Journal of the Marine Biological Association of the United Kingdom

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Research Article

Cite this article: Dinh YHT, Lam NH, Lishchenko FV (2023). Life-history traits variation of *Lutjanus malabaricus* (Bloch & Schneider, 1801) in the waters off Northern Vietnam. *Journal of the Marine Biological Association of the United Kingdom* **103**, e45, 1–13. https://doi.org/10.1017/S0025315423000346

Received: 5 January 2023
Revised: 29 March 2023
Accepted: 22 May 2023

Keywords:
growth; life-history; *Lutjanus malabaricus*; Malabar blood snapper; maturity; seasonal variation; South China Sea

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Life-history traits variation of *Lutjanus malabaricus* (Bloch & Schneider, 1801) in the waters off Northern Vietnam

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Abstract

Lutjanus malabaricus represents a widely distributed and intensively exploited snapper species. The present article is the first attempt to describe the life-history traits of *L. malabaricus* in Vietnamese waters and estimate their variability. The fish were collected at the landing sites of Nghe An and Ha Tinh provinces from June 2020 to May 2021. The standard length of fish ranged from 10 to 74 cm, weight varied between 18.53 and 8972.89 g, age ranged from 1 to 17 years and all three parameters were subjected to a significant seasonal variation. A similar seasonal pattern was observed in the variation of maturity and gonadosomatic index. We assume that the observed variation of the stock structure is the result of spawning migrations when large fish migrate inshore from the foraging grounds. Growth and weight gain of fish were described via the von Bertalanffy function, constants of the equations were as follows: $L_\infty = 76.2$, $K = -0.077$, $t_0 = -2.26$ in males and $L_\infty = 56.9$, $K = -0.176$, $t_0 = -0.48$ in females; $W_\infty = 6498$, $K = -0.100$, $t_0 = -1.96$ in males and $W_\infty = 8317$, $K = -0.100$, $t_0 = -1.31$ in females. The growth constants of the North Vietnamese stock of *L. malabaricus* are similar to the ones of the North-eastern Australian stock. A general tendency for the reduction of the growth rate and asymptotic size from equatorial waters to higher latitudes was observed.

Introduction

Snappers (family Lutjanidae) are among the most economically important fishery resources in coastal tropical and subtropical waters such as the Caribbean and Indo-Pacific waters (Allen, 1985). Since 2000, annual catches increased from 215,031 to 505,108 tons worldwide (FAO, 2021). Moreover, as top-level predators, snappers play a very important role in the ecosystems they inhabit, especially shallow coastal waters and coral reefs (Arreguín-Sánchez *et al*., 1996; Newman and Williams, 1996; Oktaviyani, 2018).

In Vietnam, Lutjanidae is represented by 10 genera, which include 25 species. Most of them are found in the Gulf of Tonkin (18 species of four genera), where *Lutjanus argentimaculatus*, *L. erythropterus*, *L. vitta* and *L. russelli* are intensively fished by local artisanal fisheries (Thi and Tu, 1994; Phấn *et al*., 1999). Malabar blood snapper, *Lutjanus malabaricus* (Bloch and Schneider, 1801) is slightly less exploited but significantly less studied representative of the family, inhabiting these waters.

Malabar blood snapper is widely distributed in the Indo-West Pacific from the Fiji Islands to the Arabian Sea and Persian Gulf, and from Australia to southern Japan (Allen, 1985; Phấn *et al*., 1999; Anderson and Allen, 2001; Newman, 2002; Andamari *et al*., 2004; Vadziutsina and Riera, 2021). In Vietnam, *L. malabaricus* reaches the greatest abundance in the central coastal area (Phấn *et al*., 1999). According to Allen (1985), Masood and Farooq (2011) and Nurulludin *et al*. (2019), the Malabar blood snapper, similar to other Lutjanidae, is a vital component of coastal ecosystems, regulating the abundance of fishes, cephalopods, crustaceans and other benthic invertebrates.

It is an important market species throughout a significant part of its range and a major recreational and commercial species in northern Australia and parts of Asia and the Pacific (Allen, 1985; Phấn *et al*., 1999; Anderson and Allen, 2001; Newman, 2002; Andamari *et al*., 2004; Fry *et al*., 2009; Wibisono *et al*., 2019; Rapi *et al*., 2020). Total annual catches of Malabar blood snapper alone increased from 445 tons in 2000 to 1742 tons in 2019, according to the Food and Agriculture Organization of the United Nations (FAO, 2021). It is also an aquaculture species in Southeast Asia in general and in Vietnam in particular, where it is cultured in brackish water ponds and marine cages (Emata *et al*., 1999; Phấn *et al*., 1999).

