Reproduction-temperature nexus influencing spawning of pectinids in tropical and temperate waters

Christian D. Cabiles, Victor S. Soliman

Coastal Resource Management Unit, Bicol University, Tabaco Campus, Tayhi, Tabaco City, 4511, Philippines. Corresponding author: V. S. Soliman, vssoliman@bicol-u.edu.ph

Abstract. This paper aims to summarize the current state of knowledge on key environmental factors in the marine environment influencing reproduction in Pectinidae. Sixteen most relevant published studies were examined as the source of secondary information wherein 62% of which are in temperate waters and 38% are in tropical waters. Spawning of scallops from tropical and temperate environments were reportedly affected by and correlated to mostly variations in water temperature, the most influential factor identified to naturally activate spawning. In temperate waters, about 90% of the spawning of different species occurs during warm months or when highest temperature was recorded (summer), while only 10% of the temperate species reproduce during fall (autumn) when water temperature was decreasing. Similarly in tropical waters, 67% of the spawning activities of scallops occur during warm months with few species spawning during cold months (33%). The transition or shift from cold temperature to warm temperature and vice versa seemingly served as “trigger” to spawning. A strategy to maximize collection of scallop spats for stock enhancement or grow-out mariculture should consider the warm months such as summer (i.e., March, April and May) in the Philippines when aquaculture planning and associated activities are afforded with many advantages.
Key Words: thermal shift, latitudinal differences, reproductive biology, culture purposes.

Introduction. Reproduction is an important aspect of the life history of any species. Like other marine bivalves, reproductive cycle of pectinids is genetically controlled response to the environment (Sastry 1979; Barber & Blake 2006). The control of reproduction involves both the combination of exogenous and endogenous factors which have different effect on the gametogenesis as well as synchronizing the reproduction (Gosling 2003). Depending upon the environmental conditions and the presence of strong cue to act as a trigger, scallops switch from protracted to highly synchronized spawning (Langton et al 1987). Natural stimuli such as but not limited to temperature, light, food, lunar periodicity and tidal cycle are appropriate environmental signals (zeitgeber) for the spawning to occur which was well documented both from the field and laboratory observations (Sarkis et al 2006). Variations of these factors can easily be perceived by animals such as pectinids and take advantages of these cues to synchronize their reproduction (Yamahira 2004). The coupling of invertebrate spawning with environmental cues impart the idea of an ecological or evolutionary advantage based on enhancing probability of fertilization success or optimization of subsequent larval survival (Olive 1992).

Many environmental factors have been suggested to influence reproduction of marine invertebrates. One of the most cited environmental factors that influence timing of spawning is temperature. Either an increase or decrease, it is considered as the most important factor in the initiation of spawning (Naidu 1970; Morillo-Manalo et al 2016). Temperature is often suggested as a signal based on the observation that spawning occurs at about the same temperature in different locations or years (Barber & Blake 1991). Orton (1920) suggested that critical temperature determines the start and end of the breeding season of a species. However, many studies demonstrated that latitudinally separated populations breed at different temperatures (Korringa 1957; Sastry 1970;

Newell et al 1982; MacDonald & Thompson 1988). For instance, the scallop *Argopecten irradians irradians* spawned when water temperature was increasing. In contrast, spawning of *Argopecten irradians concentricus* was initiated when water temperature was decreasing (Taylor & Capuzzo 1983). This simply indicates that variation in temperature is an essential stimulus for the spawning to occur.

Scallops (family Pectinidae) are a diverse group of bivalve molluscs which are ecologically and commercially important occurring both temperate and tropical waters (Gosling 2003; Telahigue 2018). They are filter feeding bivalve molluscs that live mainly on sandy gravel or gravel seabed (Telahigue 2018). Its shell comes in a variety of colors and used in the shell craft industry (Laureta 2008). In the Philippines, scallop is one of the important fishery commodities that support the needs of people in terms of food and livelihood. For instance, the senatorial scallop *Chlamys senatoria* (hereafter *Mimachlamys sanguinea*) is an important part of the fishery resources of Asid Gulf in Masbate. It is generally termed as "tikab" (in bicol dialect) which is one of the five commercially important species of scallop present in the gulf (Soliman & Dioneda 2004; Bobiles & Soliman 2018). They are harvested by people primarily for food and source of income of the islanders. At present, studies on the biology and ecology of different scallop species is very scarce in the Philippines as well in other tropical species. Unlike with temperate scallop species, their ecology and reproductive biology were extensively studied (Morillo-Manalo et al 2016).

