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香港未经净化的食用水管道中附着沼蛤的生殖周期*

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沼蛤 *Limnoperna fortunei* (Dunker, 1857) 是淡水贻贝科的一种软体动物。Miller 和 McClure (1931) 曾记录产于广东珠江，Morton (1975) 曾记录产于香港。

Limnoperna lacustris 可能是这一种的同物异名 (Habe, 1977)，曾分别报道产于长江南、北岸的洞庭湖(湖南省)和花马湖(湖北省)[41,8]以及长江的中、下游[13]一带。

Mizuno 和 Mori (1970) 记录了产于泰国 Kwai 河的同一种[19]。Brandt(1974) 记载了采自泰国 Sopa Falls, Pitsanuloke 的一个新种——*L. supoti* 和采自老挝、柬埔寨湄公河的另一个新种——*L. depressa*[5]。

沼蛤有可能成为与欧洲的饰贝 (*Dreissena polymorpha*)[11,22] 和美国的河蚬 (*Corbicula fluminea*)[40] 相类似的区域性重要淡水污损双壳类。沼蛤自 1965 年在香港大量繁殖以来，作者等对其解剖学、种群动态、附着和生长以及控制等方面进行了一系列的研究[23,25,26,32]。通过对这种贻贝类在香港的配子形成周期与船湾水库 28 个月期间的季节水文条件的研究，增加了我们对这种贻贝类的认识。

虽然沼蛤在香港不是严重的污损生物(在泰国也不是)，据中国未经证实的报道指出，在其分布范围的北部，这一种已成为有害的污损附着生物。

显然，沼蛤在中国的分布范围极为广泛，因此很有必要了解其在香港的配子形成周期、产卵季节和这些过程与水文的季节变化的相互关系，以便说明这一种在其分布区中部、亚热带部分的分布情况。

本文的研究结果为防止这种双壳类在家用、工业用和农业用淡水供应系统中的附着和对水质处理方法提供了极为重要的参考资料。

材 料 和 方 法

从 1971 年 10 月至 1974 年 2 月，每月平均从放置在船湾水库的试板上 (Morton 以前曾描述过，1977a) 采 10 个沼蛤标本。

在贻贝总科中，生殖腺不仅在外套膜中大量发育，而且在内脏块中也发育，从每一标本取一块组织，固定于布昂氏液 (Bouin's fluid)，作 6 微米厚的切片，用 Ehrlich 氏或 Heidenhain 氏苏木精染色。

从切片上看到的生殖腺，无论是雄或雌的发育指标均被确定为以下 5 期中的 1 期:

* 本文研究资料与有关船湾水库的水温和溶解氧资料均为香港政府公共工程部供水办公室提供的。
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1. 原胞期；2. 发育期；3. 成熟中期；4. 成熟期；5. 排放期。这些指标大致是根据 Loosanoff，Shaw[38,39] 和 Morton[31] 等划定的界限而确定的。

结　　果

沼蛤为雌雄异体，迄今尚未发现有雌雄同体者，总计 291 个体中有 100 个(即 34.3%)为雄体。沼蛤每年产卵两次。

1972—1974 年的 1 月和 2 月与 1972 年 8 月或 1973 年的 7 月和 8 月间，雄性和雌性生殖腺均不活跃，含有小的原精小管或卵泡(第 1 期)(图版 I: A1, B1)（表 1)，后者在卵泡中，稍发育的卵母细胞每个均具有一个清楚的囊状核和一个明显的在生殖上皮上的核，而在精小管则包含一个生殖上皮正在形成的圆形而轻度着色的直径 5 微米的原精母细胞。

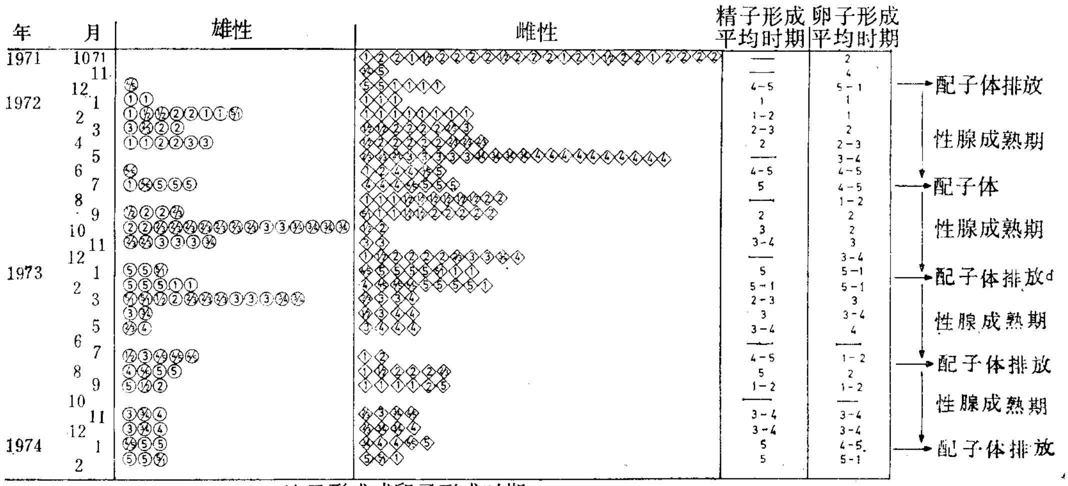
1972 和 1973 年，活跃的配子形成均开始于 3 月和 9 月。这时(第 2 期)(图版 I: A2, B2)(表 1)，精小管增大并在空腔中具有原精母细胞和更深染色的、直径为 2.5 微米的次级精母细胞，并带有少数直径为 1.5—2.0 微米的精子细胞。这时卵泡亦形成窄腔，腔壁产生宽柄的卵原细胞，其中有些直径达 10 微米。