Several studies have addressed basic life-history traits, age, growth, maturation and spawning of the Malabar blood snapper across southern, central and western parts of its range (Edwards, 1985; Newman *et al*., 2000, 2002; Andamari *et al*., 2004; Fry *et al*., 2009; Fry and Milton, 2009; Masood and Farooq, 2011; Raeisi *et al*., 2011; Mazumder *et al*., 2016; Ernawati and Budiarti, 2019; Nurulludin *et al*., 2019; Rapi *et al*., 2019, 2020; Wibisono *et al*., 2019; Ben-Hasan *et al*., 2021). According to these studies, the life-history parameters of *L. malabaricus* may vary significantly, depending on the region.

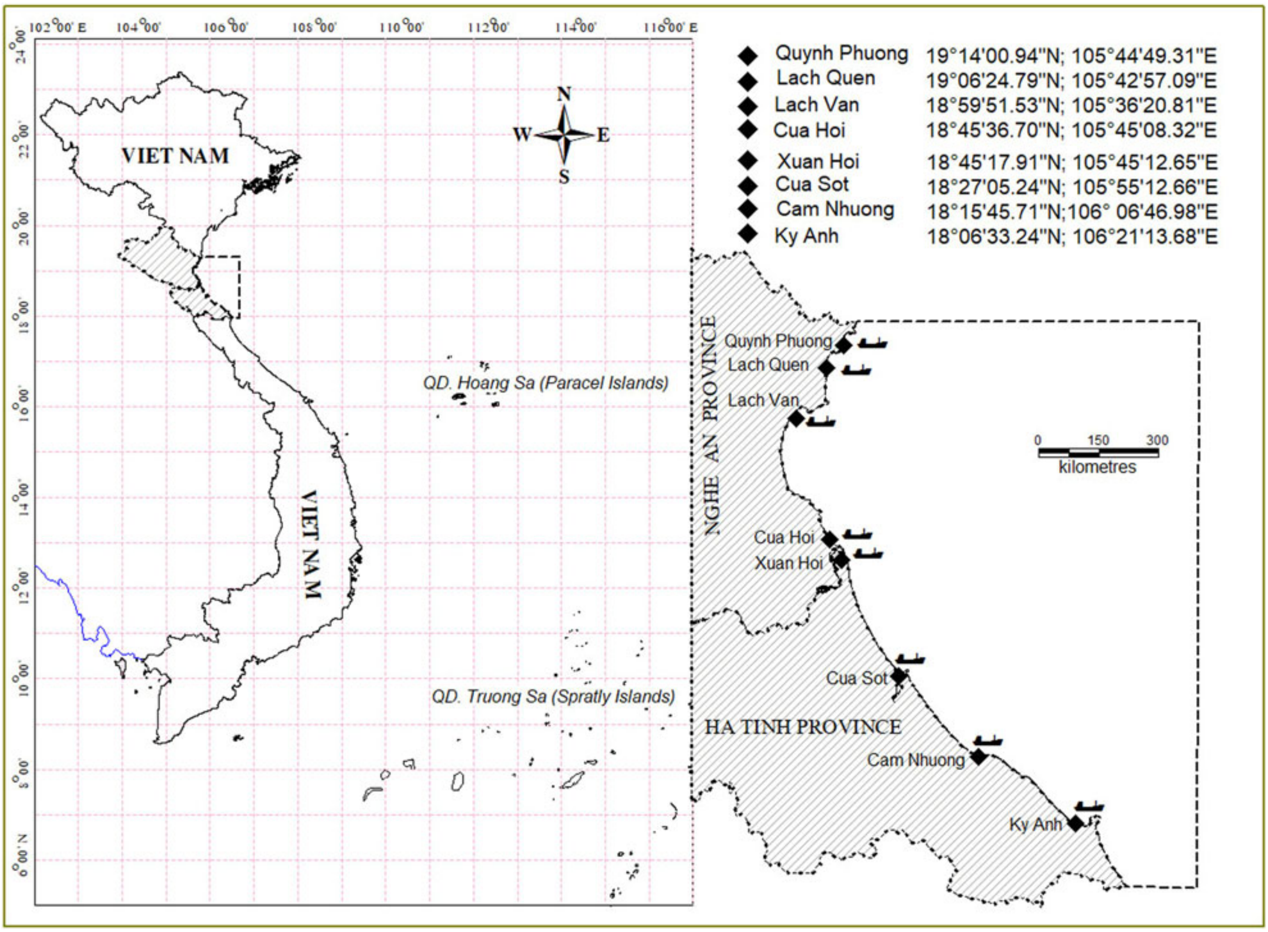

Figure 1. Area of research. Diamonds stand for landing sites where sampling of *Lutjanus malabaricus* was carried out.

Despite its high economic value, no studies on the life-history traits of *L. malabaricus* were performed in Vietnam. Existing studies are focused on the taxonomy and distribution of snappers (Thi and Tu, 1994; Phấn *et al*., 1999; Thanh, 2013). There is an urgent need to develop a management strategy based on scientific evidence to prevent the depletion of snapper stocks. Therefore, an in-depth study of the life-history traits of *L. malabaricus* was performed to fill this knowledge gap.

