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RESEARCH ARTICLE OPEN ACCESS

Mollusc fisheries and length–weight relationship in Tonle Sap flood pulse system, Cambodia

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Abstract – Molluscs are important for ecological function, livelihoods and fisheries, but are often forgotten in research and management. Here, we investigated intra-annual variation in the landing and growth patterns of three mollusc species, *i.e., Corbicula moreletiana*, *Pila virescens* and *Pila ampullacea*, using one-year daily data on landing catches and values, recorded in Kampong Chhnang province of Tonle Sap (TS) Lake. Overall, 8330 tonnes with a first sale landing value of US$ 1.4 million for the three species were reported. Also, we found that *C. moreletiana* was abundant during the dry season with high temperature and less precipitation. By contrast, the two *Pila* species were abundant from the early rainy to early dry seasons when precipitation and water levels increase. The length–weight relationship analysis indicated that a faster growth in weight of *Pila* species occurred in the rainy season, and a general negative allometric growth was observed for the three species. This implies that their populations were intensively fished. Our preliminary results suggest that molluscs in the TS Lake (i) are important resources in support of people's livelihoods, (ii) respond differently to intra-annual variation in temperature, precipitation and hydrology and (iii) are being intensively exploited with significant reduction in growth rate. Therefore, it is necessary to conduct further comprehensive research describing status of mollusc stocks and their ecology to support long-term management and conservation of this important aquatic fauna. Our study contributes to establishing the first important baseline data and information on key mollusc species for the TS.

Keywords: snail and bivalve / catch and value / *Corbicula moreletiana* / *Pila virescens* / *Pila ampullacea*

1 Introduction

Molluscs are one among the four most diverse groups of invertebrates in freshwater ecosystems (Balian *et al.,* 2008). Freshwater molluscs are divided into two main groups: the Bivalvia and Gastropoda (Sangpradub and Boonsoong, 2006). Over 5000 species are estimated worldwide, representing ~4% of the total freshwater faunal diversity (Balian *et al.*, 2008). Moreover, freshwater molluscs have a high variation in life history strategies and complex ecological interactions, and inhabit a wide range of habitats such as rivers, lakes, streams, swamps, ponds and rice fields (Köhler *et al.*, 2012).

The Lower Mekong Basin (Fig. 1) is known as a rich biodiversity hotspot for molluscs and other aquatic fauna (MRC, 2003; Sodhi *et al.,* 2004; Strong *et al.*, 2008). This basin supports ~121 species of gastropods and ~39 species of bivalves (Davis, 1988). Amongst these species, at least 111 gastropods and 5 bivalves are endemic to the basin (Davis, 1981). This great diversity is due to the tropical monsoon rainfall system, which is characterized by regular dry (November–April) and rainy (May–October) seasons, and to the extensive floodplains as well as broad tributaries of the Lower Mekong Basin. The largest floodplain of the Lower Mekong Basin is the Tonle Sap (TS) Lake, which is also the biggest freshwater wetland in Southeast Asia (Sarkkula *et al.*, 2003; Adamson *et al.,* 2009). In the TS Lake and River system, molluscs are the second largest fishery after fishes (Rainboth, 1996). They are widely abundant, for centuries, around the