每年 4—5 月和 10 月配子形成进行至第 3 期(图版 I: A3, B3)（表 1)，精小管和卵胞更增大，前者具有一些精子，后者具有窄柄的卵原细胞，这些卵原细胞的基部仍固着于卵胞壁上，其直径约 30 微米，具有一个增大而清晰的核和明显的核仁。

每年 5—6 月和 11—12 月，精巢和卵巢成熟(第 4 期)(图版 I: A4, B4)(表 1)，这时

表 1　沼蛤（*Limnoperna fortunei*）1971 年 10 月至 1974 年 2 月在香港船湾水库采获个体的性发育时期、配子形成平均时期和排放次数

Table 1. *Limnoperna fortunei*. The sex and stage of development of individuals collected from Plover Cove Reservoir, Hong Kong from October 1971 to February 1974. Mean stages of gametogenesis and times of spawnings are also given.



1→5 精子形成或卵子形成时期

○ —雄性　1 —— 原胞期　4 —— 成熟期
◇ —雌性　2 —— 发育期　5 —— 排放期
3 —— 成熟中

精小管具有很多初级和次级精母细胞和精子，但中腔（Central lumen）充满放射状排列、形成密板的拖鞋状的精子，它们的头伸向生殖上皮，其长鞭毛伸至腔中。卵胞充满分离的、有的直径达 60 微米的圆形卵，卵具有一个清晰的最大直径达 40 微米的囊状核，核中有一个着色深的、直径 10 微米的核，卵具少量卵黄，为少黄卵（Oligolacithal egg）。

在 1971 年 12 月，1972 年 7 月，1973 年 1 月、7 月和 1974 年 1 月，生殖腺排尽（第 5 期）(图版 I: A5, B5）(表 1)，包含经受整体萎缩的空的精小管和卵泡，并有像硬壳蛤（*Mercenaria*）和巨蛎（*Crassostrea*）[14,15] 与许多其他贻贝类[37]那样的配子细胞分解和再吸收现象。在香港，沼蛤第一次排空后其生殖上皮几乎即刻准备另一次的殖繁期。

图 1 表示配子形成和产卵与船湾水库平均水温的季节变化的关系，从图中可以看出这一种在春季水温上升时开始性成熟，1972 年和 1973 年 6 月，当水温分别上升到 25.5℃ 和 27℃ 时，生殖腺成熟，1972 年和 1973 年 6—7 月温度在 27—28℃之间时进行排放。

配子形成的第 2 期几乎立即开始，当温度从夏季高峰下降、接近秋季时，生殖腺逐渐成熟。1972 年和 1973 年 12 月，当平均水温分别下降到 19℃ 和 17.5℃ 时，生殖腺成熟并在 1—2 月温度最低，在 16—17℃ 时开始排放。

图 1 亦表示同一时期水库中溶解氧的季节变化，这正如我们所预料的：它和以前对河蚬[27]观察到一个明显地与温度相反的关系一样，即：在夏季水温高、溶解氧低时与在冬季水温低、溶解氧高时产卵。其它随温度的季节变化而变化的一些因子，像 Seed（1976）所论述的不同种的贻贝类一样，也影响配子形成和排放。