Materials and methods

Area of research and sampling protocols

The study on Malabar blood snapper was performed in the waters of Nghe An and Ha Tinh provinces. Fish specimens were collected from the catches of selected local commercial fishers at fish landing sites across these provinces (Figure 1). The fish were caught using traditional fishing gears, including drift nets (mesh size 60–100 mm), bottom drop-lines or artisanal fish traps at depths from 10 to 100 m.

Sampling was done following two obligatory requirements:

1. The fish was caught only in the waters adjacent to the sampling site (within the nearest ten nautical miles);
2. No preliminary sorting of catches was performed.

The sampling was carried out from June 2020 to May 2021 on a monthly basis. Every month at least 30 randomly selected individuals were dissected, if total catches were not sufficient (e.g. due to poor weather conditions in October–November 2020 and April–May 2021), all caught specimens were studied.

The fish were measured, weighed and dissected at the sampling site, gonads and recording structures were preserved according to the standard methods (Pravdin, 1966) and transported to the laboratory of the Coastal Branch of the Russian-Vietnamese Tropical Center for further analysis.

In total, 365 specimens of *L. malabaricus* were examined.

Basic measurements

Standard examination of *L. malabaricus* included measurement of total length (TL, to the nearest 0.05 mm), standard length (further SL, to the nearest 0.05 mm), total body weight (further TBW, to the nearest 0.01 g), gutted weight (further GW, to the nearest 0.01 g), gonad weight (further gw, to the nearest 0.01 g) and determination of sex and stage of maturity.

Since the total length was too much affected by random factors (damage on rays of the caudal fin in particular), the SL was used in all analyses and modelling. Total body weight was applied to estimate the gonadosomatic index (GSI) of fish, using the following equation (Pravdin, 1966; Schimose and Tachihara, 2005): $GSI = \frac{gw}{TBW} \times 100$.

For the rest of the analyses and modelling of the weight gain, GW was used because it is not affected by stomach fullness and gonad maturation.

After dissecting the fish, gonads were preserved in Bouin's fixative. Since the gonads are developing synchronously, and examination of ovaries allows clearer determination of the maturity stage and spawning season, in the framework of the present research, only ovaries were studied (Piñón *et al*., 2009). Ovaries maturity stage was determined according to Pradeep's five-point maturity scale for Lutjanids (Pradeep, 2017), where I stands for

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Table 1. Sex ratio of the *Lutjanus malabaricus* stock in Nghe An and Ha Tinh provinces, June 2020–May 2021

Month	*N* male	*N* female	% Male	% Female	Yates corrected χ^2	*P*
January	16	14	53.3	46.7	0.01	0.91
February	21	22	48.8	51.2	0.00	0.96
March	20	20	50.0	50.0	0.04	0.85
April	10	15	40.0	60.0	0.45	0.50
May	7	9	43.8	56.3	0.04	0.85
June	**24**	**6**	**80.0**	**20.0**	**7.29**	**0.01**
July	12	18	40.0	60.0	0.57	0.45
August	20	16	55.6	44.4	0.14	0.71
September	18	12	60.0	40.0	0.57	0.45
October	13	16	44.8	55.2	0.08	0.78
November	13	13	50.0	50.0	0.05	0.83
December	10	20	33.3	66.7	1.95	0.16

Significant differences are highlighted in bold.

immature, II is a maturing fish, III is a mature fish, IV stands for ripe fish and V represents spent individuals. Gonad maturity assessments were validated by the investigation of histological samples following the protocols described by Saber *et al.* (2019).

Recording structures, namely scales and otoliths, were collected for estimation of age. After collecting, both structures were preserved dry. The increments in the otoliths were poorly visible without additional processing, so in the framework of the present study, only scales were used as a tool for age determination (Pravdin, 1966). Nevertheless, the subsample of otoliths (20 left sagitta otoliths in total, 5 units of fish smaller than 35 cm, 10 units between 35 and 50 cm and 5 units of fish larger than 50 cm) was used for validation of the age estimation based on scale readings. Since the otolith-based and scale-based estimations provided the same result, the latter were applied for the age determination of the remaining individuals.

