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Original Article

Reproductive cycle of *Laevistrombus canarium* (Littorinimorpha: Strombidae) in Krabi Province, Andaman Sea, Thailand

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Abstract: The mesogastropod *Laevistrombus canarium*, or dog conch, is a commercially valuable species in the Indo-Pacific region. However, there is no information on its reproductive cycle in Thailand. From December 2012 to January 2014, specimens of dog conch were sampled monthly from Ao Thung beach, on the Andaman Sea, southern Thailand. Seawater pH, temperature and salinity during the sampling period ranged 6.97-8.1, 28-30.8°C, and 27-34 ppt, respectively. Spawning times were investigated through standard gonadal histology and calculation of the gonad index (GI). The population's sex ratio departed from 1:1 and females dominated. Five stages of gonad development were found in both sexes: resting, developing, mature, spawning and spent. Monthly variations in these stages and GI showed that this species exhibited two major spawning periods: December to April and August to September, and synchronicity existed between the sexes. However, spawning in females was less frequent and of shorter duration than in males. The results also revealed that spawning times of *S. canarium* were not related to the environmental conditions recorded at the study site. The present study classified this population of *L. canarium* that spawn in two clear pulses. The collected data provide baseline information to manage the resources and conservation of *L. canarium* in the Andaman Sea.

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Introduction

The dog conch, *Laevistrombus canarium* L., 1758, of the family Strombidae is an economically significant mesogastropod species. Indigenous to the Indo-Pacific region, this species occurs from southern India eastward to Melanesia, from Japan in the north to Australia in the south (Abbott, 1960; Poutiers, 1998). In many parts of Southeast Asia, *L. canarium* is found within seagrass beds and lives on muddy and sandy bottoms (Cob et al., 2008a, 2009c; Uneputty et al., 2021). The dog conch is a delicacy and popular seafood in Southeast Asia. It is also traditionally picked for its shell, which has decorative value (Poutiers, 1998; Said et al., 2013).

Due to the commercial value of *L. canarium*, many aspects of its biology have been extensively determined, including age, growth, survival, distribution, mortality, sexual maturity, sex determination, population structure, species description, imposex, sex ratio, food consumption, polyculture, and metal accumulation (Cob et al., 2008b, 2009a, b, c, 2011; Hassan et al., 2019; Ramses et al., 2019; Maxwell et al., 2020; Chang et al., 2021; Kobkeatthawin et al., 2021). However, studies of its reproductive cycle are relatively scare. Most information in this field has generally been found elsewhere in the Strombidae family, particularly in the economically important Caribbean species. Data for *Strombus gracilior* from Conception Bay, Baja California, and Mexico show two main spawning periods (Aranda et al., 2003a). *Strombus pugilis* from Seybaplaya to Campeche city, Mexico exhibited continuous spawning (Aranda et al., 2003a; Cardenas et al., 2005). *Aliger gigas* from the Alacranes reef and Banco Chinchorro, Quintana Roo, Mexico (Aranda et al., 2003a, b) and the Caribbean region (Boman et al., 2018) displayed one short spawning, whereas *A. gigas* from the Archipelago of San Andres, Providencia and

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Santa Catalina, Colombia displayed two main spawning periods (Avila-Poveda and Baqueiro-Cárdenas, 2009).

By comparison, data on the reproductive cycle of *L. canarium* in the Indo-Pacific region is limited despite the fact that it is a commercially exploited species. Indeed, only the reproductive cycle of *L. canarium* in waters of the Philippines has been investigated, where continuous spawning behavior was identified (Libutaque, 2000). The current work aims to describe the reproductive cycle of *L. canarium* off Ao Thung beach, Andaman Sea, Thailand. The information from the current study will be crucial to managing the fishing and conservation of dog conch in the region. Environmental factors, sex ratio, gonad developmental stages, and spawning periods were investigated.

Figure 1. Location of sampling site of *Laevistrombus canarium* off Ao Thung beach, Krabi province, Thailand.

Materials and Methods

Study site and sampling: Specimens of dog conch were collected from Ao Thung beach, Krabi Province on the Andaman Coast of southern Thailand (8°02'N, 98°45'E) (Fig. 1). At monthly intervals during a 14-month study period (December 2012 – January 2014), thirty to forty adult individuals were collected randomly by hand among seagrass beds during low tide. Using a thermometer, manual optical refractometer, and pH meter, respectively, sea temperature, salinity, and pH within each sampling site were measured at a 2 m depth during specimen collection.

In the laboratory, the total weight (TW) of whole individuals was measured with a digital balance (with a precision of 0.001 g), and shell length (SL) and shell width (SW) were measured using a vernier caliper to the nearest 0.05 mm. After breaking the shell in a vice, the soft part of the specimens was separated, the flesh weight (FW) was measured and individuals were sexed. Males were recognized by the presence of a penis and a prostate gland, and females were recognized by the presence of a vagina and a capsule gland.

Reproductive cycle and gonad index: For histological investigations of the gonads, small pieces of the tissue were removed and fixed in Bouin's solution. After 24 hours, the collected tissues were rinsed with tap water and preserved in 70% ethyl alcohol. The gonad samples were dehydrated using a sequence of ascending alcohol series (70-100%), cleared with xylene, and embedded in paraplast. Sections of 6 μm thick were cut with a rotary microtome and counterstained with Harris's haematoxylin-eosin. All sections were observed under a light microscope. Identifying the stages of gonadal development was based on the categories defined for *A. gigas* by Aranda et al. (2003b) and *S. pugilis* by Cardenas et al. (2005). These categorizations comprised five stages: resting, developing, mature, spawning, and spent. Mean gonad indices (GI) were calculated based on the methods described by King et al. (1989) using the following formula:

GI = sum [number of specimens in each stage x numerical ranking of that stage] / [total number of specimens in the sample].