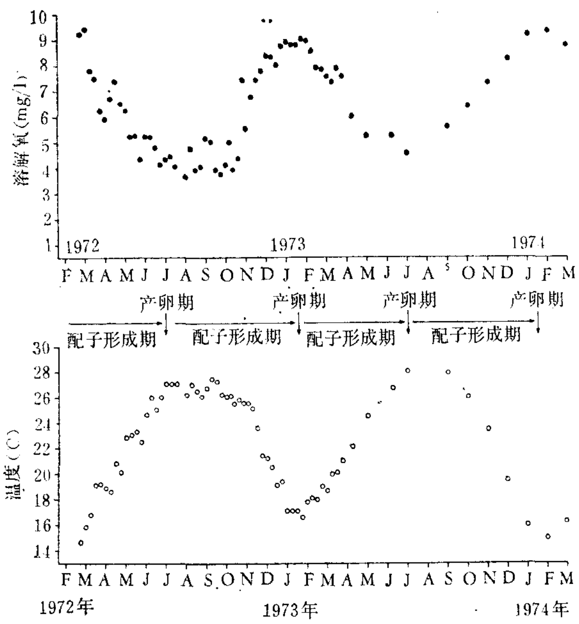


图 1 1972 年 2 月至 1974 年 2 月船湾水库沼蛤配子形成周期和排放与水温和溶解氧高低的关系

Figure 1. *Limnoperna fortunei.* The cycles of gametogenesis and spawning related to water temperature and dissolved oxygen level changes in Plover Cove Reservoir during the period February 1972 to February 1974.

讨　　论

通常双壳类，特别是淡水、河口和潮间带种类的配子形成和产卵过程与温度变化相关[35,12,36]，虽然常有其他相伴的水质变化，如 pH，盐度以及正如本文所指出的溶解氧等环境因子亦有关。因此，不能绝对地以某一单独因子或某一个多因子确定配子形成的开始和速率。经常各种外部因子，包括化学的和机械的刺激可以引起同时排放。一些潮间带种类的排放与月周期有关，牡蛎的传染性的排放可以由其他配子的进入而产生。虽然如此，温度应该被视为影响生殖周期的临界因子。这种临界温度在许多双壳类中是极为特殊的[34]。

通常浅水的双壳类一年繁殖一次或多次。在欧洲，*Dreissena polymorpha* 每年繁殖一次，在夏季水温高时排放[21]。同样，中国珠江的河蚬 *Corbicula* cf. *fluminalis* 也是在每年冬季水温降至最低时繁殖一次。而在船湾水库，河蚬每年则在初夏和秋季高温时先后繁殖两次[27]。美国引进的这一种，也保持其同样的繁殖式样[7,6]。

很难说明沼蛤，饰贝和蚬的一些种的繁殖式样与产地的关系，因为它们一般是“随意的”，甚至粗略地分为流水和静水都是不适当的，因为它们似乎都能在流水和静水中生活。

另一种区分适应于两种绝然不同环境的生物的方法曾被 MacArthur 和 Wilson (1967) 描述为 r 或 K-选择。属于 r-型的种类常居于高度变化的难以预料的境地，其中发育快成熟早产而生命期短的种为典型种。相反，属于 K-型的种类通常栖于可以预测的稳定产地，成熟慢，常延迟繁殖，其生命较长，很少有确切适合于这两个范畴的某一种生物，但沼蛤更接近于定为 r-型，它是短命的、早熟的且具有高繁殖力的[26]。同样理由，河蚬大概也是 r-型[6]，而 *C.* cf. *fluminalis*[31] 更适合定为 K-型。

然而，关于淡水双壳类的性的表现，这些一般的规律常被打破，如河蚬是雄性先熟的雌雄同体，即很多小的雄性个体与少数较老的雌体受精[27]，而 *C.* cf. *fluminalis* 是雌雄异体的，并有趋于雌性先熟的雌雄同体的趋势[31]。相反，*Dreissena polymorpha* 与沼蛤一样为雌雄异体[21]，虽然前者大约有 4.5% 的个体为雌雄同体[3]，但在这次调查中未发现沼蛤有雌雄同体的。

在河蚬[27]，其幼体在内鳃瓣孵化至 220μm (这种情形可能在 *C.* cf. *fluminalis* 亦有，但不经常)[31]。相反，*Dreissana polymorpha* 不在鳃间孵化幼体。刘、张、王、王报道[13]沼蛤在所有的 4 个鳃瓣孵卵，但在本文中我没有确定这一点。如果事实真是如此的话，在这种鳃丝仅由微弱的纤毛连接的贻贝是不寻常的[23]。

从很多方面看，沼蛤都是明显地与欧洲的饰贝 (*Dreissena polymorpha*) 几乎完全相同的亚洲种，但其产卵次数和时间却迥然不同，这可能是分布式样的不同所致。配子体形成和排放的基本进程，通常被认为是受温度支配的，其繁殖式样的变化常是因为居于整个分布范围的不同地区(虽然小生境相同)所致。因此，贻贝的繁殖随纬度变化而异[16,42]。南方种类在一年中通常繁殖较晚，并且向北逐渐缩短繁殖季节，而北方种类恰好相反，愈向南，产卵愈早，其繁殖季节延长，这也是一个一般的规律。然而，在所有这些情况下，一般只有一个繁殖季节，这一季节又可分为若干期，通常为两期。因此，贻贝在整个冬季配子形成，春季有部分排放，然后生殖腺很快成熟至初夏完全排放[36]。同样，*Dreissena polymor-*

pha 亦在夏季繁殖一次[30]，它同贻贝极其相似。在香港沿岸 *Anomalocardia squamosa* 在夏季各月中排放时，有一个高峰，可以分为两个期(Morton, 1978)，与巴西种 *A. brasilliana* 一样[33]。贻贝科的 *Musculista senhausia*，在香港也是一年排放一次，是在冬季温度低的时候[20]。*Mya arenaria* 主要在秋季，有时接着在第二年春季排放，如果有春季这次排放，其精子来自秋季排放保留的精子球 (Shaw, 1964, 1965)。

