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Reproductive ecology, gametogenic cycle, and spawning dynamics of *Leukoma asperrima* (Sowerby, 1835) in the Gulf of Panama

Ecología reproductiva, ciclo gametogénico y dinámica del desove de *Leukoma asperrima* (Sowerby, 1835) en el Golfo de Panamá

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ABSTRACT

Synchronization between bivalve reproductive cycles and primary productivity is fundamental for recruitment success in regions subject to seasonal upwelling. The gametogenic cycle of *Leukoma asperrima* was investigated using histometric indicators and physiological indices under the influence of thermal and salinity variability in the Panamanian Pacific. Analysis revealed a bimodal reproductive strategy, with a primary spawning period between October and February and a secondary event between April and June, coinciding with water cooling and increased phytoplankton density. The average annual Gonadosomatic Index (GSI) was 31.39, peaking in April (34.26). Histometrically, oocyte diameter ranged from 55.32 µm to 65.83 µm, reflecting intense vitellogenic activity prior to spawning peaks. The population was identified as dioecious, with a mean sex ratio of 1:1.2 (F:M) and no evidence of hermaphroditism. Sex determination was validated via gonadal smears, an essential technique given the absence of macroscopic chromatic dimorphism. It is concluded that temperature acts as the primary modulator of gonadal conditioning, while food availability regulates the rate of gamete maturation. This study provides novel data on the reproductive ecology of the species, essential for understanding its resilience to climate change and anthropogenic pressure.

Keywords: Bimodal, gametogenic cycle, dioecy, reproductive strategy, Gulf of Panama, oceanographic factors, gonadal smear, gonadosomatic index, vitellogenesis.

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RESUMEN

La sincronización entre los ciclos reproductivos de los bivalvos y la productividad primaria es fundamental para el éxito del reclutamiento en regiones sometidas a afloramientos estacionales. Se investigó el ciclo gametogénico de *Leukoma asperrima* mediante indicadores histométricos e índices fisiológicos bajo la influencia de la variabilidad térmica y de salinidad del Pacífico panameño. El análisis reveló una estrategia reproductiva bimodal, con un periodo de desove máximo entre octubre y febrero, y un evento menor entre abril y junio, coincidiendo con el enfriamiento del agua y el aumento de la densidad fitoplanctónica. El Índice Gonadosomático (IG) promedio anual fue de 31.39, alcanzando su pico máximo en abril (34.26). Histométricamente, el diámetro de los ovocitos varió de 55.32 µm a 65.83 µm, reflejando una intensa actividad vitelogénica previa a los picos de desove. La población se identificó como dioica, con una proporción sexual promedio de 1:1.2 (H:M), sin evidencias de hermafroditismo. La determinación del sexo se validó mediante frotis gonadal, técnica esencial dada la ausencia de dimorfismo cromático macroscópico. Se concluye que la temperatura actúa como el principal modulador del acondicionamiento gonadal, mientras que la disponibilidad de alimento regula la tasa de maduración de los gametos. Este estudio aporta datos inéditos sobre la ecología reproductiva de la especie, esenciales para comprender su resiliencia ante el cambio climático y la presión antrópica.

Palabras claves: Bimodal, ciclo gametogénico, dioecia, estrategia reproductiva, golfo de Panamá, Factores oceanográficos, Frotis gonadal, gonadosomático, Índice, vitelogénesis

INTRODUCTION

Reproduction in marine filter-feeders is a physiologically demanding process requiring precise synchronization with environmental cycles to ensure recruitment success. Factors such as temperature, salinity, and phytoplankton density have been identified as the primary regulators of the gametogenic cycle in tropical bivalves. In the Gulf of Panama, the interaction between rainfall and seasonal upwelling creates an environmental gradient where salinity increases and temperature decreases during the dry season, a pattern that reverses during the rainy season. This inverse relationship ($r = -0.69$) is a determinant driver for the bioconversion of energy reserves into reproductive tissue.

Sastry (1975) postulates that these environmental cues act as physiological triggers initiating germ cell maturation. The reproductive cycle can be effectively monitored through indicators such as the Gonadosomatic Index (GSI) and oocyte histometric. Oocyte diameter is considered an excellent indicator of gonadal maturity, reflecting the increase in vitellogenesis prior to spawning. Previous studies on venerids have shown that nutrient accumulation before reproduction is reflected in significant variations in fresh meat weight, which is a more sensitive indicator of nutritional status and "fatness" than total animal weight. According to Giese & Pearse (1974), continuous reproductive cycles with seasonal peaks are common in low-latitude bivalves, where temperatures rarely drop below the metabolic arrest threshold.