The gonad index would vary from 1 (minimum) if all specimens were resting and/or spent to 3 (maximum) if all specimens were mature.

Statistical analysis: The difference in the sex ratio was evaluated monthly using the Chi-square test in SPSS program version 28.0.1 for Windows.

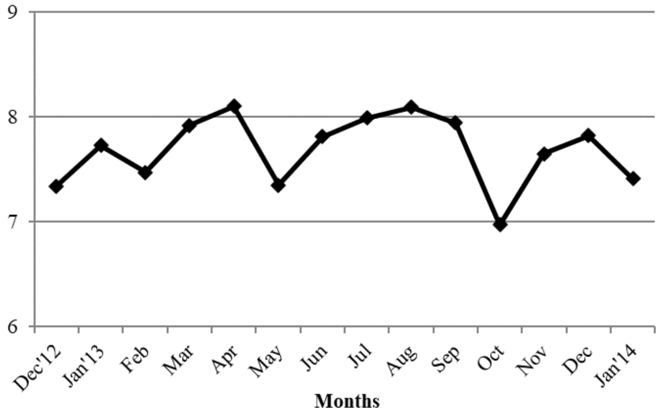

Figure 2. Monthly variation in the pH level of seawater at the sampling site off Ao Thung beach, Krabi province from December 2012 to January 2014.

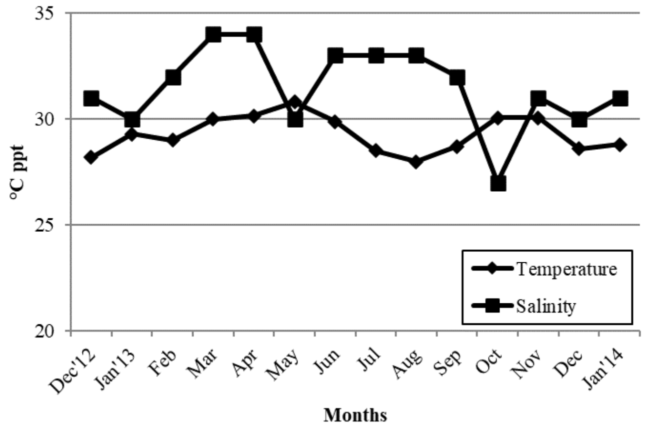

Figure 3. Monthly seawater temperature (°C) and salinity (ppt) at the sampling site off Ao Thung beach, Krabi province from December 2012 to January 2014.

Results

Environmental parameters: The pH of the seawater in the study area fluctuated between a high of 8.10 in April 2013 and a low of 6.97 in October 2013 (Fig. 2). From December 2012 to February 2013, water temperatures ranged from 28.20 to 29.30ºC, then steadily increased during March (30ºC) to reach the maximum temperature of 30.8ºC in May (Fig. 3). From June (29.87ºC), temperature declined to the minimum of 28ºC, recorded in August. The temperature increased to 28.7ºC in September and reached a steady level of 30.1ºC during October and November. In December 2013 and January 2014, the last two months of the study, sea temperature dropped to 28.6 and 28.8ºC, respectively. In December 2012, the salinity of the seawater was 31 ppt. There was a slight decrease to 30 ppt in January 2013 (Fig. 3). Salinity increased in February (32 ppt). It continued through March and April to reach the maximum level of 34 ppt. Salinity declined steeply in a single month from 34 ppt in April to 30 ppt in May but rapidly rose again to reach a steady level of 33.00 ppt through June, July and August. In September, salinity slightly decreased to 32 ppt and fell abruptly in October to the minimum of 27 ppt. During November and December 2013 and January 2014, the last three months of the study, salinity returned to levels similar to those of the previous year, ranging 30-31 ppt.

Gonad developmental stages: Gonad development in both sexes could be classified at the microscopic level into five distinct stages according to the number of different germ cells and the percentage of connective tissue between testicular tubules and/or ovarian follicles.

Testis: The testis is composed of testicular tubules. The five histological stages of the testis are described as following:

Resting stage: In this phase, testes comprised mostly reticular connective tissue, which occupied 90% of the testes. Few testicular tubules were found, and they were relatively small and irregularly shaped (Fig. 4A). They were mainly composed of the spermatogonia, which lined the thickened tubular wall and had started to fill with primary and secondary spermatocytes.

Developing stage: In this stage, about 80% of the testes were occupied by connective tissue. The testes had abundant testicular tubules which had increased in diameter and were filled with maturing cells in all stages of development (Fig. 4B). Spermatogonia were present in smaller numbers and, having grown, separated from the tubular walls and appeared in the lumen. Male germ cells within the testicular tubules were mostly primary spermatocytes, secondary spermatocytes, and dark-colored spermatids near the middle of the lumen. Spermatozoa were occasionally observed in the lumen but were not well arranged.