To address the issue on lack of information regarding biology as well as reproduction of scallops, this paper summarizes the current state of knowledge regarding major aspects of reproduction among pectinids (Pectinidae) from temperate and tropical waters. Reproduction is an important aspect of the life history of any species and understanding their reproductive processes linked to temperature is vital to the management of the commercial fishery. The justification for making this effort is that scallops are an important part of the fishery resources worldwide which serve as food and source of income by people which deserve tangible attention (Shumway et al 2006). Second, this would generate significant contribution to the body of knowledge regarding the timing of reproduction of different scallop species. Third, this article summarizes relevant information regarding the reproductive development of scallops and will give emphasis on areas that needs to be studied for future research considering Philippines, where fishery industries including scallops, is a major commodity sector that is vulnerable to over exploitation. This paper will concentrate on the description of reproduction with a brief overview on methods of assessment, timing of reproduction and factors affecting reproduction. Knowledge of spawning period is important for understanding and predicting recruitment events and maximizing the collection of scallop spat for stock enhancement in natural grounds or for mariculture.

Material and Method. Systematic reviews of relevant studies were conducted to gather empirical evidences and data regarding the reproduction of scallops using the root word "reproduction+scallop". The literature searches were conducted in August 2017 and February 2018 using Google Scholar (*htttp.scholar.google.com*). The information needed to be generated from these studies includes the methods of assessment, timing of reproduction and the factors that initiate or triggers the spawning activity of the species. In this paper, only 16 published studies were considered based on the completeness of information they can provide. These studies were grouped into two which is based on the location of the study sites and were determined whether it is temperate or tropical waters. Specific spawning season (summer, autumn, winter and spring) of temperate species were determined to properly identify and compare them to other temperate waters as well as those in tropical waters. Scientific names of the species under reviewed were verified from the website of World Register of Marine Species (WORMS); wherein in this paper, current taxonomic identification of the species was used. Data sets generated were subjected to simple analysis such as frequency, percentage and plotted using Microsoft Excel.

Results

Means of assessing reproductive activity of pectinids. Several means of assessing gametogenesis and reproduction in molluscs have been utilized. These include microscopic (histological), macroscopic (visual) gonadal staging, oocyte size-frequency distribution, sex steroid measurement and gonado-somatic index (GSI).

From the 16 relevant studies reviewed, it was revealed that determination of GSI in combination with histological analysis were the most common methods used to assess the reproductive pattern of scallops (50%). The combination of these methods for reproductive assessment gives reliable information whereby histological analysis was used to provide a direct snapshot on developmental stages of individual gametes within the gonads and supported the findings from the GSI. On the other hand, 31.25% used histological analysis while 18.75% used GSI only to determine reproductive activity (Figure 1).

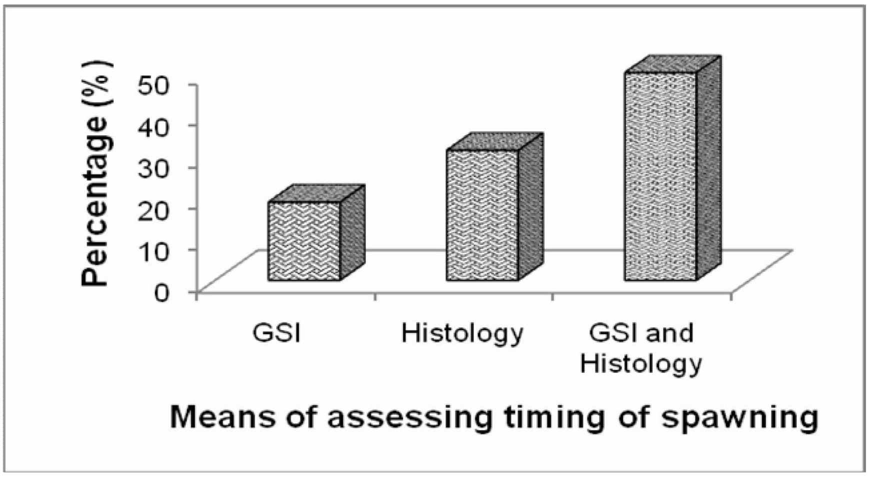

Figure 1. Papers on the means of assessing reproductive activity in pectinids (N = 16).