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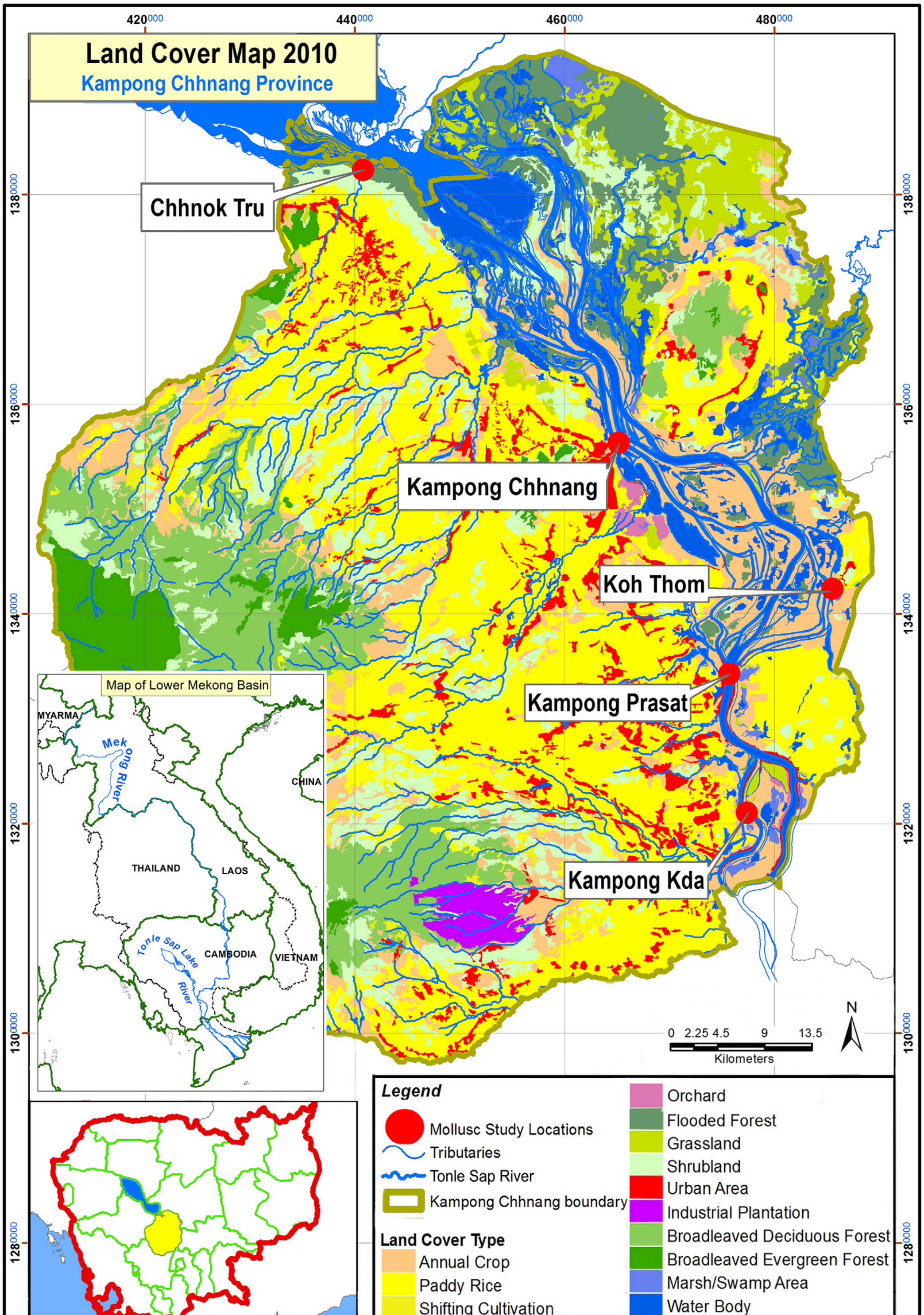

Fig. 1. Map showing major mollusc-landing sites covered in the study and land cover in Kampong Chhnang province, Cambodia (modified from Ngor *et al.*, 2016).

TS Lake (Zhou, 2002), and their biomass is exceptionally high compared to other zoobenthos (Chea *et al.*, 2016).

In the TS Lake, bivalves (*e.g.*, Asian clam *Corbicula* spp.) are reported to be abundant during the dry season (MRC, 2003), while the gastropods (*e.g.*, apple snails *Pila* spp.) are numerous during the rainy season and in the beginning of the dry season when floodwaters recede and the temperature reaches its minimum of the year (MRC, 2003). Despite the high estimated mollusc diversity and production in the TS Lake, little attention has been paid to the study of mollusc fisheries regarding landing catches, values and other aspects of the mollusc stocks, *i.e.,* length–weight relationship. This leads to the ignorance of the importance of molluscs in support of both food security and ecology, *e.g.,* when discussing about the impacts of water development or aquatic faunal management and conservation issues.

The lack of focus on mollusc fisheries is a concern as they functionally contribute to enhancing food availability and security, providing physical structures for other aquatic organisms (Gutiérrez *et al.,* 2003; Halwart, 2006; Vaughn *et al.,* 2008) and removing particulate organic matters from water columns (Sousa *et al.,* 2008; Musig *et al.,* 2012). Furthermore, molluscs provide a source of protein intake and income for local people in some developing countries, *e.g.,* Cambodia, Laos, Thailand and Vietnam, that share the Lower Mekong Basin (Coates *et al.*, 2003; Köhler *et al.*, 2012). Subsequently, changes in their abundances and biomass can directly or indirectly influence ecosystem functioning and the livelihoods of local people.

Biomass and production of molluscs are closely linked to their morphological characteristics, *e.g.,* body length and weight (Froese, 2006). Analyses of these characteristics, *i.e.,* length–weight relationship (LWR), are useful for informing the management of the stocks (*e.g.,* stock assessment) and are important to determine individual and population conditions (Hilborn and Waiters, 1992; Simon *et al.,* 2014). Moreover, the analyses of LWR of molluscs can also provide an indication of environmental conditions in which they inhabit because their maturity stages are affected by surrounding environmental variables, *e.g.,* hydrology, food availability, water quality and temperature (Simon *et al.,* 2014; Saleky *et al.,* 2016).