Despite the importance of *Leukoma asperrima*, a knowledge gap exists regarding its specific reproductive strategies in Panamanian waters. While some authors suggest high temperatures induce spawning, others, such as Vélez & Epifanio (1981), have demonstrated that optimal gonadal development occurs under low-temperature conditions in other regional species. Furthermore, sex determination in this species represents a taxonomic challenge due to the lack of macroscopic chromatic dimorphism, necessitating gonadal smear techniques for accurate identification.

Researchers like Palacios (1985) and Pizarro & Cruz (1987) have highlighted that sex ratio and spawning synchrony are critical factors for mitigating larval dispersal effects. This work delves into the sexual maturity cycle, sex ratio, and the influence of oceanographic parameters on the reproductive effort of *L. asperrima*.

MATERIALS AND METHODS

Sample Processing and Environmental Parameters

A monthly subsample of 35 to 45 adult specimens was selected for reproductive analysis. Simultaneously, *in situ* physicochemical parameters—sea surface temperature (ºC) and salinity (psu)—were recorded, along with phytoplankton density using a standardized filtration method.

Physiological Indices and Gonadal Histometry

Nutritional condition was evaluated using the Gonadosomatic Index (GSI), calculated as:

$$IG = \left(\frac{\text{Peso de la gónada}}{\text{Peso total del tejido fresco}} \right) \times 100$$

This index allows for the normalization of gonadal weight variations relative to animal size. For histometric, the diameter of at least 50 oocytes per female was measured using an optical microscope equipped with a calibrated ocular micrometer, considering only oocytes with a visible nucleus to ensure precise equatorial measurement.

Sex Determination and Sex Ratio

Given the absence of chromatic dimorphism in *L. asperrima* gonads, sex identification was performed using the gonadal smear technique. Tissue was observed under a microscope at 40x; the presence of spherical, granular gametes identified females, while motile spermatozoa or fluid tissue identified males. The sex ratio was analyzed using the Chi-square (x^2) test to determine significant deviations from the theoretical 1:1 parity. Pearson correlation analysis was used to evaluate the relationship between oocyte diameter, GSI, and environmental variables ($P < 0.05$).

RESULTS

Sample Processing and Synchrony with Environmental Parameters

Analysis revealed that the reproductive physiology of *L. asperrima* is closely modulated by the Gulf of Panama's upwelling regime. A significant inverse correlation was observed between sea surface temperature and salinity ($r = -0.69$, $P < 0.05$), acting as the primary trigger for gonadal conditioning.

- **Upwelling Response:** The accelerated increase in GSI toward April (34.26) coincided with the 1996 upwelling period, characterized by minimum temperatures and high phytoplankton densities.
- **Gonadal Conditioning:** Gonadal development showed a direct response to food availability; high chlorophyll and nutrient concentrations during the dry season favored an increase in gonadal biomass prior to spawning.
- **Thermal Influence on Spawning:** Peak spawning periods (October–February) synchronized with water temperature decreases, suggesting that environmental cooling induces massive gamete release.

- **Condition Indicators:** Fresh meat weight and GSI proved to be more sensitive indicators of "fatness" and nutritional status than total animal weight.
- **Histometric Relationship:** Despite vitellogenic activity, no significant statistical correlation was detected between oocyte diameter and GSI, indicating that gonad weight variations depend on connective tissue proliferation and glycogen reserves rather than just germ cell size.
- **Seasonality Effect:** During the rainy season (May–October), rising temperatures and salinity stability allowed for progressive somatic recovery, preparing individuals for the second reproductive peak in October.

Gonadosomatic Index (GSI) Dynamics and Maturity

The average GSI for the total population was 31.39. Marked seasonal fluctuation was detected, with an accelerated increase toward April, reaching a maximum of 34.26, followed by a second peak in October (30.61). Individuals classified as "indeterminate" (post-spawning) showed a significantly lower GSI of 25.53 (Figure 1 and Table 1).

Figure 1.