在船湾水库沼蛤是少见的，与河蚬相似。后一种通常在6月和7月释放幼虫，但因受精卵是在内鳃瓣孵化，所以排放发生较早，可能是在春季和夏末。然而沼蛤的性周期并不复杂，每年排放两次，极不寻常地与夏季最高温和冬季最低温相关。很清楚，升温和降温支配这一种的配子形成。两个温度标准 (大约 27—28℃ 和 16—17℃) 刺激排放。极端的温度可以阻止排放是众所熟知的，虽然这种情形看来在较暖的气候限制较少[2,10,20] (Young, 1945)，但温度的两个极端可以刺激排放则是较少知道的，以往记载双壳类的排放典型的是仅有一个临界温度范围，而这个范围每一种都是固定的[34]。

Limnoperna 的不寻常的生殖周期可以据其分布的资料说明，看来它在中国北部是广分布的[8,41]，但也分布在热带的泰国[4,19]，可能亦分布于老挝和柬埔寨[5]。陈[8]指出在花马湖 1959—1960 年温度变化于 8℃ (1 月) 和 30℃ (7 月) 之间，这是大陆水体的特征，与香港船湾水库的记录相近，可以想像在这里沼蛤亦有冬季和繁殖周期，然而，刘、张、王、王的观察指出[13]，在这种双壳类分布范围的北部仅在冬季 9—11 月，当温度界于 16—21℃时有一个繁殖周期，这就给这里提出的香港是 *Limnoperna* 整个分布范围的中部亚热带部分，且在北方它每年只有一个生殖周期出现的争论予以了某些支持，在南方 (即泰国、老挝、柬埔寨)它可以有更延长的夏季繁殖期。

在其整个分布范围内，搞清这种双壳类繁殖的详细研究是需要的，特别是 *Limnoperna* 有很大可能成为一个重要的污损种，这种双壳类的异筋类型和它在生境中以足丝开拓的特点，在其他淡水双壳类 (欧洲的 *Dreissena polymorpha* 除外)都没有的，这就已经肯定它是一个潜在的害虫，其广泛的繁殖潜力这一点是不容忽视的。

本文所包括的资料连同以前的沼蛤幼虫附着时期的资料[26]一起考虑，现在，至少是在其总分布范围的这一分布区内可以提出经济的控制方法。Morton, Au and lam[32] 曾确定有效控制 *Limnoperna* 的剩余的氯浓度，本资料确定了应用的时间。对控制淡水双壳类附着还有一些其他有效的方法[28,30]，本资料也对这些控制方法的应用有所帮助。

最后以警惕沼蛤意外地从其分布范围向外传播来结束本文。河蚬传至北美[6]的例子足以说明这个严重问题是可以发生的。在淡水水域中，一个种，若不控制它在所有可能生长环境中的迅速开拓和适当的生长方式及繁殖周期，这个种就可以成为一个真正的灾害。

(齐钟彦 译， 邓 昂 校)

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THE REPRODUCTIVE CYCLE IN *LIMNOPERNA FORTUNEI* (DUNKER 1857) (BIVALVIA: MYTILIDAE) FOULING HONG KONG'S RAW WATER SUPPLY SYSTEM

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Limnoperna fortunei (Dunker 1857) is a freshwater mytilid and has been recorded from the Pearl River around Canton (People's Republic of China) by Miller and McClure (1931) and from Hong Kong (Morton, 1975).

Limnoperna lacustris, which is probably synonymous with *L. fortunei* (Habe, 1977) has been reported from Dongting Lake (Hunan province) and Lake Huama (Hubei province) respectively located south and north of the Changjiang River (Yangtze River) (Tchang Si and Liu, 1955; Chen, 1979). It also inhabits the middle and lower reaches of the Yangtze itself (Liu, Zhang, Wang and Wang, 1979).

Mizuno and Mori (1970) record the same species from the Kwai River, Thailand. Brandt (1974) records a new species, *L. supoti,* from Sopa Falls, Pitsanuloke, Thailand, and a further new species, *L. depressa,* has been recorded from the Mekong River of Laos and Cambodia (Brandt and Temcharoen, 1971).