In this study, we aimed to (1) investigate intra-annual variation (*i.e.,* on a daily and monthly basis) in landing catches of three mollusc species: *C. moreletiana* (Cyrenidae), *Pila virescens* and *Pila ampullacea* (Ampullariidae), (2) examine the relationship between the monthly landing catches and key environmental variables and (3) describe the LWR of the three species based on observed monthly length–weight data. Due to high variation in water levels, precipitation and temperature, which all influence molluscs' body development (Simon *et al.,* 2014; Saleky *et al.,* 2016), we expected that the monthly growth patterns of the three species significantly change within the year. This study is an expansion of a previous study by Ngor *et al.* (2016), who reported the total landing catches and values of five key mollusc species in Kampong Chhnang province. Based on this paper, we further investigate the details of the three above-mentioned species (out of the five species recorded in Ngor *et al.,* 2016) that form the largest mollusc landing in Kampong Chhnang province of the TS River and Lake.

2 Materials and methods

2.1 Study area

The study area is located in Kampong Chhnang province, covering a surface area of 5521 km^2 (NIS, 2013), of which ~48% is attributed to rice paddy and annual crop production, ~24% to shrubland and broad-leaved deciduous forest and 12% to water body and flooded forest (Fig. 1). The rest of the land cover is made up of broad-leaved evergreen forests (~6%), urban (~5%), grassland and swamp area (~3%), shifting cultivation (0.8%), industrial plantation (0.8%) and orchard (0.3%) (Fig. 1).

Kampong Chhnang province is considered as a transition zone, linking the TS Lake with the TS River, the river with a flow-reversal system. The TS River plays an important role in bringing the excess water from the Mekong River to the TS Lake during the rainy season, and in draining the water from the TS Lake back to the Mekong River during the dry season when the rain ceases and water levels in the Mekong drop (Kummu *et al.,* 2014). As such, most of the area in this province is covered with fertile land (alluvial plain) and is almost an ever-wet heart of Cambodia. This condition is naturally suitable for a diverse aquatic fauna to inhabit and for local people to closely engage with agricultural productions including fisheries. About 87% of population are primarily involved in agricultural activities including rice farming, crop gardening, fishing and livestock (NCDD, 2010).

Our study covers five major commercial mollusc landing sites in Kampong Chhnang province in the TS floodplains, *i.e.,* Kampong Kda, Kampong Prasat, Koh Thom, Kampong Chhnang and Chhnok Tru (Fig. 1). Data collected from these sites roughly represented the annual mollusc landings (for the three study species) in the province.

2.2 Hydrology

The hydrological cycle in Kampong Chhnang province is strongly influenced by seasonal variability of the Mekong floods. During the flooding season (May–October) when higher water levels occur in the Mekong, the water in the TS River flows into the TS Lake. In the dry season (November–April), the TS River reverses its flow direction from the TS Lake to the Mekong River. Based on a 12-year record (2000–2012), the lowest water levels take place in April (mean: 2.5 m) and peak in October (mean: 10.3 m). During this period, the lowest water was 2.02 m in 2006 and the highest was 11.8 m in 2011. See Supplementary Information Figure S1 for the intra-annual variability of the 12-year daily water levels in the TS River at Kampong Chhnang hydrological station.

2.3 Data collection

Daily data of the three species were recorded from commercial traders at the five commercial landing sites that were determined by focus group discussions with Kampong Chhnang Fisheries Administration Cantonment (Provincial level), Fisheries Administration Section (District level) and Fisheries Administration Unit (Commune level). Technical details about fishing gears and collection methods of molluscs are described in Deap *et al.* (2003: 84–86). Five field research officers participated in the daily field-data collection process; each was based at one of the five commercial landing sites over the period from 1 February 2014 to 31 January 2015. Prior to field data collection, data recording forms and a checklist of ecological questions were prepared to record daily catches, prices and weight–length data and collect ecological information on the study species in each site. The field research officers were then trained how to (i) fill in the data collection forms, (ii) take samples and subsamples for estimating the total landings of molluscs by species, *e.g.,* when large landings of snail

Table 1. Total landings (kg) of the three mollusc species and their correspondent first sale landing values (US$) from February 2014 to January 2015.