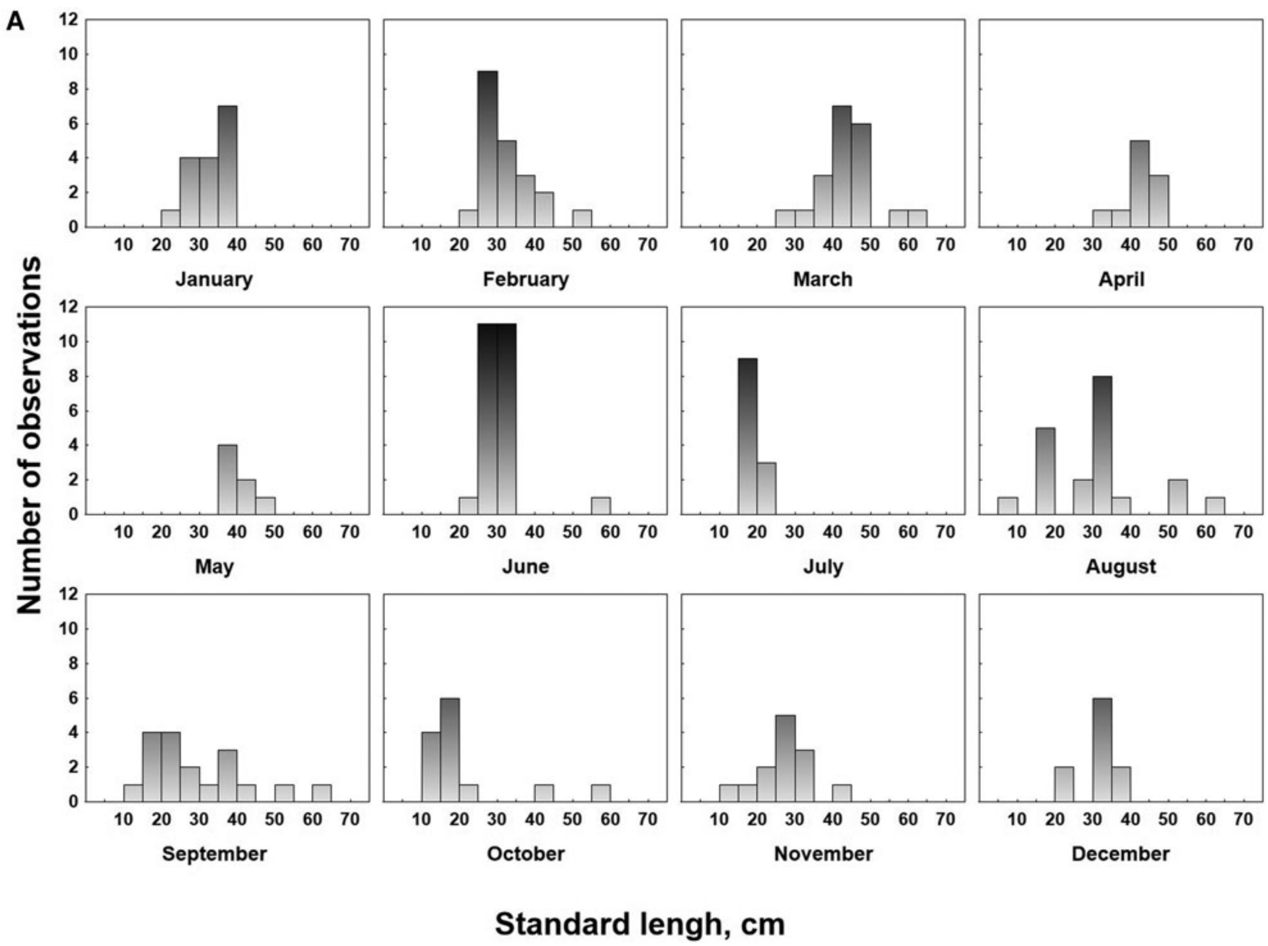

Figure 2. Size structure of *Lutjanus malabaricus* stock ((A) males, (B) females) in the waters off Ha Tinh and Nghe An provinces in June 2020–May 2021.