***Mature stage*:** The testes contain numerous expanded testicular tubules. Connective tissue occupied the testicular tubules walls and markedly decreased in size (Fig. 4C, D). The testicular tubules were typically

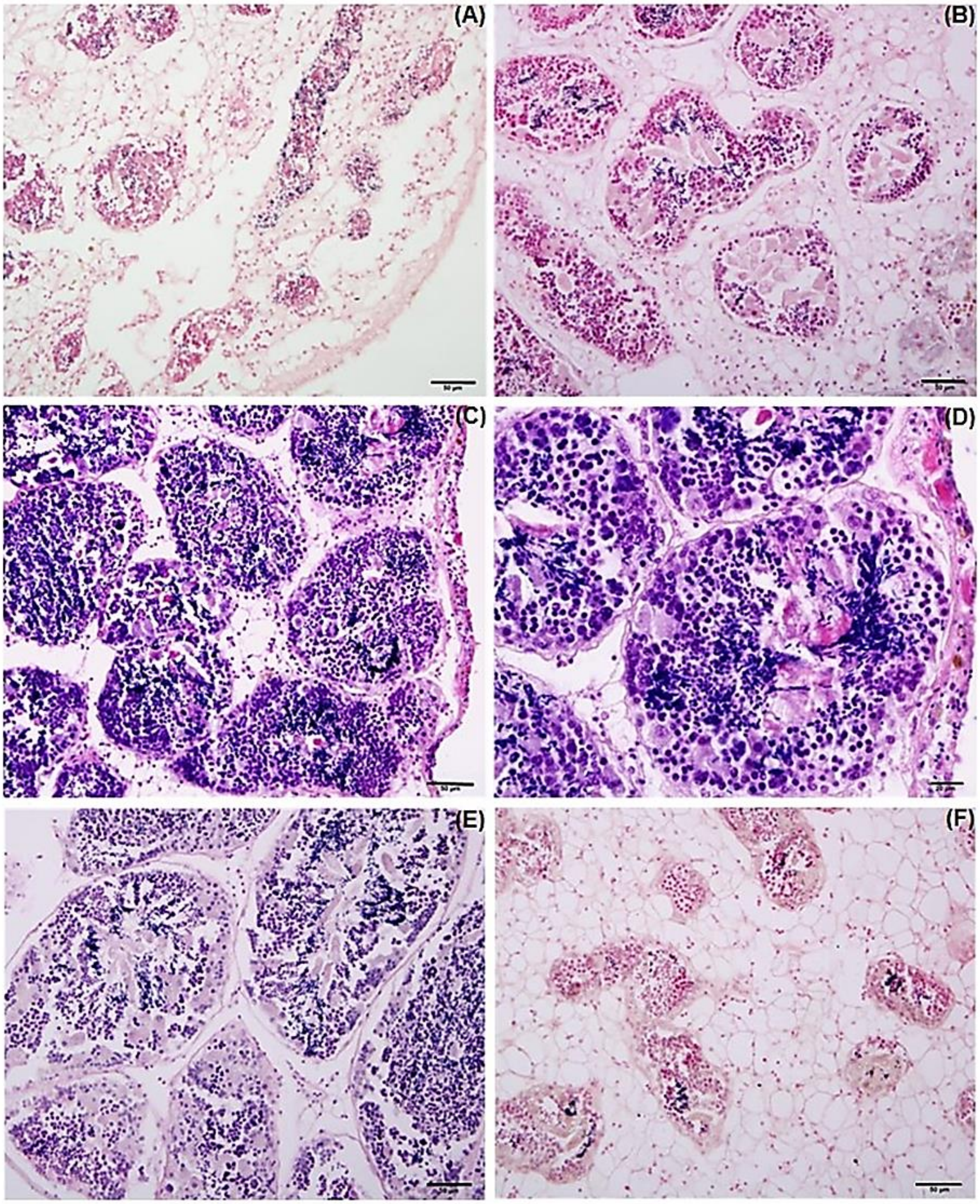

Figure 4. Photomicrographs of testicular phases of collected male dog conchs stained with H&E: (A) resting stage; (B) developing stage; (C and D) mature stage; (E) spawning stage; (F) spent stage. Scale bars = 50 μm (A, B, C, E, and F) and 20 μm (D).

fused, and apparent cells were spermatids and mature spermatozoa, which were more numerous than spermatids and formed a compact mass with the tails close to the middle of the lumen. In contrast, spermatogonia were scarce and close to the tubular walls, and spermatocytes were also less abundant than spermatozoa.

Spawning stage**:** The testicular tubules continued to fuse. A dense band of spermatozoa at the center of tubular lumens was still apparent but spermatozoa were less than in the mature stage because some had been discharged and were located in the testis duct

(Fig. 4E). The release of these spermatozoa caused empty spaces in the testicular tubules. At the same time, the walls of the testicular tubules erupted, resulting in the formation of large irregular lumens containing cells at almost all stages. Most of the lumen was empty, and although some spermatids remained, they were fewer in number than at the previous stage.

Spent stage**:** The testes had collapsed and degenerated. The testicular tissue was inhabited by reticular connective tissue. This stage was distinguished by broken and degenerated testicular tubules with mostly empty lumens that contained some reproductive cells at different stages of development (Fig. 4F). Very few spermatogonia were found close to tubular walls, and remaining spermatozoa were visible in the lumen. Abundant phagocytes were observed among the rest of the testicular tubules and residual reproductive cells.

Ovary: The ovary is composed of ovarian follicles. The five histological stages of the ovary are described in the following.

Resting stage**:** Ovaries presented mostly reticular connective tissue that occupied 90% of the ovaries. It was hard to distinguish this tissue from digestive gland tissue. Low numbers of irregularly shaped follicles were found in this stage (Fig. 5A). Follicles mainly were lined with oogonia and a few small, developing pre-vitellogenic oocyte buds from the follicular wall.

Developing stage**:** Ovaries became thicker and occupied 30% of the ovarian section. The follicles were well-developed and contained reproductive cells in all stages of development: oogonia, pre-vitellogenic oocyte, vitellogenic oocyte and mature oocyte (Fig. 5B). Oogonia were found in clusters of four to five cells and they had a spherical nucleus with a clear nucleolus. In the early stage, small ovaries and thickening follicles were evident. These follicles were mainly filled with pre-vitellogenic oocytes. In the late stage, the ovary was larger, and vitellogenic oocytes and mature oocytes were usually present in the follicles.