Timing of spawning of pectinids. Scallops occur throughout the world's aquatic ecosystem both from tropical and temperate countries showing distinct pattern on the timing of reproduction. For instance, *Patinopecten caurinus* from Alaska, USA reaches sexual maturity at about 103.3 mm and shows one annual spawning pattern. The species spawns during summer primarily during June extending into July (Hennick 1970). Similarly, *Chlamys opercularis* (hereafter *Aequipecten opercularis*) from Plymouth, England shows continuous spawning throughout the year. This species began to mature in March and major spawning period occurs in June to July, September to October and January to February (Broom & Mason 1978). In the southwest lagoon of New Caledonia, scallop *Annachlamys flabellata* and *Mimachlamys gloriosa* show similar timing in reproduction. *A. flabellata* reaches its sexual maturity at about 45 mm whereas *M. gloriosa* reach its sexual maturity at about 50 mm. The major spawning of these two scallop species commences during January and February. On the same fishing ground (southwest lagoon), *Comptopallium radula* (hereafter *Decatopecten radula*) reaches sexual maturity at about 60 mm and major spawning event occur during April and May (Lefort & Clavier 1994). In *Argopecten irradians*, spawning occurs during October in Florida (Barber & Blake 1983) while May to July in Massachusetts, USA (Taylor & Capuzzo 1983). The breeding season of *Pecten opercularis* from Plymouth, Southwest England occurs from January to June (Amirthalingam 1928), while spawning of *Pecten maximus* from Ireland commences during September (Salomonsen et al 2015). In the giant scallop *Placopecten magellanicus*, different breeding seasons were reported. This scallop species spawns from September to October in Port au Port Bay, Newfoundland (Naidu 1970); July to mid-September in Charles Arm, Notre Dame Bay, Newfoundland (Penney & McKenzie 1996), August to September in Georges Bank, USA (Almeida et al 1994), July to September in Passamaquoddy Bay, New Brunswick, Canada (Parsons et al 1992) and St. Lawrence, Canada (Bonardelli et al 1996). In the Philippines, spawning of *Chlamys* *senatoria* (hereafter *Mimachlamys sanguinea*) from Gigantes Island (Morillo-Manalo et al 2016) and *Amusium pleuronectes* from Visayan Sea (Del Norte 1988) both occur from January to February (Table 1).

Out of the 16 studies reviewed, 62% are studies done in temperate waters while only 38% are from tropical waters. Spawning of scallop species from temperate waters mostly occurs during summer with 90% while only 10% occurs in the fall (Figure 2); while in tropical waters, spawning mostly occurs during warmer months of the year (67%), while only 33% occurs during cold months (Figure 3).

Table 1

Timing of spawning of pectinids

Species	*Location*	*Season*	*Source*
Patinopecten caurinus	Alaska, USA	Summer	Hennick (1970)
Placopecten magellanicus	Port au, Port Bay Newfoundland	Fall	Naidu (1970)
Aequepecten opercularis	Plymouth, England	Summer	Broom & Mason 1978)
Argopecten irradians	Florida	Warm months	Barber & Blake (1983)
Placopecten magellanicus	Charles Arm, Notre Dame Bay, Newfoundland	Summer	Penney & McKenzie (1996)
Placopecten magellanicus	St. Lawrence, Canada	Summer	Bonardelli et al (1996)
Pecten opercularis	Plymouth, England	Summer	Amirthalingam (1928)
Placopecten magellanicus	Georges Bank, USA	Summer	Almeida et al (1994)
Placopecten magellanicus	Passamaquoddy Bay, New Brunswick Canada	Summer	Parsons et al (1992)
Pecten maximus	Ireland	Summer	Salomonsen et al (2015)
Mimachlamys sanguinea	Philippines	Cold months	Morillo-Manalo et al (2016)
Argopecten irradians	Massachusetts, USA	Summer	Taylor & Capuzzo (1983)
Annachlamys flabellata	Southwest lagoon, New Caledonia	Warm months	Lefort et al (1994)
Decatopecten radula	Southwest lagoon, New Caledonia	Warm months	Lefort & Clavier (1994)
Mimachlamys gloriosa	Southwest lagoon, New Caledonia	Warm months	Lefort & Clavier (1994)
Amusium pleuronectes	Visayan Sea, Philippines	Cold months	Del Norte (1988)

