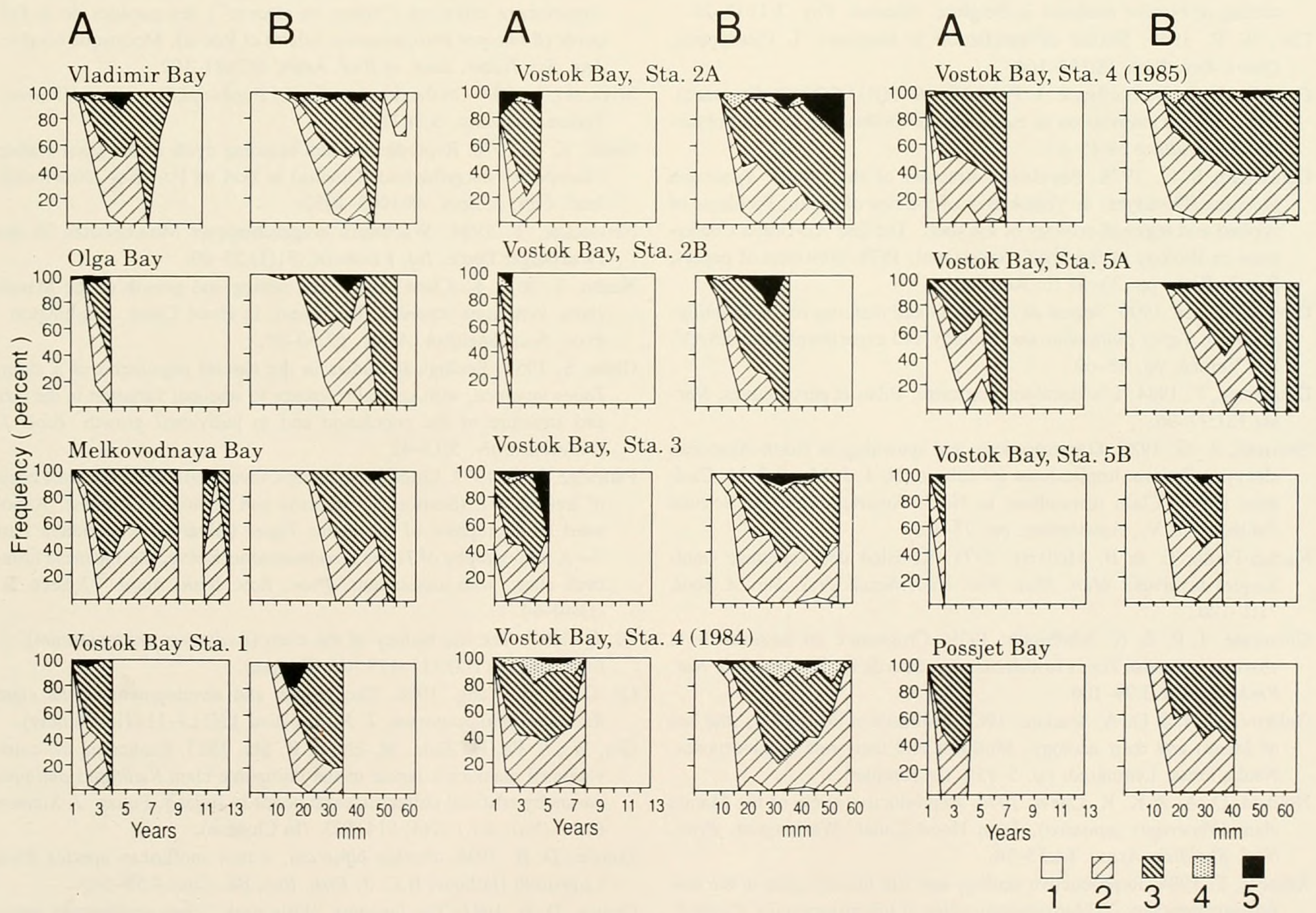

Figure 8. Stages of development in the gonadal cycle of manila clams, *Tapes philippinarum*, in Vostok Bay, 1985. 1. Active 2. Ripe 3. Partially Spent 4. Spent 5. Resting.

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