Mature stage**:** As the ovary ripened, occupying 40-50% of the section, ovarian follicles were spherical, and their thin walls exhibited no germinal cells. The connective tissue between follicles had almost disappeared (Fig. 5C, D). In this stage, most of the follicles were in contact with other follicles, and some had fused to form a large lumen. Most follicles were filled with vitellogenic and mature oocytes. Pre-vitellogenic oocytes were also seen in the follicles but were less than in the developing stage. Mature oocytes or eggs exhibited granular cytoplasm containing many yolk or vitelline globules stained red to pink with eosin.

Spawning stage**:** The irregularly shaped follicles contained partially empty spaces in the lumen, and follicular walls were thin and degenerated. Vitellogenic oocytes were usually detected close to the follicle walls and were less abundant than in the mature stage (Fig. 5E). Connective tissue reappeared, starting from the external wall of the ovary and in the middle of the ovary and digestive gland. Mature oocytes packed with vitelline in the cytoplasm were still present in the follicular lumen, but their numbers were less than in the previous stage. Sometimes the walls of these cells were broken or burst, and phagocytes could be identified among them. Reabsorption of residual oocytes was common.

Spent stage**:** Ovaries had collapsed and contained more reticular connective tissue. This stage showed broken and degenerated follicles, and their lumens usually contained remaining gametes and cellular debris but were sometimes empty (Fig. 5F). The residual female gametes within the follicles were mostly mature oocytes exhibiting autolysis and broken and wrinkled walls. A great number of phagocytes were found among the rest of the ovarian follicles and unspawned gametes. New oogonia production occurred in the follicles' periphery in the late stage.

Reproductive cycle: In males, resting, developing and spent testes were observed during eleven to twelve months of the study period. In contrast, the testes in the mature stage were only noted for four months. Resting testes were present throughout the year. Low percentages of resting testes were detected during January and February 2013 (5.0-14.3%), with an increase from March (25.0%) to June (89.3%) (Fig. 6A). A steep decline occurred during July (12.0%).

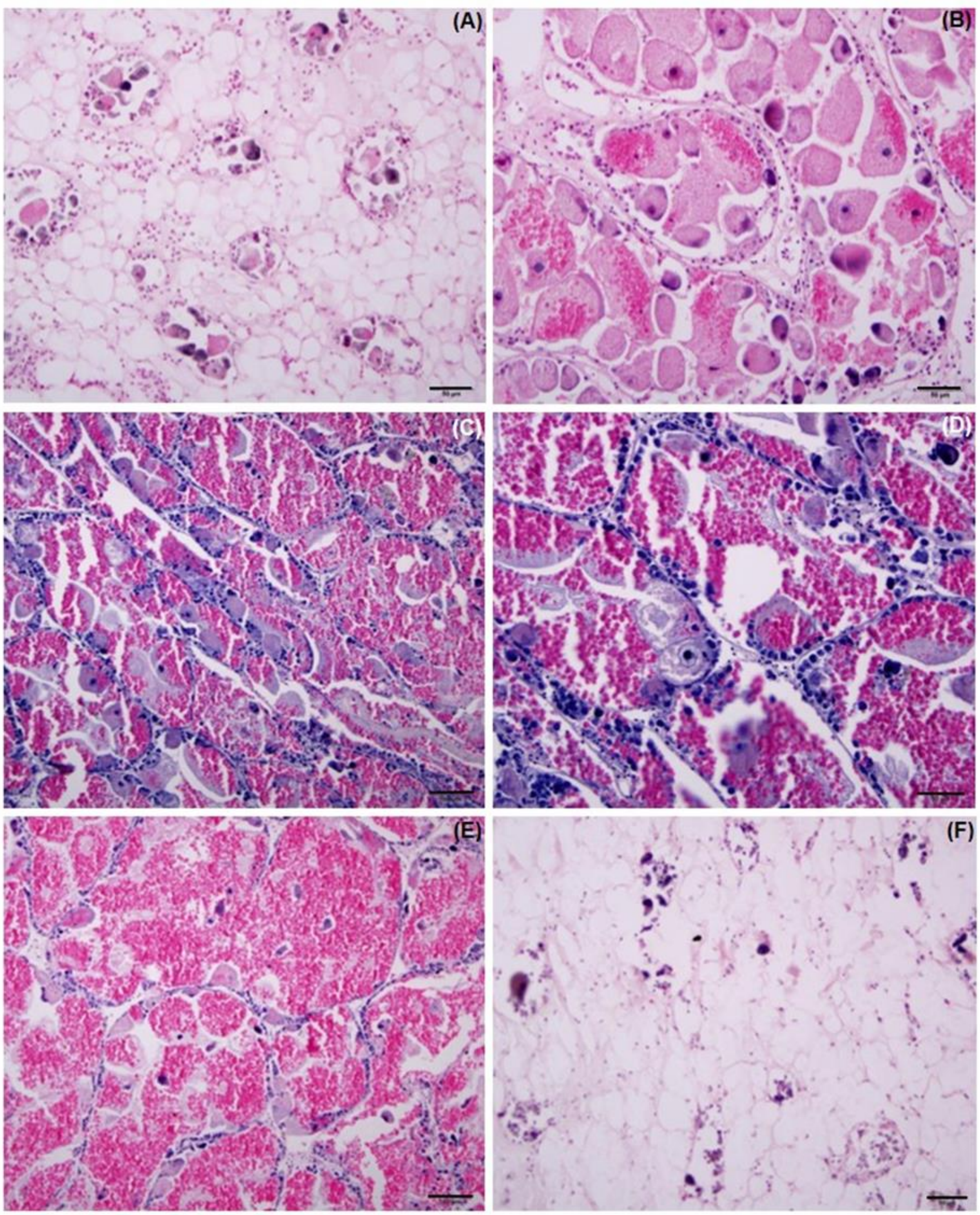

Figure 5. Photomicrographs of ovarian phases of collected female dog conchs stained with H&E: (A) resting stage; (B) developing stage; (C and D) mature stage; (E) spawning stage; (F) spent stage. Scale bars = 50 µm (A, B, D, and F) and 100 µm (C, and E).