L. fortunei has the potential to become a freshwater fouling bivalve of regional importance comparable with *Dreissena polymorpha* in Europe (Morton, 1969b; Kerney and Morton, 1970) and *Corbicula fluminea* in the U.S.A. (Sinclair and Isom, 1963).

A series of studies (Morton, 1973; 1975; 1977a; Morton, Au and Lam, 1976) has elucidated aspects of the anatomy, population dynamics, settlement and growth, and control of *Limnoperna fortunei* following its colonisation of Hong Kong in 1965. This study adds to our knowledge of this unique mytilid by investigating its cycle of gametogenesis in Hong Kong and relating this to the seasonal hydrological conditions prevailing in Plover Cove Reservoir over a period of 28 months.

Though *L. fortunei* is not a serious fouler in Hong Kong (nor Thailand), unconfirmed reports from the People's Republic of China indicate that in the northern parts of its range, the species has become a fouling pest.

Clearly *L. fortunei* occurs over a very wide range in China and it is therefore important to establish the cycle of gametogenesis, the season of spawning and the relationship between these processes and seasonal hydrological changes in Hong Kong as representative of the species in the middle, sub-tropical component of its range.

Such information is important because it allows for the selective treatment of raw water to prevent settlement of the bivalve within freshwater domestic, industrial, and agricultural water supply systems.

MATERIALS AND METHODS

On average, 10 specimens of *Limnoperna fortunei* were collected every month from test panels (earlier described in Morton, 1977a) immersed in Plover Cove Reservoir, Hong Kong, over the period from October 1971 to February 1974 inclusive.

In the Mytilacea, the gonads develop largely in the mantle but also in the visceral mass and a piece of tissue was removed from each specimen, fixed in Bouin's fluid, sectioned at 6 μm and stained in either Ehrlich's or Heidenhain's haematoxylin.

The gonads, as seen in the sections, were assigned to one of 5, either male or female development indices approximately equivalent to either 1, primordia; 2, developing; 3, maturing; 4, mature or 5, spent. These indices are based approximately upon those defined by Loosanoff (1937; 1942), Shaw (1964; 1965) and Morton (1982) and will be defined later.

The data obtained from the above study has been considered in relation to water temperature and dissolved oxygen levels in Plover Cove Reservoir and routinely obtained by the Water Supplies Office of the Public Works Department of the Hong Kong Government.

RESULTS

Limnoperna fortunei is dioecious; no hermaphrodites have been found. Of a total of 291 individuals, 100 or 34.3% were male. *L. fortunei* spawns twice every year.

During January and February (of 1972, 1973 and 1974) and again in August or July and August in 1972 and 1973 respectively, both male and female gonads were inactive and comprised small, primordial seminiferous tubules or ovarian follicles (Category 1) (Plate I: A1; B1) (Table 1). In the latter, small developing oocytes each with a clear vesicular nucleus and a distinct nucleolus line the germinal epithelium while the former comprises a germinal epithelium producing round, lightly staining, primary spermatocytes 5 μm in diameter.

In both 1972 and 1973 active gametogenesis began in March and September. At these times (Category 2) (Plate I, A2; B2) (Table 1) the seminiferous tubules had enlarged and possessed primary and, more darkly staining, secondary spermatocytes 2.5 μm in diameter with a few spermatids 1.5—2.0 μm in diameter occurring in the lumen. At this time also the ovarian follicles possed narrow lumina, the walls of which were producing broadly stalked oogonia, some of which were 10 μm in diameter.

By April—May and October of each year, gametogenesis (Category 3) (Plate I: A3; B3) (Table 1) was progressing, the tubules and follicles were much larger and possessed in the former case a number of spermatozoa and, in the latter case, narrowly stalked oogonia, still basally attached to the follicle wall and approximately 30 μm in diameter with an enlarged clear nucleus, with a distinct nucleolus.

The testis and ovary were considered ripe (Category 4) (Plate I, A4; B4) (Table 1) from May to June and from November to December in each year. At these times the seminiferous tubules possessed many primary and secondary spermatocytes and spermatids but the central lumen was full of slipper-shaped spermatozoa, arranged in radial cords, forming dense lamellae, their heads projecting towards the germinal epithelium, their long flagellae into the lumen. The follicles were packed with, detached, rounded eggs some 60 μm in diameter possessing a clear, vesicular nucleus a maximum of 40 μm in diameter with a darkly staining nucleus 10 μm in diameter. The eggs possess but a little yolk and are thus oligolecithal.

By December 1971, July 1972, January and July 1973 and January 1974, the gonads were spent and comprised (Category 5) (Plate I, A5; B5) (Table 1) empty tubules and follicles undergoing a general reduction in overall size and with cytolysis and reabsorption of gametes as occurs in *Mercenaria* and *Crassostrea* (Loosanoff, 1937; 1942) and most other mytilids (Seed, 1976). In *L. fortunei*, in Hong Kong, the germinal epithelium almost immediately, prepares itself for another phase of activity.