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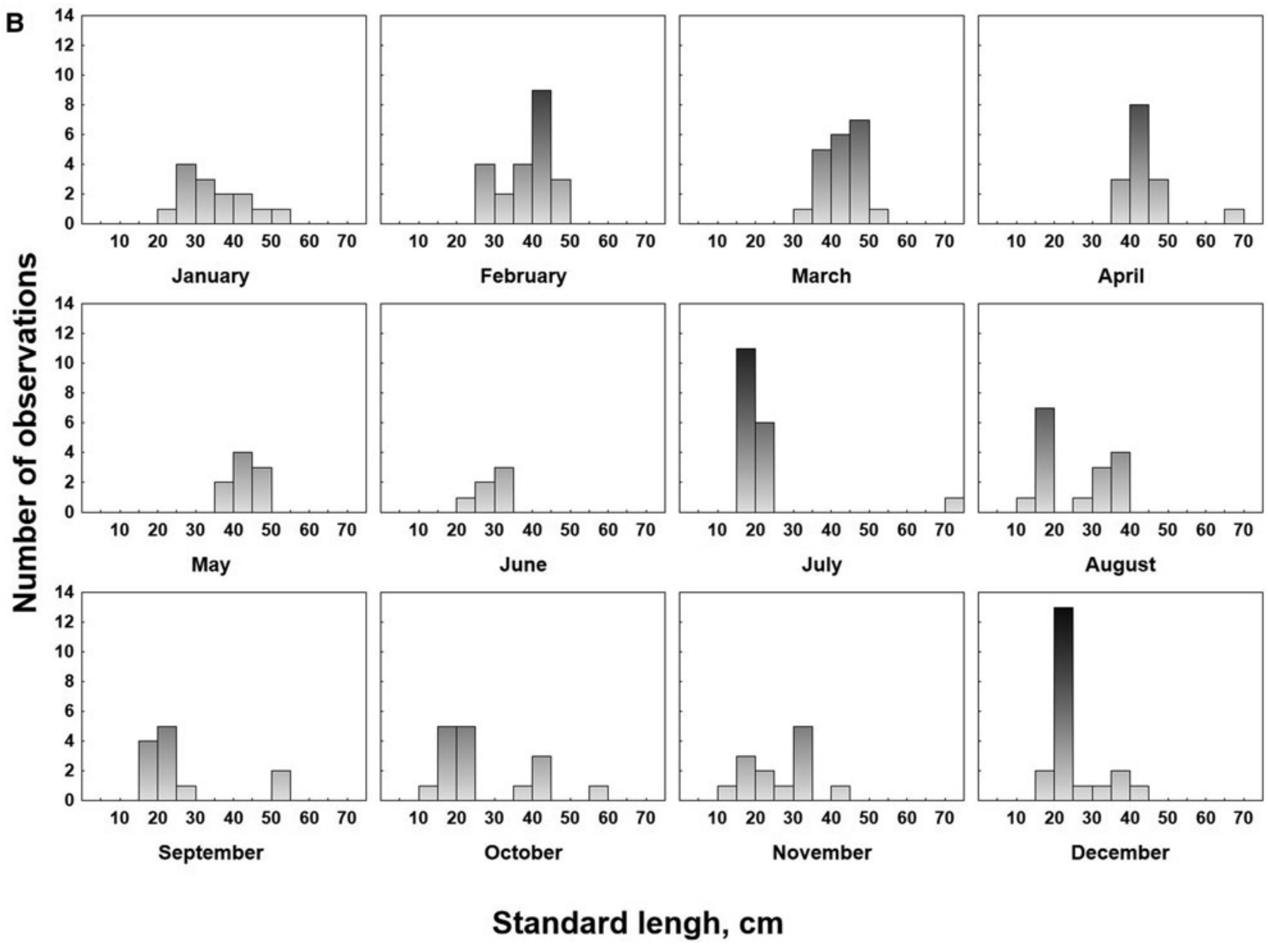

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Data analysis

The sex ratio was tested on the monthly basis, in order to check if it corresponds to 50% male:50% female, using χ^2 test with Yates correction (Hays, 1988).

Data on monthly maturity, size and weight ratio were tested for normality, using the Shapiro–Wilk test (Shapiro *et al.*, 1968). Distributions were considered normal when W was higher than 0.5 and P was higher than 0.05.

In cases when the distribution of the variable was assumed normal (in particular, in cases of size, weight and age of fish, pooled by sex), a simple t-test for independent samples was applied to check if the differences between the groups were significant (Hays, 1988).

The Mann–Whitney U test was used to test the differences between pairs of the groups when the distribution of the variable was assumed not normal (sex differences in maturity stage ratio and GSI value, sex differences in all measures within monthly samples).

Finally, when the null hypothesis on the normality of the distribution of the variable was not confirmed, and multiple groups were compared (differences between months or differences in GSI between maturity stages), a non-parametric Kruskal–Wallis test and multiple comparisons of mean ranks for all groups matrix were applied to test the differences (Siegel and Castellan, 1988).

Since most of the analysed parameters had distributions different from the normal one, the mode was applied to describe samples instead of the mean.

The growth pattern was modelled by fitting the von Bertalanffy function (von Bertalanffy, 1938):

$L_t = L_\infty\,(1 - \exp\,(-K(t - t_0)))$, where L_∞ is the asymptotic length, K is the growth coefficient and t_0 is the theoretical age at zero length, to standard length at age data of each sex separately, least squares loss function was applied to estimate the accuracy of the model (Wald, 1939).

To model weight gain, the von Bertalanffy function for weight gain was applied:

$W_t = W_\infty\,(1 - \exp\,(-K(t - t_0)))^3$, where W_∞ stands for the asymptotic weight, K is the growth coefficient and t_0 represents the theoretical age at zero length. Similarly to linear growth modelling, least-squares loss function was used for estimation of the model's accuracy.

The relationship between the linear size of fish and its weight was described by fitting the coefficients of a power function to weight at length data (Newman, 2002).