The resting testes frequency started to recover in September (31.0%) and was at the maximum level in October (90.0%). Developing testes were also observed throughout the year but presented low proportions, with a maximum in July 2013 (65.5%) and a minimum in January 2014 (5.0%). Mature testes were registered in two periods which were December 2012 (23.1%), February 2013 (5.0%), and August 2013 (45.7%, maximum).

Spawning testes were found with variable

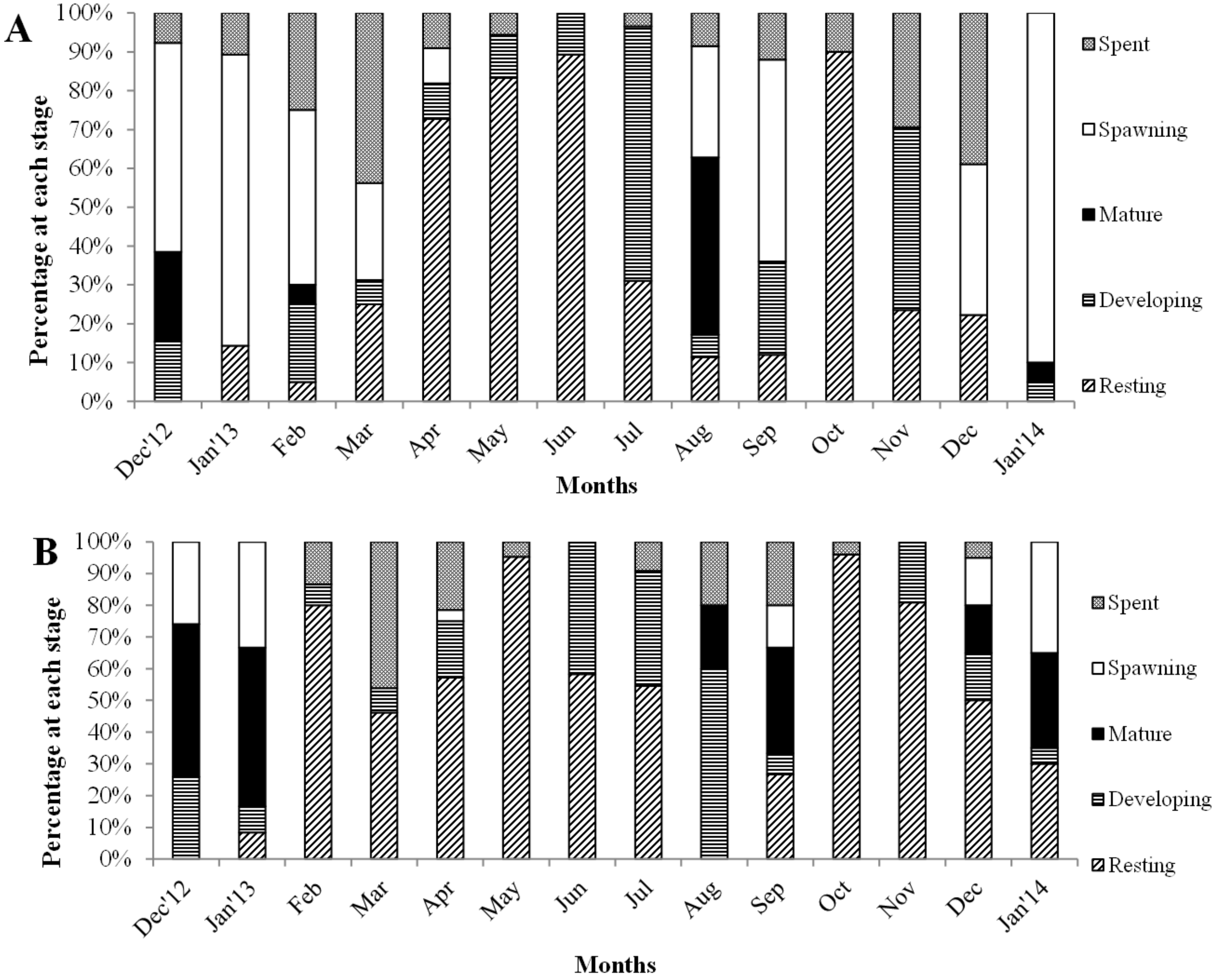

Figure 6. Percentage frequency of five gonad developmental stages in (A) male and (B) female *Laevistrombus canarium* specimens collected monthly from December 2012 to January 2014.

frequencies during nine months of the study period. Two main spawning periods were noted, the first from December 2012 to April 2013 (ranging from 9.1% in April - 75.0% in January 2013), and the second from August (28.6%) to September 2013 (52.0%). After that, the dog conch started a new phase of spawning in December 2013 (38.9%) and the frequency of spawning testes was highest in January 2014 (90.0%). Testes in the spent stage were first encountered in December 2012 (7.7%) and percentages of spent testes increased to a maximum level in March 2013 (43.8%). After that, during the remaining months spent testes presented at low percentages, ranging from 3.4% in July to 38.9% in December.