Species	Total landing (kg)	Mean daily landing (kg)	Total value (US $)*	Mean daily value (US $)
C. moreletiana	6,436,439	23,900 (±14,660)	369,805	1,375 (±1,028)
P. virescens	1,511,280	4,140 (±2,437)	781,025	2,140 (±1,399)
P. ampullacea	381,899	1,046 (±2,267)	218,053	598 (±1,423)

* At the time of sampling, the average exchange rate was about Cambodian Riel 4000 to US$1.00.

species were not sorted, (iii) identify key mollusc species and (iv) measure the weight–length of the individual mollusc species. Mollusc identification was based on the Mekong River Commission's (MRC) guide: "Identification of Freshwater Invertebrates of the Mekong River and Its Tributaries" (Sangpradub and Boonsoong, 2006) and applesnail.net at each landing site. It is noted that *P. virescens* in this study is the accepted scientific name of *Pila polita* in the MRC identification guide and at applesnail.net and in Ngor *et al.* (2016). For photos, length measurement and identification keys of mollusc species presented in this study, see Supplementary Information Table S1.

A 100-kg scale, accurate to 100 g, was used to weigh the molluscs landing at each site. The collected daily landing catches (by species) from each site were then aggregated to obtain the overall daily and monthly landings for the entire province. Correspondingly, daily landing prices by species per kilogram at each site was also recorded for calculating the overall daily mollusc landing values by species for the province. Additionally, length–weight data at each landing site were recorded using a 1-kg electronic scale and a caliper accurate to 1 g and 1 mm, respectively. Mollusc maximum body size (height) was applied for the length measurement. As much as possible, at least 30 individuals of each study species from sub-daily landings within each month were randomly selected for the height measurement, and all collected individuals were analyzed in this study. The sample size of *C. moreletiana* was small, compared to the *Pila* species, as the species was mainly landed in Chhnok Tru. In the case of small landing (*i.e.,* <30 individuals), all samples were used for the measurement. The scales and calipers were calibrated before use. The descriptive statistics on monthly length and weight of the study species are provided in Supplementary Information Table S2.

Daily water levels at the hydrological station of Kampong Chhnang (latitude: 12.25053; longitude: 105.6859) were registered by the Mekong River Commission (MRC, 2010). In addition, we included the monthly temperature and precipitation, which were obtained from bioclimatic data (http://www.worldclim.org), for further analysis.

2.4 Statistical analysis

To investigate daily and monthly variations in the mollusc landing catches (*i.e.,* the catch of each species in kg), the package "ggplot2" of R was used to plot the catches against time. The differences in monthly landing catches were tested using a one-way ANOVA (when residuals of the models were normal: Shapiro-Wilk test, $p > 0.05$, and homoscedasticity: Bartlett's test, $p > 0.05$), or otherwise the non-parametric test (Kruskal–Wallis) was used.

The nonmetric multidimensional scaling (NMDS) and the function "envfit" from "vegan" package were applied to associate the monthly mollusc landing catches with the recorded water levels and the monthly precipitation and temperature. The function "ordispider" of R was employed to visualize the monthly variability of mollusc catches on the NMDS ordination plot. In the NMDS analysis, missing values were not accepted and thus were removed to enable the analysis. Therefore, only data from February to May 2014 and from September 2014 to January 2015 (for the three mollusc species and environmental variables) were used for the analysis. Every test for significant differences, p values <0.05 were considered. We performed all analyses in the R language program (R Development Core Team, 2017).

The length–weight relationship (LWR) of each species was expressed by an exponential equation $W = aL^b$, where W is the body weight (g) and L is the total length (mm). This equation can be linearized as $\log W = \log a + b \log L$, where a is the intercept and b *is* the slope (regression coefficient), which is used to indicate the growth patterns, *i.e.,* isometric ($b = 3$) or positive allometric ($b > 3$) or negative allometric ($b < 3$). The LWR of each species was computed on a monthly basis in order to increase the sample size, and thus improve the reliability of the analysis of the LWR.

3 Results

3.1 Overall landings and economic values

C. moreletiana was the most abundant species as it formed the largest landings of all species recorded with a total landing of 6,436,439 kg across the study period. *P. virescens* ranked second with the total landing of 1,511,280 kg, and *P. ampullacea* was the least abundant among the three species with the total landings of 381,899 kg. The species that provided the highest total landing values (based on the first sale landing prices) was *P. virescens*, followed by *C. moreletiana* and *P. ampullacea* (Tab. 1).