All tests were performed using Statistica v. 12.0 software.

Results

Basic life history traits

In total, 184 male and 181 female individuals of *L. malabaricus* were sampled during the study period. No statistically significant predominance of one sex over another was observed except for June 2020, when the stock was significantly dominated by males (Table 1).

SL of male fish ranged from 10 to 64 cm, while the SL of females ranged from 13 to 74 cm. Unlike the sex ratio, the size class composition of the *L. malabaricus* stock experienced noticeable seasonal variation (Kruskal–Wallis test, H (11) = 85.6, P =

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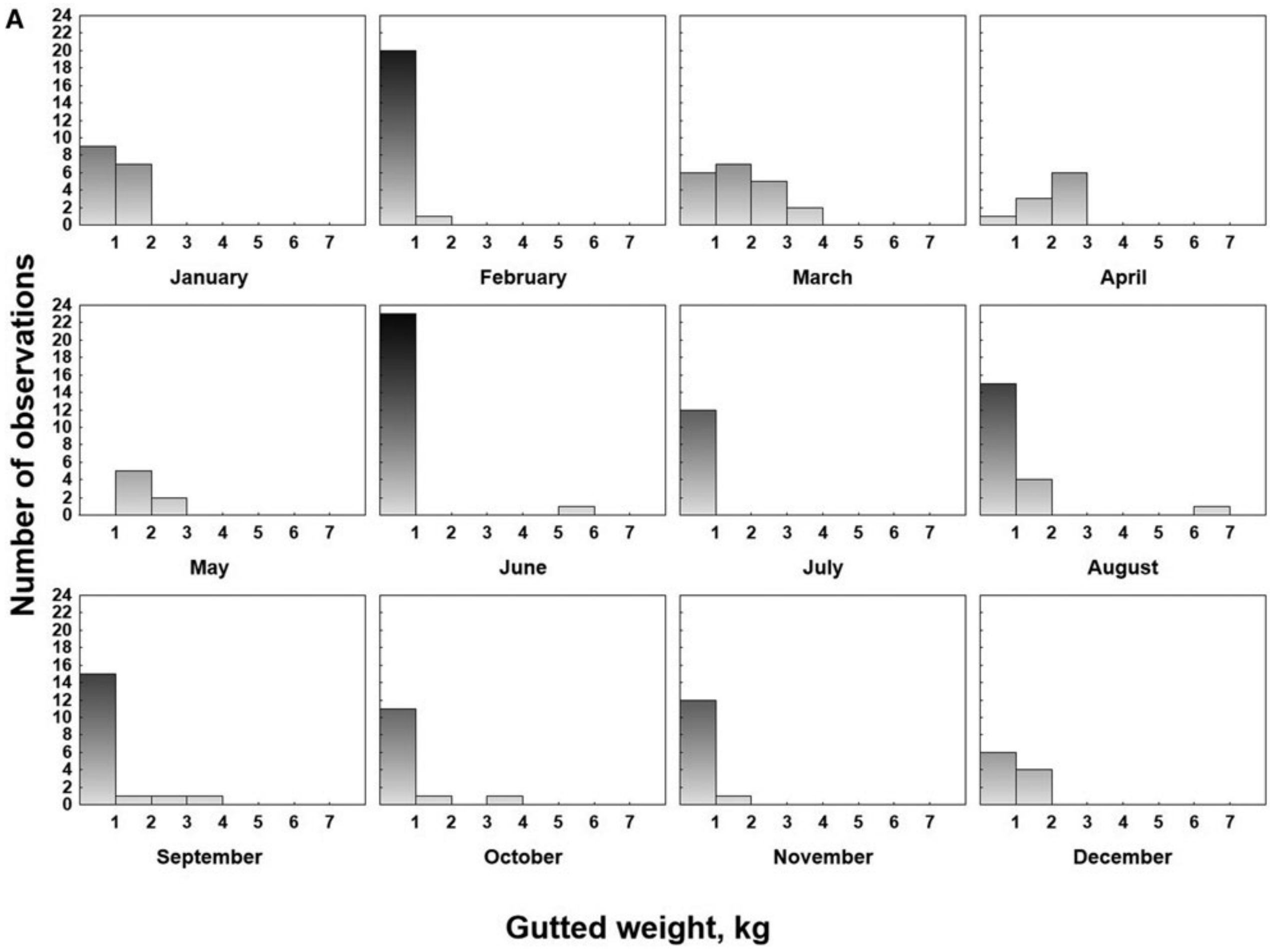


Figure 3. Weight structure of *Lutjanus malabaricus* stock ((A) males, (B) females) in the waters off Ha Tinh and Nghe An provinces in June 2020–May 2021.

0.001 in males; H (11) = 93.4, P = 0.001 in females). In general, size class dynamics could be determined as a seasonal succession of small-sized, large-sized and mixed groups of fish.