In females, the resting and developing ovaries were observed during the twelve months of the study period. Mature and spawning ovaries were noted during six months. Resting ovaries were present throughout the year. In the four months of April, June, July, and December 2013, resting ovaries ranged from 50.2 to 58.3%. In the four months of February, May, October, and November, ovaries in this stage were observed, ranging from 80.1 to 96.0% (Fig. 6B). In the remaining months, the resting ovaries were found in

8.3-46.2% of the specimens.

Developing ovaries were also marked throughout the year but represented small proportions with a maximum in August (60.0%) and a minimum in January 2014 (5.0%). Mature ovaries were found in two periods: December 2012 (15.0%) to January 2013 (50.0%), and August (20.0%) to September (33.3%). Whereas spawning testes were present in nine months of the study phase, spawning ovaries were only present in six months. Similar to testes, the spawning ovaries were found in two main periods. The first period was from December 2012 (25.9%) to January 2013 (33.3%), while the second time of spawning was in September (13.3%). After that, a new spawning phase started in December 2013 (15.0%) and peaked in January 2014 (35.0%). Spent ovaries were noted in nine months of the year but occurred at low percentages, with a maximum in March (46.2%) and a minimum in October (4.0%).

GI: The GI of both males and females displayed a similar pattern with two major peaks annually. The first peak was in December 2012 and January 2013, while the second one was in August. In males, GI values ranged from a minimum of 1.0 in October to a maximum of 2.3 in August. In females, the highest GI value occurred in December 2012 (2.5), while the lowest value (1.0) was observed in May and October 2013. GI values ≥ 2.0 were only noted over short periods of three and four months in males and females, respectively (Fig. 7). The male GI decreased slightly from December 2012 (2.2) to January 2013 (1.8). Female GI was higher during these months (2.4-2.5). In February, the male GI remained fairly stable, whereas the female GI decreased sharply to 1.1 and was stable from March to May, ranging from 1.0 to 1.2. During these three months and in June, the male GI decreased to the same level as the female GI (ranging from 1.1-1.3). The female GI increased to a steady level during June and July (1.4) and then rose steeply to a high value in August (2.0), while the male GI increased sharply from July (1.7) to an annual high in August (2.3). After that, a similar trend between males and females was observed in which there were steep declines in GI values of both sexes between September (1.8 in males and 1.9 in females) and October (1.0, both sexes), followed by a steady increase in GI values in both sexes between November 2013 and January 2014 (ranging from 1.4-2.1 in males and 1.2-2.0 in females).

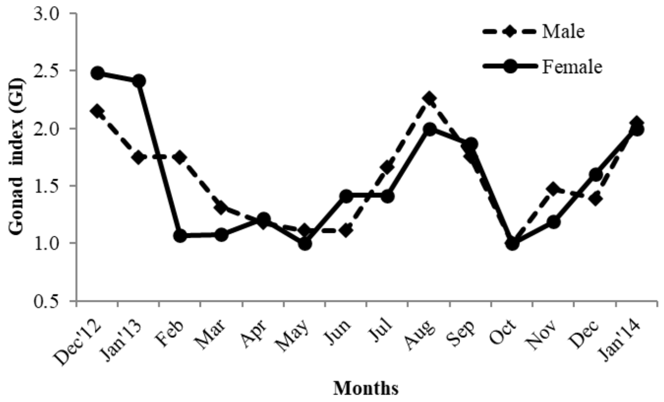

Figure 7. Monthly gonad index (GI) of *Laevistrombus canarium* males (squares) and females (circles) from a population sampled off Ao Thung beach, Krabi province, southern Thailand from December 2012 to January 2014.

Sex ratio: A total of 551 adult specimens (238 males and 313 females) were observed between December 2012 and January 2014. The male/female ratio of the population collected over 14 months was 0.76, which differed significantly from a 1:1 ratio ($X^2 = 11.022$, $P<0.05$) and revealed that females were dominant (Table 1). There were no differences in sex ratios from January 2013 and February, April and May, September, and between December and January 2014 (X^2-test, $P>0.05$). The sex ratios showed more males than females in July and August (X^2-test, $P<0.05$), whereas females outnumbered males in December 2012, and in March, June, October and November 2013 (X^2-test, $P<0.05$).

Discussions

The sex ratio of the *L. canarium* population from the Ao Thung beach, Andaman Sea, Thailand was unequal, with an obvious dominance of females. This female-biased sex ratio is in agreement with previous studies conducted on this species along the Johor Straits, Malaysia (Cob et al., 2009b), on the reefs in Far North Queensland, Australia (Maxwell et al., 2017) and in the waters of Kota Batam, Indonesia (Ramses et al., 2019). The findings of the present

Table 1. Monthly variation in the sex ratios of *Laevistrombus canarium* collected from Ao Thung beach, Krabi province during December 2012 to January 2014.