3.2 Intra-annual variation in mollusc landings and their association with environmental variables

The daily landings of the three species were highly varied within the observed complete hydrological cycle (Fig. 2). The highest landing catch of *C. moreletiana* occurred from February to April 2014 and from December 2014 to January 2015, covering almost the entire dry season. Its lowest landing

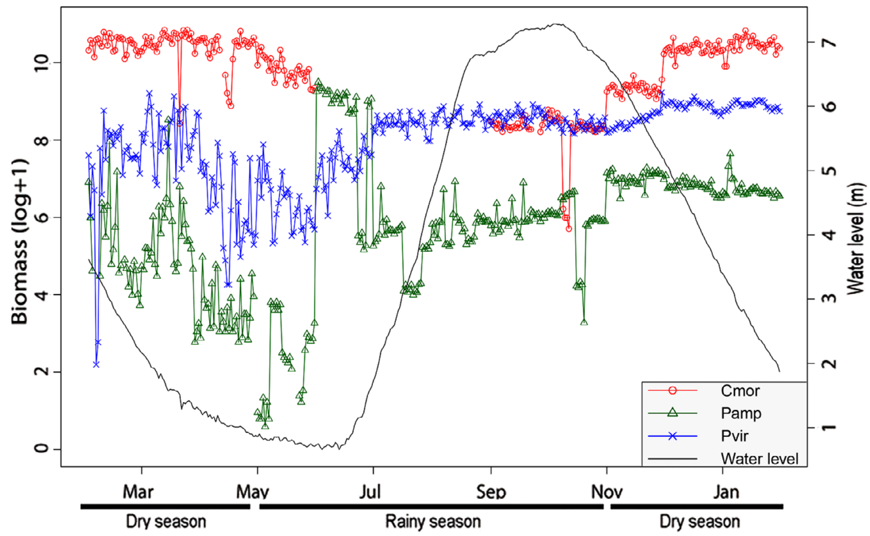

Fig. 2. The variation in landing catches of *Corbicula moreletiana* (Cmor), *P. ampullacea* (Pamp), *P. virescens* (Pvir) over a complete hydrological cycle from February 2014 to January 2015.

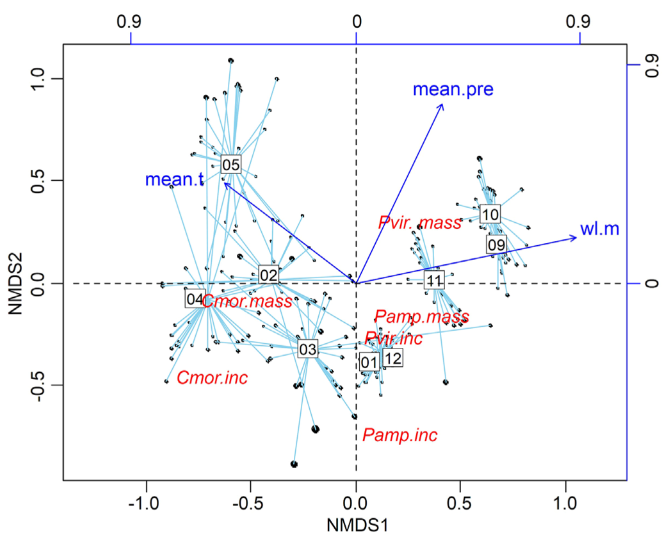

Fig. 3. The NMDS ordination of all samples based on Bray–Curtis dissimilarity matrix of monthly landing catches and vectors of *Corbicula moreletiana* (Cmor), *P. ampullacea* (Pamp) and *P. virescens* (Pvir) and their recorded landing values. The monthly mean temperature (mean.t), precipitation (mean.pre) and water levels (wl.m) were fitted using the envfit function on the NMDS ordination map. mass and inc denote the catches and values of each species, respectively. The two-digit number represents each month of the year, *i.e.,* 01 = January etc.

was observed between September and October 2014 during the high flow period. For *P. virescens* and *P. ampullacea*, relatively high landings were recorded from June 2014 to January 2015, partly during the increasing water levels (inflow) between June and October, and partly during the falling water levels when TS River resumes its normal flow direction (outflow); whereas decreased landing catches were observed from February to May 2014 during the low flow period (Fig. 2).

The daily landing values of each species was found to be autocorrelated with the daily landing catches (see Supplementary Information Fig. S2).

The monthly variation in the landing catches within the year was significant for each species: *C. moreletiana* (ANOVA, $F = 426$, $p < 0.001$), *P. ampullacea* ($F = 284$, $p < 0.001$) and *P. virescens* ($F = 306$, $p < 0.001$) (Fig. 3). The relationship between each species' monthly catches and the analysed variables is shown in Figure 3. The bivalve *C. moreletiana* that was mostly abundant from February to May was positively correlated to the monthly mean temperature of the year and negatively correlated to the water levels. The NMDS ordination map clearly showed contrasting patterns between the bivalve and the two gastropod species. The bivalve *C. moreletiana* that was mostly abundant from February to May was positively correlated to the monthly mean temperature of the year and negatively correlated to the water levels; whereas *P. ampullacea* and *P. virescens*, mostly abundant from September to November, were positively associated with the water levels and negatively associated with the monthly mean temperature. *P. virescens* was a unique species linked to the high precipitation.