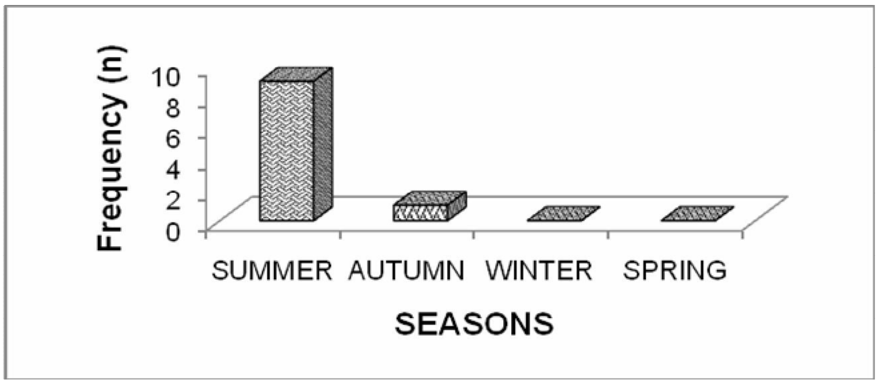

Figure 2. Papers on the spawning season in temperate waters (N = 10).

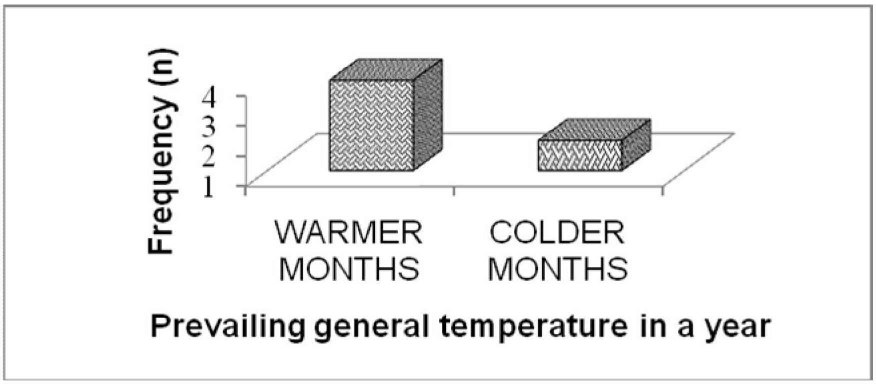

Figure 3. Papers by prevailing general temperature in tropical waters (N = 6).

Factors affecting reproduction in pectinids. Reproduction of scallops like other marine bivalve is triggered by different natural stimuli which include such as but not limited to temperature, light, food, lunar phases and tidal fluctuations. Among these environmental parameters, temperature is the most influencing factor that triggers the spawning event based from the literatures that were reviewed (Table 2).

In the present study, the initiation of spawning of pectinids has been observed to occur both increasing and decreasing water temperature. In temperate waters, species of scallop where the spawning coincides with the increase in water temperature includes *Patinopecten caurinus* (Hennick 1970), *Aequipecten opercularis* (Broom & Mason 1978), *Argopecten irradians* (Taylor & Capuzzo 1983), *Placopecten magellanicus* (Naidu 1970; Penney & McKenzie 1996; Almeida et al 1994; Bonardelli et al 1996), *Pecten opercularis* (Amirthalingam 1928) and *Pecten maximus* (Salomonsen et al 2015). In contrast, spawning associated with a decrease in temperature includes *Placopecten magellanicus* from Newfoundland. In tropical waters, species of scallop where the spawning coincides with the increase in water temperature includes *Argopecten irradians* (Barber & Blake 1983), *Annachlamys flabellata, Decatopecten radula* and *Mimachlamys gloriosa* (Lefort & Clavier 1994), whereas spawning in conjunction with a decrease in temperature includes *Mimachlamys sanguinea* (Morillo-Manalo et al 2016) and *Amusium pleuronectes* (Del Norte 1988).

Table 2

Factors influencing reproduction of pectinids

Species	*Location*	*Factors inflencing reproduction*
Patinopecten caurinus	Alaska, USA	Temperature
Placopecten magellanicus	Port au, Port Bay Newfoundland	Temperature
Aequepecten opercularis	Plymouth, England	Food supply
Argopecten irradians	Florida	Temperature
Placopecten magellanicus	Charles Arm, Notre Dame Bay, Newfoundland	Temperature
Placopecten magellanicus	St. Lawrence, Canada	Temperature
Pecten opercularis	Plymouth, England	Temperature
Placopecten magellanicus	Georges Bank, USA	Lunar periodicity
Placopecten magellanicus	Passamaquoddy Bay, New Brunswick Canada	Temperature
Pecten maximus	Ireland	Temperature
Mimachlamys sanguinea	Philippines	Temperature
Argopecten irradians	Massachusetts, USA	Temperature
Annachlamys flabellata	Southwest lagoon, New Caledonia	Temperature
Decatopecten radula	Southwest lagoon, New Caledonia	Temperature
Mimachlamys gloriosa	Southwest lagoon, New Caledonia	Salinity
Amusium pleuronectes	Visayan Sea, Philippines	Temperature