Month	**Total**	**Males**	**Females**	**Sex ratio (M:F)**	**P-value**
December 2012	40	12	28	0.43 : 1	0.011*
January 2013	40	24	16	1.50 : 1	0.160
February	40	22	18	1.22 : 1	0.527
March	34	11	23	0.48 : 1	0.040*
April	40	14	26	0.54 : 1	0.058
May	40	14	26	0.54 : 1	0.058
June	40	9	31	0.29 : 1	0.001*
July	40	30	10	3.00 : 1	0.002*
August	40	28	12	2.33 : 1	0.011*
September	40	20	20	1.00 : 1	1.000
October	40	6	34	0.18 : 1	0.000*
November	40	11	29	0.38 : 1	0.004*
December	37	15	22	0.68 : 1	0.250
January 2014	40	20	20	1.00 : 1	1.000
Total	**551**	**238**	**313**	**0.76 : 1**	**0.001***

*Indicates samples with statistically unbalanced sex ratios (X^2 – test) ($P<0.05$)

study is also in agreement with a study on *S. pugilis* collected from Seybaplaya to Campeche city, Mexico (Cardenas et al., 2005). In contrast, the studies on *S. gracilior* from Playa Panamá, Costa Rica (Jiménez-Arce, 1993) and *Canarium labiatum* population on Green Island, located near Cairns, Queensland, Australia (Maxwell et al., 2020) found an equal sex ratio (1:1). Although most monthly samples in the present study showed a balanced sex ratio, females dominated in December 2012, March, June, and in October and November and males dominated in July and August. The monthly alteration in the sex-ratio can be related to the species' behavior during the reproductive cycle. For example, the high proportions of females observed during the major spawning seasons of *Bolinus brandaris* (Vasconcelos et al., 2012; Elhasni et al., 2013) was accompanied by the establishment of packed collections of females to lay down collective spawns (Martín et al., 1995; Vasconcelos et al., 2008a). The congregation of females for this purpose is absolutely accountable for the female-biased sex ratios found in late spring and early summer. Recently, it is evident that *Crepipatella dilatata* has a high reproductive potential, considering a large number of months that individuals are actively reproducing and the number of brooding events per female each year (Chaparro et al., 2019), whereas in *Haliotis gigantea,* the female proportion (F/F+M) of the 290 specimens was 36.6%, indicating a distinctly higher proportion of males (Shin et al., 2020). In *Hexaplex trunculus* (Elhasni et al., 2010), high numbers of males were discovered mostly during maturation and copulation and agreed with the peak of copulative activity in *B. brandaris* (Vasconcelos et al., 2012). However, this correlation was not the case in the present study.

Based on known spawning intensity and duration, all three types of gastropod spawning patterns are found among species in the *Strombus* group: one very extended spawning period, with or without a dominant peak, two or more clear peaks or spawning pulses, and one short defined pulse as proposed by Aranda et al. (2003a). The population of *L. canarium* in the present study showed two main spawning periods with simultaneous gametogenesis and spawning between sexes: one period from December 2012 to April 2013 and another from August to September 2013. This synchrony between males and females produced coincident gametic releases in both sexes.

In the Andaman Sea, Thailand, however, male dog conchs spawned for 9 months (December 2012 – April 2013, August – September 2013, and December 2013 – January 2014) for a total of 14 months, whereas females spawned only for 6 months: from December

2012 to January 2013, in April and September 2013, and from December 2013 to January 2014, indicating that periods of maximum spawning were less regular in females and lasted for shorter periods than males. In the oyster, *Crassostrea rhizophorae*, males also recovered and ripened faster than females.

It is believed that oogenesis needs more time and more energy than spermatogenesis, owing to the necessity for yolk creation (Nascimento and Lunetta, 1978; Eckelbarger and Hodgson, 2021). This difference would explain the variations between sexes in the frequency and span of spawning observed in the present work. The annual dual spawning periods observed in the present study of *L. canarium* differ from the populations of Miag-ao, Iloilo, the Philippines (Libutaque, 2000), which exhibited continuous or constant spawning, in which males and females spawned monthly during the thirteen-month study period. Spawning peaks in that study occurred in January, April and May for males and in April, August, September and October for females. This pattern of constant spawning of *L. canarium* along the Philippine coast was also observed in populations of *S. pugilis* from Seybaplaya to Campeche city, Mexico, where spawning organisms were found in June 1990, from June to September 1996, in February 1997 and from May to July 1997 (Aranda et al., 2003a). Also, in the same location (from July 1996 to July 1997), spawn was present throughout the year in over 70% of the male population, with a maximum of 100% in August and 2 periods of low intensity in July (15%) and October (40%), while spawning in females was discontinuous, with 4 pulses of low intensity in February and June 10%, and August and October 20%. (Cardenas et al., 2005). Similar behavior to the present population of *L. canarium* was exhibited by a population of *S. gracilior* from Conception Bay, Baja California, Mexico. Two spawning pulses were observed, the first at the beginning of both years from February to March 1979 and 1980, and the second from August to November 1979 (Aranda et al., 2003a). When compared to spawning patterns of other species, the spawning pattern observed in *L. canarium* and *S. gracilior* is different from that reported for *A. gigas.*

Most studies have suggested that *A. gigas* displayed one short, defined spawning pulse. A population from Seybaplaya to Campeche city, Mexico exhibited this type of spawning from June to August with a peak during July and another population on the Alacranes reef, Quintana Roo, Mexico (Aranda et al., 2003a) spawned from June to October. A similar observation in the Banco Chinchorro, Quintana Roo, Mexico also found that the male *A. gigas* produced a short spawning period during June and July, with a maximum of 60% in July and a spawning period in females limited to the months of July and August in 20 and 33% of the population, respectively (Aranda et al., 2003b). In addition, *A. gigas* collected from the Caribbean region, also had a significantly shorter reproductive season (Boman et al., 2018). In the case of *A. gigas*, only a study in the Archipelago of San Andres, Providencia and Santa Catalina, Colombia demonstrated a different spawning pattern, in which spawning occurred twice, once from March to April (6%) and again in September (6%) in males and from March to April (20%) and in September (43%) in females (Avila-Poveda and Baqueiro-Cárdenas, 2009).