3.3 Length–weight relationships

The monthly LWRs estimated for each species were significant and strongly explained by the linear regression models with relatively high values of the coefficients of determination (R^2) (Tab. 2). The regression coefficients *b* were mostly lower than 3, except for the *b* value of *P. ampullacea* in October. The *b* values of *C. moreletiana* in the dry season (April, November and December) were slightly higher than they were in the rainy season (May, September and October). Interestingly, opposite findings were observed for the *Pila* species where the *b* values were found to be higher in the rainy season (May–October) than they were in the dry season (November–April).

Table 2. Monthly length–weight relationships (LWR) for each study species.

	C. moreletiana				*P. ampullacea*				*P. virescens*			
Month	*N*	*a*	*b*	R^2	*N*	*a*	*b*	R^2	*N*	*a*	*b*	R^2
February	–	–	–	–	137	0.731	1.035	0.85**	509	0.084	1.542	0.69**
March	–	–	–	–	279	0.002	2.488	0.93**	524	0.052	1.662	0.68**
April	80	0.086	1.769	0.96**	168	0.011	2.056	0.79**	398	0.005	2.241	0.78**
May	121	0.219	1.274	0.93**	10	0.001	2.682	0.92**	248	0.001	2.627	0.88**
June	–	–	–	–	39	0.006	2.174	0.93**	298	0.002	2.456	0.78**
July	–	–	–	–	25	0.001	2.627	0.89**	294	0.002	2.505	0.92**
August	–	–	–	–	68	0.0003	2.850	0.92**	290	0.009	2.068	0.70**
September	40	0.020	1.719	0.27**	20	0.002	2.504	0.77**	204	0.001	2.503	0.63**
October	57	0.007	2.027	0.17**	133	0.003	2.400	0.83**	139	0.001	2.583	0.76**
November	63	0.058	1.292	0.70**	31	0.0004	3.063	0.93**	188	0.003	2.327	0.63**
December	24	0.003	2.323	0.09	93	0.037	1.744	0.68**	170	0.615	1.003	0.24**

** $p < 0.01$, *N*: number of individuals, *a*: intercept, *b*: slope, R^2: coefficient of determination.

4 Discussion

4.1 Mollusc fisheries and economic values

We found substantial daily harvests of three mollusc species from the TS Lake. *C. moreletiana* was the most abundant species, making up the highest catches over the study period. The great abundance of this species may reflect the widespread ability and diverse reproductive strategies of its genus, ranging from free-swimming larvae to incubation of larvae in gills (Vaughn and Hakenkamp, 2001; Glaubrecht *et al.*, 2006). Therefore, they can reach their optimal number when suitable habitat conditions are available. For the *Pila* species, their numerous abundance could be attributed to their ability to tolerate water deficiency and to be capable of prolonged periods of aestivation in the soil during the dry season (Köhler *et al.*, 2012; Hayes *et al.*, 2015). According to Köhler *et al.* (2012), ampullariids are ubiquitous and reproduced rapidly, which makes them widespread, abundant and easy to collect by the locals, as well as resilient to high collection pressure.

In the Lower Mekong Basin, at least seven mollusc species are known to be abundant and are harvested at considerable levels. These species include *P. scutata, P. virescens* and *P. ampullacea* (Ampullariidae), *Mekongia swainsoni* and *Filopaludina martensi cambodiensis* (Viviparidae) and *C. fluminea* and *C. moreletiana* (Cyrenidae) (Claridge, 1996; Ngor *et al.*, 2014, 2016). Local people of the Lower Mekong Basin exploit molluscs for food and trade on a daily basis (Campbell and Parnrong, 2001; Ngor *et al.*, 2014). In Cambodia, however, up to 10 bivalve and 12 gastropod species are exploited (Lim, 1995). These species contribute significantly to the daily, monthly and annual yields of other aquatic animals (OAAs) (Halwart, 2006; Ngor *et al.*, 2014). For example, an estimation of 121,000 tonnes of the annual yield of OAAs, which mainly comprised molluscs, crustaceans, amphibians and reptiles, was reported in Cambodia for the year 2008 (MRC, 2010). From the annual yield of OAAs, Cambodian people are known to consume 9.2 kg/person/year (Hortle, 2007), of which 3.5 kg are molluscs (MRC, 2010). This suggests that OAAs including the three species belonging to Ampullariidae and Cyrenidae are an important source of food nutrition, security and part of income generation for the local people.