Of the 16 published studies reviewed, 81% of which states that spawning activity was initiated by the variation of temperature whereas spawning occurs during warmer months or during the maximum temperature of the year (summer) (Hennick 1970; Broom & Mason 1978; Taylor & Capuzzo 1983; Naidu 1970; Penney & McKenzie 1996; Almeida et al 1994; Parsons et al 1992; Bonardelli et al 1996). In contrast, food supply (Broom & Mason 1978), salinity (Lefort & Clavier 1994) and lunar periodicity (Parsons et al 1992) shows the least percentage among the environmental factors that affects and trigger spawning activity which comprise only of 6% of the papers reviewed (Figure 4).

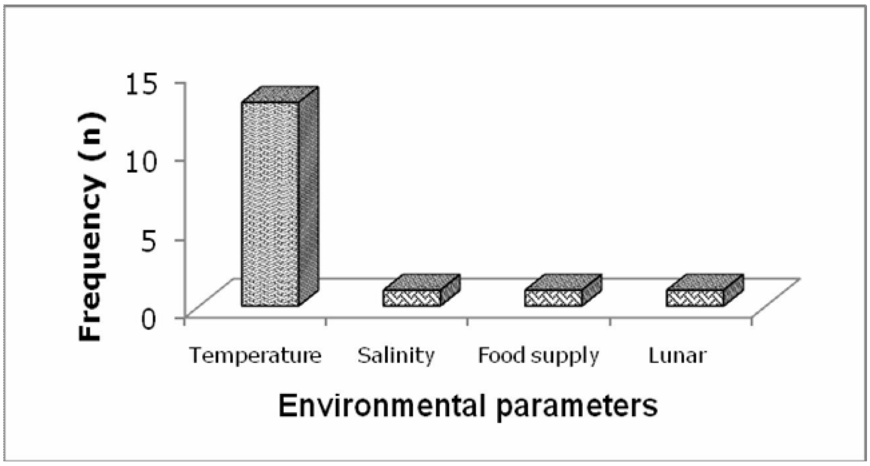

Figure 4. Papers on environmental factors influencing the reproduction of pectinids (N = 16).

Discussion. Scallops, like other marine bivalves, have reproductive cycles that are genetically controlled response to the environment (Sastry 1970). For a marine invertebrate which releases its gametes into the water, one criterion which is likely important in the evolutionary selection of an environmental spawning cue is its "distinctiveness". To ensure coordination of gamete release within a population, the individuals must be able to distinguish the signal from other environmental variations. Fertilization success is only likely to be achieved if there is a high degree of spawning synchrony (Pennington 1985; Olive 1992; Sewell & Levitan 1992). Latitudinal differences in reproduction have been recorded within a species of pectinids. Spatial differences in environmental influences namely those of food, temperature, salinity, lunar periodicity, tides and current are some of the important factors that could passively initiate spawning (Sarkis et al 2006). Coupling reproduction within these environmental parameters provides significant advantages for fertilization and survival.

Shifting of temperature from cold to warm water or vice versa serves as an important spawning cue that triggers the onset of spawning in pectinids both from temperate and tropical regions. Most of the species reviewed from these two geographical regions prefer to spawn during summer when water temperature was increasing (*P. caurinus, A. opercularis, A. irradians, P. magellanicus, P. maximus, A. flabellata, D. radula, M. gloriosa*, Table 1). Scallops most probably spawned under this condition because their sensitivity to temperature increases with increasing temperature (Bonardelli et al 1996). During summer, the main environmental factor that shows major sudden change is temperature. During this season, the beds is strongly stratified with temperatures and undergoing greater fluctuations than at the surface (Bonardelli et al 1996). Variations on temperature can be easily perceived by marine organisms like pectinids where their spawning is initiated. Coupling reproduction during this condition could enhance fertilization success and larval survival, since fertilization success and embryonic development are optimal at temperatures characteristic of the warm water mass. Similarly, reproduction during summer enhances larval survival due to the high level of photosynthetic activity favorable to production of natural food for the larvae. On the other hand, low temperature retard larval development (Bonardelli et al 1996). In contrast, rise in temperature does not provoke a spawning response in some pectinids.