In this context, three seasonal cohorts were identified in males (Figure 2A): the large-sized group, which predominated in March–May and had modal size classes larger than 40 cm; the small-sized group, which was the most abundant in June–November and included fish with the modal classes smaller and equal to 35 cm; and the mixed group which included individuals of both small- and large-sized groups, to which fishes sampled in December–February and June can be attributed.

In females, these differences were even more pronounced (Figure 2B). Similar to males, three size groups were observed: the group composed of large-sized individuals (modal size classes 40–50 cm), predominant in February–May; the small-sized group, the most abundant in July–December (modal size classes were less than 35 cm); and mixed group, observed in January and June.

Size differences between sexes were insignificant (t value = −0.4, P = 0.6873). Within monthly samples, significant differences in standard length between sexes were observed twice, in February (Mann–Whitney U test, Z value = −3.1, P = 0.0019), when the mixed group still was the most abundant among males, while in females large-sized group already became predominant, and in December (Mann–Whitney U test, Z value = 2.1, P = 0.0407), when the mixed group was predominant among males and small-sized group was the most abundant among females.

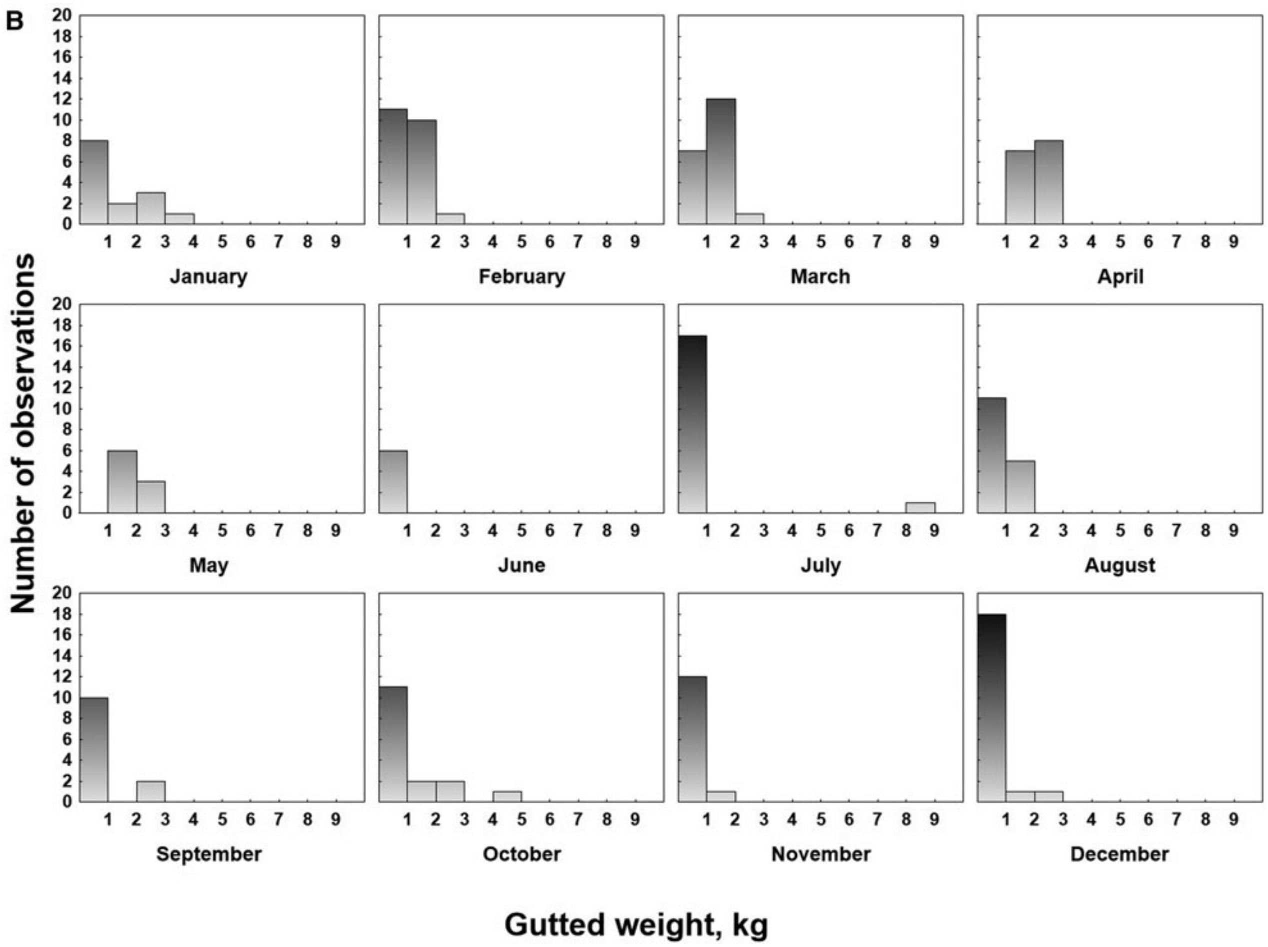
GW of *L. malabaricus* ranged from 18.53 to 8972.89 g (34.26–6809.00 g in males and 18.53–8972.89 g in females). Similarly to the length of fish, no significant differences between the mean GW of males and females were observed (t-value = −0.4, P = 0.7142).