We found that, over the year of the survey, some 8330 tonnes of mollusc landings for the three study species were reported from the five major landing sites in Kampong Chhnang province, with the corresponding total first sale value recorded at around US$ 1.4 million. Our results provided strong evidence and strengthened the results of previous studies that mollusc fisheries are among the important sources of employment and income generation as well as food security in the region. For example, poor households in many Cambodian provinces (*e.g.,* Kampong Cham, Kampot, Kratie, Battambang and Kampong Thom) earn some 60–70% of their daily income from OAAs, of which molluscs contribute a large quantity (Persson *et al.*, 2010; RUPP, 2010). The harvested molluscs can be sold to traders with the first sale value earned by each local family between US$ 90–180 (MRC, 2003). Specifically, of all reported OAAs collected from the rice field in Battambang province in nine 25-ha study sites of TS Lake over the 7-month period from August 2003 to February 2004, molluscs made up of ∼10% of the total economic value, which was about US$ 22,912 (Hortle *et al.*, 2008). In general, local people living in Cambodia and countries sharing the Lower Mekong Basin earn their daily income from selling the excess harvest of OAAs, particularly mollusc species (*e.g., P. virescens* and *P. ampullacea*) which have high economic values (MRC, 2003).

4.2 Relationship between landing catches and water levels, temperature and precipitation

Our results demonstrated that the landing catches of the bivalve species were positively correlated to temperature. This finding supports a previous survey in Kampong Cham province that a high harvest of bivalve species mainly took place during the dry season (MRC, 2003), which is comparatively hot. High temperatures provide good conditions for increases in phytoplankton abundance (Vannote *et al.*, 1980; Statzner and Higler, 1985; Hecky and Kilham, 1988), which in turn enhances the abundance of phytoplankton feeders (*e.g., Corbicula* spp.) (Vaughn and Hakenkamp, 2001). Moreover, a high nutrient load (when the water recedes and therefore nutrients are concentrated) also supports a high abundance of *Corbicula* spp. (Vanderploeg *et al.,* 1995; Vaughn and Hakenkamp, 2001; Sor *et al.,* 2017). Bogan (2008) also reported that a dense aggregation of bivalves was observed in the period of high temperature and when large quantities of algae, diatoms, bacteria, fine particulate and organic particles were present. These combined factors therefore likely explain the high production of bivalves that we found during the dry season.

A contrasting result was found for the gastropod species; the landing catches of *P. virescens* and *P. ampullacea* were positively associated with precipitation and water levels, and negatively associated with temperature. During the dry season, these snails are able to withstand water shortage and hot weather by aestivating (Köhler *et al.*, 2012; Hayes *et al.*, 2015), and hence are not collected in large numbers. During the rainy season, water levels in the TS Lake is highly influenced by floods from the upstream Mekong. A large area of Kampong Chhnang province which is connected to the TS Lake is usually flooded, covering the belt of flooded forests, degraded forests and wetlands surrounding the lake and river (Lieng *et al.*, 1995; Poulsen *et al.*, 2002; Ngor *et al.*, 2018a). These conditions enable the snail species to gain access to breeding and nursing grounds for reproduction and growth, and therefore drive their enormous production during the rainy season. In addition, the rains may increase the abundance of food sources (*e.g.,* aquatic plants), as the snails, being ampullariids, are primarily macroherbivorous (Strong *et al.,* 2008).

Our findings also support previous studies conducted in the tropics and in some temperate areas. In the Lower Mekong Basin and in Indian Gho-Manhasan stream, Cyrenidae (*e.g., C. cashmeriensis*) were mostly found in dry season when high temperatures were observed (IUCN, 2013; Sharma *et al.,* 2013). Similarly, they have been found to occur abundantly between summer and autumn, which is the warmest period of the year (Pigneur *et al.*, 2014). For *Pila* species, they can be found in both dry and rainy seasons, *e.g.,* for the case of *P. scutata* found in Indonesia (Priawandiputra *et al.*, 2017) and of *P. globosa* found in Bangladesh (Huq *et al.*, 2002). To the best of our understanding, however, there appear to be no clear seasonal changes in the abundance found for the *Pila* species from other regions, except for the case of our present study in the TS Lake.

4.3 Length–weight relationships

Our study, using the length–weight data by month, found that there was a general negative allometric growth for the three study species, as reflected by low *b* values (*i.e.,* <3). For *C. moreletiana,* although there were higher *b* values found in the dry season, due to nutrient accumulation that supports their growth (Vanderploeg *et al.,* 1995; Vaughn and Hakenkamp, 2001), the *b* values were still lower than 3. This was also observed for *P. virescens* and *P. ampullacea* in most cases. However, in contrast to *C. moreletiana,* higher *b* values of the two gastropod species were found in the rainy season. As explained earlier, this could be due to suitable habitat conditions, *e.g.,* more available space due to increasing water levels and food availability – water plants and other vegetation – which can better support their growth. The same analysis on daily measurements confirmed the similar findings with regards to the growth patterns for the three study species (see Supplementary Information Fig. S3). Overall, although a negative allometric growth was generally observed for each species, our results suggest that the growth in weight of the two gastropod species is faster during the rainy season than during the dry season. At the same time, there is little evidence of seasonal growth patterns of the bivalve species due to insufficient data.