From Figure 1, which relates gametogenesis and spawning to seasonal changes in mean water temperature in Plover Cove Reservoir, it can be seen that the species begins to sexually mature in the Spring as water temperatures progressively rise. By June 1972 and 1973 when the temperature had reached 25.5°C and 27°C respectively the gonads were mature and from June to July in both 1972 and 1973 spawning took place at temperatures of between 27—28°C.

A second phase of gametogenesis begins almost immediately, the gonads progressively maturing as the temperature falls from the Summer high, with the approach of Autumn. By December 1972 and 1973 when the mean water temperature had fallen to 19.5°C and 17.5°C respectively, the gonads were mature and typically, in January to February, spawning began when temperatures were lowest and between 16°—17°C.

Figure 1 also shows the seasonal variation in dissolved oxygen levels in the reservoir over the same period. This demonstrates, as would be expected, a clear inverse relationship with temperature so that as noted earlier for *Corbicula fluminea* (Morton, 1977b) spawning takes place at times of high temperature and low dissolved oxygen levels in summer and at low temperatures with high dissolved oxygen levels in winter. Other factors may also vary with seasonal changes in temperature and could also influence gametogenesis and spawning as reviewed for various mytilids by Seed (1976).

DISCUSSION

Generally, the processes of gametogenesis and spawning in the Bivalvia, especially freshwater, estuarine and intertidal species, are related to changes in temperature (Orton, 1920; Kinne, 1963; Seed, 1975), though there is often other associated water quality changes, e.g. pH, salinity and, as this study has shown, dissolved oxygen, so that it is not absolutely certain whether a single or a multiplicity of factors determines the onset and rate of gametogenesis. Very often simultaneous spawning may be triggered by a variety of extraneous factors including chemical and mechanical stimuli. Some intertidal species spawn in relation to lunar cycles. Epidemic spawning in oysters may result from inhalation of other gametes. Nevertheless temperature must be seen as the critical factor responsible for and influencing the broader aspects of the reproductive cycle. In many bivalves this critical temperature is extremely specific (Nelson, 1928).

Generally, shallow water bivalves reproduce one or more times a year. Thus, in

Europe, *Dreissena polymorpha* reproduces once a year, spawning in Summer when temperatures are high (Morton, 1969a). Similarly *Corbicula* cf fluminalis from the Pearl river, People's Republic of China, breeds once a year, but when temperatures are falling to a Winter minimum (Morton, 1981). On the other hand, in Plover Cove Reservoir, *Corbicula fluminea* spawns twice a year, in early Summer and Autumn, again when temperatures are high (Morton, 1977b). In the introduced component of its range- the U.S.A.- a similar breading parttern is maintained (Aldrich and McMahon, 1978; Britton *et al.*, 1979).

It is very difficult to relate breeding patterns in *Limnoperna*, *Dreissena* and species of *Corbicula* to habitat, because they are generally "opportunistic", even the broad divisions of lotic and lentic are inappropriate because they all seem capable of living in both running and standing water bodies.

Another way of classifying organisms adapted to one or other of two habitat extremes has been described by MacArthur and Wilson (1967) as r and K-selection. r strategists occupy highly variable, often unpredictable habitats, in which rapid development and early reproduction in a short-lived species is typical. Conversely, K strategists occupy stable, usually predictable habitats and are slow to mature often with delayed reproduction and have longer life spans. Few organisms fit exactly into one or other of these categories, but *Limnoperna fortunei* is more closely identifiable as an r-strategist being short lived, maturing early and with a high fecundity (Morton, 1977a). For similar reasons, *Corbicula fluminea* is probably also an r-strategist (Britton and Morton, 1979) whereas *C.* cf. *fluminalis* (Morton, 1982) is more appropriately defined as a K-strategist.

These generalizations often break down, however, with regard to the expression of sexuality in freshwater bivalves. Thus, *Corbicula fluminea* is a protandric hermaphrodite i.e. many small males fertilizing a few established older females (Morton, 1977b) while *C.* cf. *fluminalis* is dioecious with a tendency towards protogynous hermaphroditism (Morton, 1981). On the other hand *Dreissena polymorpha* is dioecious (Morton, 1969a) as is *Limnoperna fortunei,* though in the former case but not the latter approximately 4.5% of individuals are hermaphrodite (Antheunisse, 1963). No hermaphrodites have been found in this survey of *Limnoperna fortunei.*

In *Corbicula fluminea* (Morton, 1977b), the young are incubated in the inner demibranch to a length of 220 μm (this facility is also possibly possessed but rarely used in *C.* cf. *fluminalis*) (Morton, 1981). Conversely *Dreissena polymorpha* does not incubate its young. Liu, Zhang Wang and Wang (1979) report that *L. fortunei* incubes eggs within all four demibranchs, but I have not confirmed this in this study and if true would represent a most unusual facility on the part of this mytilid with ctenidial filaments only weakly united by ciliary junctions (Morton, 1973).