The gonadal development, gametogenesis, and spawning of molluscs are regulated by endogenous factors, including the endocrine system (Euler and Heller, 1963: Horiguchi et al., 2021), genetics and nutrition (Horiguchi et al., 2021), and exogenous factors, including seawater temperature (Morriconi, 1999; Vélez-Arellano et al., 2009; Elhasni et al., 2010; Vasconcelos et al., 2012; Elhasni et al., 2013; Boman et al., 2018; Panchenko and Balanov, 2020; Horiguchi et al., 2021; Popović et al., 2021), food supply (Jaramillo and Navarro, 1995), day length (photoperiod) (Elhasni et al., 2010, 2013; Horiguchi et al., 2021), salinity (Cain, 1974; Stephner, 1981), storms (Cronin, 2000), currents (Davis and Chanley, 1955; Ino, 1970; Guallart et al., 2020; Horiguchi et al., 2021), specific gravity of seawater (Taki, 1949), presence of microalgae (Breese and Robinson, 1981), onshore wind (Horiguchi et al., 2021) and geographical location (Cronin, 2000). Among environmental factors, day length, seawater temperature, and food availability establish in many marine gastropods the most significant environmental cues for the regulators of reproduction such as maturation and spawning (Sternberg et al., 2010). In the present study at Ao Thung beach, the recorded environmental parameters of pH, temperature, and salinity ranged in 2013 from 6.97 (October) to 8.1 (April), 28 (August) to 30.8ºC (May), and 27 (October) to 34 ppt (March and April), respectively. As mentioned earlier, the dog conch in Ao Thung beach, Andaman Sea, Thailand produced two main spawning periods. However, there was apparently no association between these factors (pH, temperature and salinity) and the reproductive cycle of the dog conch. The findings of the present study are in agreement with the population of *S. pugilis* from Seybaplaya to Campeche city, Mexico where there was no correlation between environmental factors (temperature and salinity) and the reproductive cycle of *S. pugilis* displaying continuous spawning (Baqueiro-Cardenas et al., 2005). The small amplitude of annual fluctuations in temperature and salinity (range = 33.5-35.0 ppt) in tropical regions may also explain why dog conchs occupy the inshore waters of Miag-ao, Iloilo, Philippines spawning continuously throughout the year (Libutaque, 2000). Continuous spawning in the limpet *Acmaea scabra* (Gould) had a direct connection with food abundance (Sutherland, 1970), whereas in endangered freshwater snail *Heleobia atacamensis* would reproduce continuously throughout the year; it is not known what ecological parameters (e.g., feeding, microhabitats, abundance) influence its reproduction (Collado et al., 2021). In Ao Thung beach, the temperature is around 29.29°C with an annual thermal amplitude of around 2 to 3°C and salinity is around 31.5 ppt with an annual amplitude of around 7 ppt. These values are approximately steady and hence, they might not affect the gametogenesis and spawning periods in *L. canarium*.

Information about the mechanisms that control the annual reproductive cycles in gastropods is limited but most studies have concluded that these cycles are induced by temperature. For example, the spawning season of *Nacella (P.) deaurata* in Lapataia Bay, Argentina was synchronous with a rise in water temperature (Morriconi, 1999). Similarly, in Conception Bay, Baja California, Mexico, the periods of highest maturation and spawning in *Tegula eiseni* concurred with the seasonal temperature rise from July to November (Vélez-Arellano et al., 2009) and in *Bolinus brandaris* sampled from the Ria Formosa lagoon (southern Portugal), spawning coincided with rising seawater temperatures (Vasconcelos et al., 2012). Furthermore, *A. gigas* collected from the Caribbean region found that locations with a relatively high variation in water temperature had a significantly shorter reproductive season (Boman et al., 2018) and in the green ormer (*Haliotis tuberculata* L.) from the northern Adriatic Sea, off western Istria (Croatia) showed that the cycles of gametogenesis were directly correlated with the seasonal condition of the temperature change (Popović et al., 2021). Acting together, in some gastropod species, day length and seawater temperature regulate the annual reproductive cycle, such as in *Hexaplex trunculus* taken from the Gulf of Gabès (Tunisia), whose main spawning period (April–May), strictly coincided with increasing day length (from 13.2 to 14.2 h) and seawater temperature (from 19.3 to 23.4ºC) during this period (Elhasni et al., 2010) and in *B. brandaris* collected from the Gulf of Gabès (Tunisia) whose spawning season (April and July) seems to be regulated by the annual cycle in day length and seawater temperature (Elhasni et al., 2013). In *Nacella magellanica* from Punta Ninfas, Chubut, Argentina, spawning period extended over all months except June in males, while females spawned from late winter to spring, with an increase from August to November; this prolonged period of gamete release of *N. magellanica* could be related to more favourable temperature and photoperiod (Vilela et al., 2019). In addition to seawater temperature and day length/photoperiod, a recent study of gastropods has suggested that there are four exogenous factors that control the reproductive cycle (including spawning behavior) of *Thais* spp. i.e., water temperature, illumination/photoperiod, tidal cycles, and onshore winds (Horiguchi et al., 2021).

Conclusions

This study of the reproductive cycle of *L. canarium* from the Andaman Sea, Thailand, identified this gastropod population in tropical waters as a species that spawns in two major pulses. The information gathered from this study is crucial to specific ecosystem management plans, guaranteeing the conservation of the species along the coast of the Andaman Sea in Thailand. These plans should establish, for example, closed seasons during the spawning peaks, from December to April and August to September and limit the collection of small-scale snails throughout the year.

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