The LWR is commonly used as an indicator of biological fisheries, changes in individual and population status and growth patterns of organisms (Gayon, 2000; Gaspar *et al.,* 2001; Albuquerque *et al.,* 2009). We found that the weight gain in each study species is slower than the growth in length, as inferred from low *b* values. This clearly indicates that the collected molluscs were young individuals, and their populations, in particular the bivalve, were not able to reach their mature stage before being harvested. Thus, our findings may imply that the three species were intensively fished and were being overharvested.

4.4 Conclusion and management implications

Many studies recognize the importance of molluscs' contribution to food security, employment and economy, especially for the poorer segments of the society (Balian *et al.*, 2008; Strong *et al.*, 2008; Köhler *et al.*, 2012). This recognition becomes obvious when fish is less abundant and molluscs become an important alternative resource to support rural families' livelihoods. Our study recorded 8330 tonnes corresponding to US$1.4 million of the first sale value from the three mollusc species landed in one of the six provinces around the TS Lake. In Cambodia, in addition to local consumption, mollusc species are also exported to neighbouring countries such as Vietnam and China. Among the three study species, the two *Pila* species are commercially exported, due to their higher economic values, compared to *C. moreletania.* However, in terms of yield, the *C. moreletania* was by far the highest. Our current assessment on mollusc landings in Kampong Chhnang was likely still underestimated because our study covered only major commercial landing sites. There are also numerous small-scale mollusc collectors that are dispersed in space and time in the complex inland ecosystems of the TS Lake. Also, the estimated mollusc landings excluded the quantity that collectors keep for household consumption.

Habitat degradation and fragmentation resulting from flood-forest clearing and wastes from intensive rice farming and industrial crops in the TS Lake, threats from golden apple snail (*Pomacea canaliculata*), intense harvesting pressure and the ignorance from formal institutions have put the important resources in a precarious condition. Overharvesting of mollusc species, *e.g.,* as reflected by the negative allometric growth, may also enhance the abundance and spread of the invasive, noncommercial golden apple snail, due to less competition with indigenous snail species and available space. The increase of this invasive snail is, on the one hand, a threat to the high-value native snail species, and on the other hand, is a harmful species to the agricultural productivity because it mainly feeds on young seedling of rice species and other aquatic-dependent crops (Ngor *et al.,* 2014). Furthermore, the changes in the status of *Corbicula* species can alter local and regional ecosystem functioning. *Corbicula* species provide a key ecosystem service in fresh waters by filtering out large quantities of algae, diatoms, bacteria, organic particles and silt and absorbing heavy metals and large organic molecules (Bogan, 2008; Musig *et al.,* 2012). Moreover, both the bivalves and gastropods play the pivotal role in the food web dynamics, *e.g.,* being one of the main food sources for many threatened, endemic and economic species inhabiting the Mekong and TS Lake including fish (*e.g., Probarbus jullieni*, *Chitala blanci*, *Cyclocheilichthys enoplos*, *Helicophagus waandersii, Pangasius bocourti*), turtle (*e.g., Sacalia quadriocellata*), birds (*e.g., Larus ridibundus*, *Anhinga melanogaster*) (Rainboth, 1996; Poulsen *et al.*, 2004; Ministry of Agriculture Forestry and Fisheries [MAFF], 2007; Froese and Pauly, 2017) water snakes and mammals, *e.g.,* rats (applesnail.net; Brooks *et al.*, 2007). Overharvesting of any particular mollusc species is thus likely to adversely influence not only local people but also the ecological functioning and food web of the TS ecosystem and beyond.

Given the current status of indiscriminate fishing effects of the TS (McCann *et al.*, 2016; Ngor *et al.*, 2018b) and human actions, *e.g.,* hydropower developments that block fish migration routes, modify river flows and degrade habitats as well as the decline of flooded forests around the TS Lake (MRC, 2011), the seasonal catches of many fish species are declining. The declines in fish populations have led to a strong shift in the natural resources exploitation to other aquatic animals, *e.g.,* molluscs, water snakes, crustaceans – shrimps in the TS River and Lake. During our field data collection, we observed that these resources were being intensively exploited. Therefore, it is imperative to call for more research, legislative support with appropriate planning, management and conservation actions if such important resources are to be sustained for the ecosystem and for long-term support to the people's livelihoods.

Supplementary Material

Supplementary figures and tables.
The Supplementary Material is available at https://www.limnology-journal.org/10.1051/limn/2018026/olm.

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