Limnoperna fortunei is clearly in most respects the almost exact Asian equivalent of the European *Dreissena polymorpha* but with strong differences in the number and timing of spawnings possibly resulting from differences in distribution pattern.

Just as temperature is generally considered to order the basic processes of gametogenesis and spawning so it is also conceded that variations in breeding pattern often result from occupation of the same niche but in different components of the total range. Thus, reproduction in *Mytilus* varies with latitude (Wilson and Hodgkin, 1967; Lubet and Le Gall, 1967). It is also a general principle that southern species usually reproduce later in the year and have a progressively restricted season further northwards whereas northern species exhibit the reverse trend——spawning earlier and with a more extended season further south. In all of these cases, however, it is general that there is but a single reproductive season that may be divided into a number of phases, usually two. Thus gametogenesis in *Mytilus edulis* occurs over Winter and there is a partial spawning in the Spring with the gonad then rapidly maturing to fully spawn in early Summer (Seed, 1975). Simitarly *Dreissena polymorpha* reproduces once a year, again in Summer (Morton, 1979a) and thus closely matches *Mytilus edulis*. On Hong Kong shores, *Anomalocardia squamosa* spawns during the Summer months in a single peak that may be divided into two phases (Morton, 1978) as in the Brazilian species *A. brasiliana* (Narchi, 1976). The endobyssate mytilid *Musculista senhausia* also spawns once a year in Hong Kong, but in Winter when temperatures are low (Morton, 1974). In *Mya arenaria,* a major Autumn spawning is sometimes followed by a 2nd Spring spawning, the spermatozoa of this spawning, when it occurs, derived from sperm balls retained from the Autumn spawning (Shaw, 1964; 1965).

Limnoperna fortunei is unusual but resembles *Corbicula fluminea in* Plover Cove Reservoir. In the latter species larval release takes place generally in June and January, but because the fertilized eggs are retained within the inner demibranch spawning takes place earlier, probably in Spring and late Summer. In *Limnoperna* fortunei, however, where the sexual cycle is uncomplicated, spawning occurs twice and is, most unusually, correlated with Summer maximum and Winter minimum temperatures. Clearly a rising *and* a falling temperature order gametogenesis in this species and that two temperature criteria (approximately 27—28°C and 16—17°C) stimulate spawning. It is well known that extreme temperatures may inhibit spawning, though these seem to be less limiting in warmer climates (Young, 1945; Allen, 1955; Heinonen, 1962; Moore and Reish, 1969), but less well known that two extremes of temperature may stimulate spawning. As noted earlier spawning in bivalves typically only occurs over a single critical temperature range that is constant for each species (Nelson, 1928).

The unusual reproductive cycle of *Limnoperna* may be accounted for by reference to its distribution. It seems to be widely distributed in the north of China (Tchang, Li and Liu, 1955; Chen, 1979) and yet occurs in tropical Thailand (Mizuno and Mori, 1970; Brandt, 1974) and possibly in Laos and Cambodia (Brandt and Temcharoen, 1971). Chen (1979) has shown that in Lake Huama, the temperature (in 1959—1960) ranged between 8°C in January and 30°C in July. These figures characteristic of a "continental" water body, approximate those recorded from Plover Cove Reservoir Hong Kong and one would thus expect *L. fortunei* here to also possess winter and breeding cycles. The observations of Liu, Zhang, Wang and Wang (1979), however, indicate that but a single reproductive cycle occurs in the northern part of this bivalve's range, in Winter, from September to November when temperatures are between 16—21°C. This gives some measure of support to the contention here put forward that *Limnoperna* in Hong Kong is in the middle sub-tropical component of its total range and that in the north it breeds but once per annum. In the south (i.e. Thailand, Laos, Cambodia) it may have a more extended Summer breeding programme.

Clearly research is needed to clarify the reproductive strategy of this bivalve over its total range especially as *Limnoperna* has a very great potential to become a fouling species of importance. The heteromyarian form of this bivalve, its exploitation of an epibyssate niche not colonised by other freshwater bivalves (except *Dreissena polymorpha* in Europe) already confirms it as a potential pest; a wide reproductive potential magnifies this.

The information contained within this paper when considered together with earlier information on the time of larval settlement in *Limnoperna fortunei* (Morton, 1977a) does now, however, allow for the economical application of control procedures, at least within this component of its total range. Morton, Au and Lam (1976) have defined residual chlorine concentrations effective in the control of *Limnoperna*, the present information defines the time of application. A variety of other control methods are available to control settlement of freshwater bivalves (Morton, 1977c; 1979). This information assists application of these controls also.