Reproductive cycle and gonodosomatic index (GSI) for L. asperrima in the Gulf of Panama.

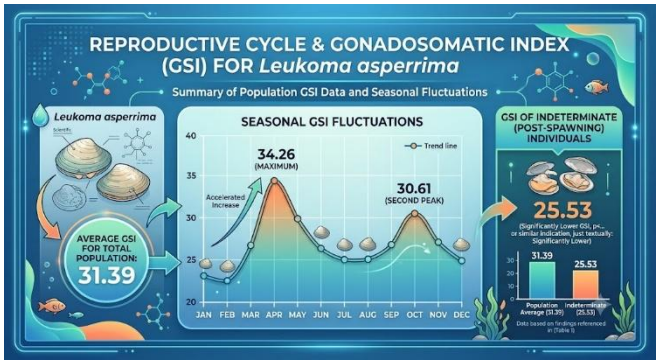

Table 1.

Reproductive and physiological indicators of L. asperrima

Parameter	Average Value / Range
Oocyte Diameter (Annual)	60.53 µm
Minimum Diameter (February)	55.32 µm
Maximum Diameter (October)	65.83 µm
IG Males	31.62
IG Females	31.23

Spawning Cycle and Environmental Variability

Two defined spawning periods were identified: a primary event from October to February and a secondary event from April to June. These periods coincided with decreasing surface temperatures and increased phytoplankton density during upwelling. No significant correlation was found between oocyte diameter and GSI ($P > 0.05$), suggesting that gonadal weight depends on factors beyond gamete size.

Sex and Sex Ratio

The species is dioecious and lacks macroscopic chromatic dimorphism; differentiation was achieved exclusively through gonadal smears (Table 2). The average sex ratio was 1:1.2 (F:M), showing no significant deviations from the 1:1 theoretical parity ($P > 0.05$), except for June and July. No hermaphroditic specimens were recorded.

Table 2.

Sexual structure of the analyzed sample (n=452)

Sex	Frequency (%)	Smear Characteristics
Males	51.99%	Fluid texture, without granules
Females	43.81%	Defined granular texture
Indeterminate	4.20%	Flaccid tissue (post-spawning)

DISCUSSION

The reproductive strategy of *L. asperrima* in the Gulf of Panama is defined as continuous with

marked seasonal bimodality, adapted to synchronize with coastal upwelling. The identified spawning peaks (October–February and April–June) coincide with reports by Palacios et al. (1986c) and Pizarro & Cruz (1987), who associate gamete release with falling surface temperatures and rising primary productivity.

GSI fluctuations, peaking in April (34.26), evidence an immediate physiological response to the phytoplankton abundance characteristic of the upwelling period. However, the lack of significant correlation between GSI and oocyte diameter suggests that gonad weight gain depends not only on germ cell size but also on auxiliary cell proliferation and glycogen accumulation in the interfollicular connective tissue, as proposed by Gómez & Villalaz (1989). The population is strictly dioecious, with a sex ratio (1:1.2 F:M) that does not significantly diverge from parity for most of the cycle. This stability, along with the absence of hermaphroditism, positions *L. asperrima* as a robust reproductive system compared to other regional species like *Argopecten ventricosus*, which show hermaphroditic variations under environmental stress.

Finally, the use of gonadal smears proved to be the most efficient methodology for sex identification in tropical venerids, given the lack of chromatic dimorphism. The histometric and physiological results presented here confirm that temperature and food availability are the primary exogenous regulators of gametogenesis, where water cooling acts as the proximal stimulus for massive spawning.

CONCLUSIONS

L. asperrima is a functional dioecious species without macroscopic chromatic dimorphism, maintaining a sex ratio balance of 1:1.2, ensuring reproductive stability in the Panamanian littoral.

The reproductive strategy is continuous with a defined seasonal bimodality, featuring peak spawning between October and February and a secondary event between April and June.

GSI and fresh meat weight are robust indicators of condition and maturity, peaking during upwelling, confirming that water cooling is the main stimulus for gamete release.

The lack of significant correlation between GSI and oocyte diameter (annual average 60.53 µm) suggests that gonadal energy investment includes vitellogenesis as well as glycogen reserve accumulation and auxiliary tissue proliferation.

These findings establish a fundamental scientific basis for understanding how venerid bivalves optimize reproductive effort in response to oceanographic variability.

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