Some of the species spawn when water temperature is decreasing (*A. pleuronectes, M. sanguinea, P. magellanicus* (Port au, Port Bay Newfoundland), Table 1). This could possibly be attributed to the faster rate of decreasing temperature than the scallops' rate of acclimation to cold temperature. This phenomenon may provide a stronger stimulus resulting in the complete extrusion of reproductive products (Naidu 1970).

On the other hand, lunar periodicity was observed to be the influencing factor in the spawning of *Placopecten magellanicus* from Georges Bank, USA (Almeida et al 1994, Table 2). Basing from the report of Skov et al (2005), reproductive synchrony with lunar cycles may have evolved because the cycles of the moon offer reliable time cues which causes environmental fluctuations such as tides, light (moon illumination) and temperature. Tides for instance are not equally distributed in relation to lunar cycles wherein water amplitude changes cyclically (Kvale 2006) as the effect of the moons gravitational pull on earth (Dronkers 1964). As the result, spring and neap tide occur which offer a reliable stimulus for spawning. The correspondence in spawning event during spring tides suggests that water amplitude act as environmental spawning cue. Spawning may be due to different local environment conditions which are correlated with the tidal cycle. These include physical composed of temperature, pressure or currents; biological in the form of food availability together with the chemical factors such as pheromones (Mac-Donald 1988). Similarly, off-shore movement of water during spring tides was strongest (Johanes 1978). Spawning in association with these fluctuating lunar induce environmental factors offers significant advantages, whereas spawning in the absence and presence of light during New Moon and Full Moon could reduce predation (Johannes 1978) as well as facilitate migration to spawning sites (Colin et al 1978) indicating that moonlight is of selective important. Strong movement of current also facilitates the speedy offshore migration of larvae away from estuaries and coastal waters where the predators and other environmental stresses are high (Johanes 1978).

Aside from temperature and lunar periodicity, food availability also plays an important role in the initiation of spawning to some of the pectinids species (Table 2). In *A. opercularies* from Plymouth Southwest England, spawning commences in conjunction with increase in food availability. This timing of spawning is very advantageous for the newly hatch larvae in assurance that they have enough food sources for survival (Pazos et al 1996; Gosling 2003).

In general, environmental factors are adaptively important for aquatic organisms in anticipating future cyclic event (De Haro & Panda 2006; Duguay & Cermakian 2009). Fluctuation of these environmental parameters can be perceived by the marine animals and affects its life histories such as behavioral, physiological as well as reproduction (Yamahira 2004). From the present study it was revealed that different timing of spawning exists between pectinids species in association with the different environmental stimulus. With such identified environmental parameters, temperature seemingly observed to be the most influential and causes the best stimulus for the reproduction to occur. Spawning of pectinids species both from tropical and temperate waters occurs both during increasing and decreasing water temperature. This is consistent with the statement of Naidu (1970) that either an increase or decrease in water temperature, it is considered to be the most important factor in the initiation of spawning event. On the other hand, different timing of spawning event for the different pectinids species is a function of environmental differences and locations (Barber & Blake 2006).

Knowledge on the reproduction of organism is an essential parameter in fishery science as an important basis for conservation of the natural stock. Thus, information provided herein will be a significant contribution to the body of knowledge specifically for pectinids having sufficiently unique form of reproduction.

Conclusions. Most of the pectinid species from tropical and temperate countries prefer to spawn during warmer months or summer primarily attributable to variations in water temperature. The transition from cold temperature to warm temperature seemingly served as trigger for the onset of spawning. A strategy to maximize collection of scallop spats for stock enhancement of wild stock or grow-out mariculture should consider the warm months such as summer in the Philippines where economic activities during this period are afforded with many advantages.

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Authors:
Christian D. Cabiles, Coastal Resource Management Unit, Bicol University, Tabaco Campus, Tayhi Tabaco City 4511, Albay, Philippines, e-mail: christian.cabiles@bicol-u.edu.ph
Victor S. Soliman, Coastal Resource Management Unit, Bicol University, Tabaco Campus, Tayhi Tabaco City 4511, Albay, Philippines, e-mail: vssoliman@bicol-u.edu.ph

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