Finally this paper concludes with a warning against the accidental introduction of *Limnoperna fortunei* outside its home range. The example of *Corbicula fluminea* introduced into North America (Britton and Morton, 1979) should suffice to demonstrate the grave problems that may arise. A species unrestrained from the controls that normally hold it in check rapidly comes to colonise almost all available niches in the freshwater domain and with adjusted growth patterns and breeding cycles can be a very real pest.

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图 版 说 明

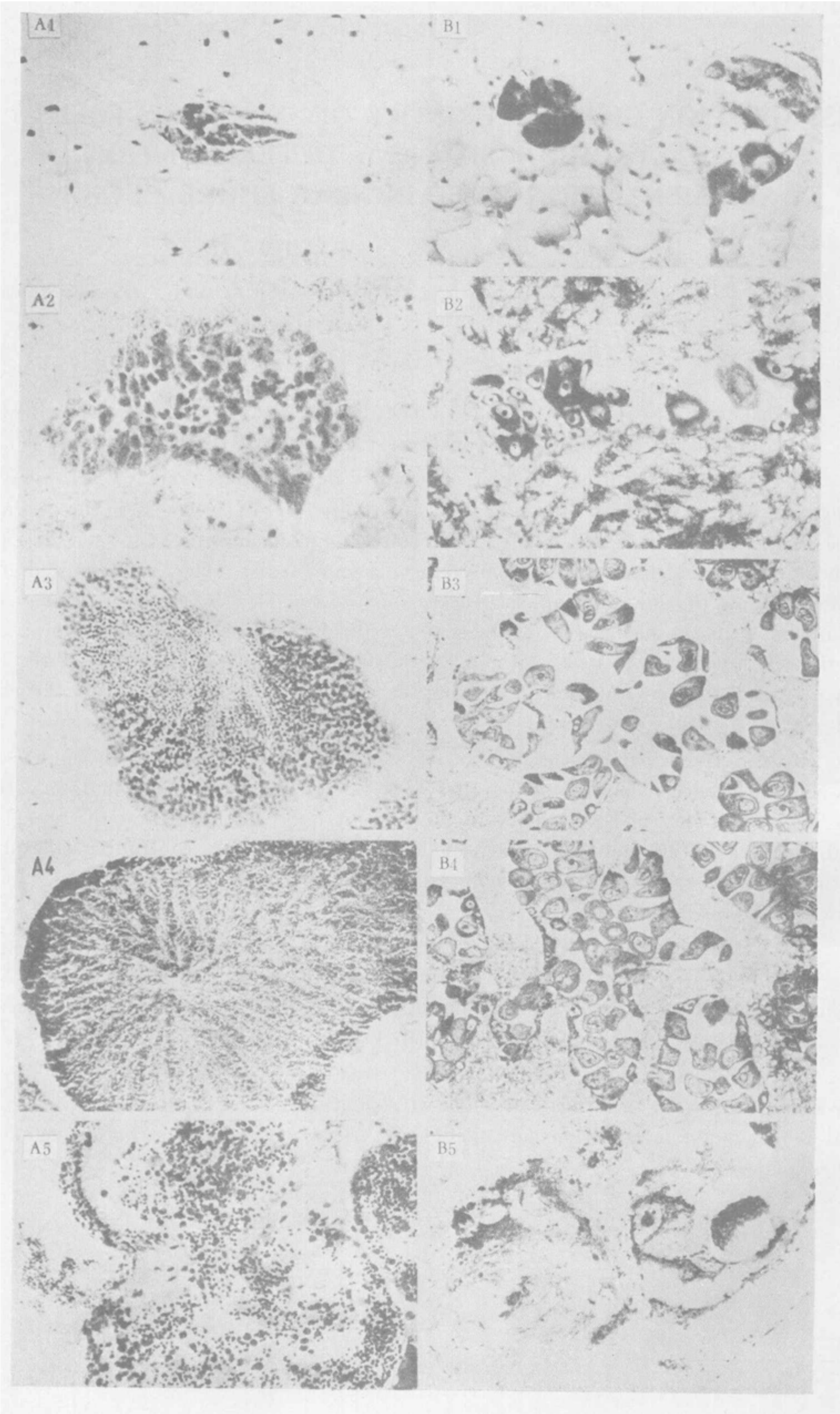
Explanation of Plate

图版 I 沼蛤配子形成五个时期的显微照片

A. 雄性; B. 雌性。

1. 原胞期; 2. 发育期; 3. 成熟中期; 4. 成熟期; 5. 排放期。

Plate I. *Limnoperna fortunei*. Photomicrographs of the five stages of gametogenesis in A, males and B, females: 1. primordia; 2. developing; 3. maturing; 4. mature; 5. spent.


A1
B1
A2
B2
A3
B3
A4
B4
A5
B5