The weight class structure of the stock was subjected to the same kind of dynamics as the size class structure (Kruskal–Wallis test, H (11) = 90.4, P = 0.0001 in males; H (11) = 85.0, P = 0.0001 in females).

Thus, the group of large males (with modal weight classes of more than 1 kg) predominated in March–May; the group of small-sized males (with modal classes of 1 kg and less) was the most abundant in June–November and February; while the mixed group prevailed in December–January (Figure 3A). In females, large-sized group also was the most abundant from March to May, small-sized one prevailed in June–December and the mixed group was observed in January and February (Figure 3B).

Regarding weight, differences between sexes within monthly samples, two months, characterized by significant differences determined by sex were identified. In February, while males were represented by the small-sized group, in females mixed group prevailed (Mann–Whitney U test, Z value = −3.1, P = 0.0021). In December, reverse situation was observed: among males, fish of the mixed group was the most abundant, while females were represented by a small-sized group (Mann–Whitney U test, Z value = 2.8, P = 0.0052).

Within the period of study, only a very limited number of spent individuals was observed, and the stock was comprised of fish in maturity stages from I to IV. Even though statistically significant monthly differences in the ratio of maturity stages were observed (Kruskal–Wallis test, H (11) = 48.0, P = 0.0001), seasonal pattern (i.e. successive predominance of immature, maturing, mature, ripe and spent fish in the stock) was found only in the first half of the year (Figure 4). Specifically, in January, the



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stock was dominated by immature fish; in February, the amount of maturing and mature fish increased, making portions of immature, maturing and mature individuals similar; in March and April, the mature and ripe individuals prevailed in the stock; finally, in May, most of the individuals were either ripe or spent. However, in the second half of the year, we didn't observe a smooth transition into the prevalence of the immature fish as could be expected. Instead, July and October were characterized by the prevalence of maturing and mature individuals; in August and September, maturing fish prevailed; and only in November and December, prevalence of immature individuals was observed.

Significant differences were observed only between January and March, April, May; February and May; March and January, November; May and November–February.

Another measure of maturity, GSI, experienced very similar dynamics. In males, GSI ranged from 0.001 to 3.834%, and in females, it varied from 0.009 to 4.848%. GSI significantly differed between sexes (Mann–Whitney U test, Z value = −9.1, $P = 0.0001$).

Significant monthly variation was observed as well (Kruskal–Wallis test, H (11) = 36.0, $P = 0.0002$ in males; H (11) = 46.0, $P = 0.0001$ in females). But the pairwise analysis did allow us to identify a clear seasonal variation. In males, significant differences were observed only between June and November–January (Figure 5A), and in females, significant differences were found between March, April, May in one group and October–January in another group (Figure 5B).

On the other hand, differences between sexes within monthly samples were observed in all months except June (Mann–Whitney U test, Z value = −0.46, $P = 0.6472$) and August (Mann–Whitney U test, Z value = −1.52, $P = 0.1293$).

Clear differences in GSI were observed between individuals at different stages of gonad development (Kruskal–Wallis test, H (4) = 79.2, $P = 0.0001$ in males; H (4) = 104.6, $P = 0.0001$ in females). With maturation, median GSI increased in males from 0.01 at stage I to 0.78% at stage V, and in females, it increased from 0.03 to 1.87%.

Finally, the age structure of the *L. malabaricus* stock was examined. The age of fish ranged from 1 to 16 years in males and from 1 to 17 years in females, and differences between sexes were insignificant (t-value = 0.7, $P = 0.4726$).

Surprisingly, significant monthly variation in age was observed in both males (Kruskal–Wallis test, H (11) = 69.4, $P = 0.0001$) and females (Kruskal–Wallis test, H (11) = 75.3, $P = 0.0001$). Stock in winter and spring was predominated by older fish (modal age 6 years and more), while in summer and autumn, younger individuals (3 and fewer years) were much more abundant. In males, older fish prevailed in December–June, the prevalence of the younger ones was observed in July–October, and in November, both groups mixed in the stock (Figure 6A). In females, older individuals were the most abundant in January, February, April and May, and younger individuals prevailed in other months (Figure 6B).

Significant differences between sexes in monthly samples were observed only once, in December, when males were represented by a mixed group, while among females, young individuals were clearly predominant (Mann–Whitney U test, Z value = 2.2, $P = 0.0263$).

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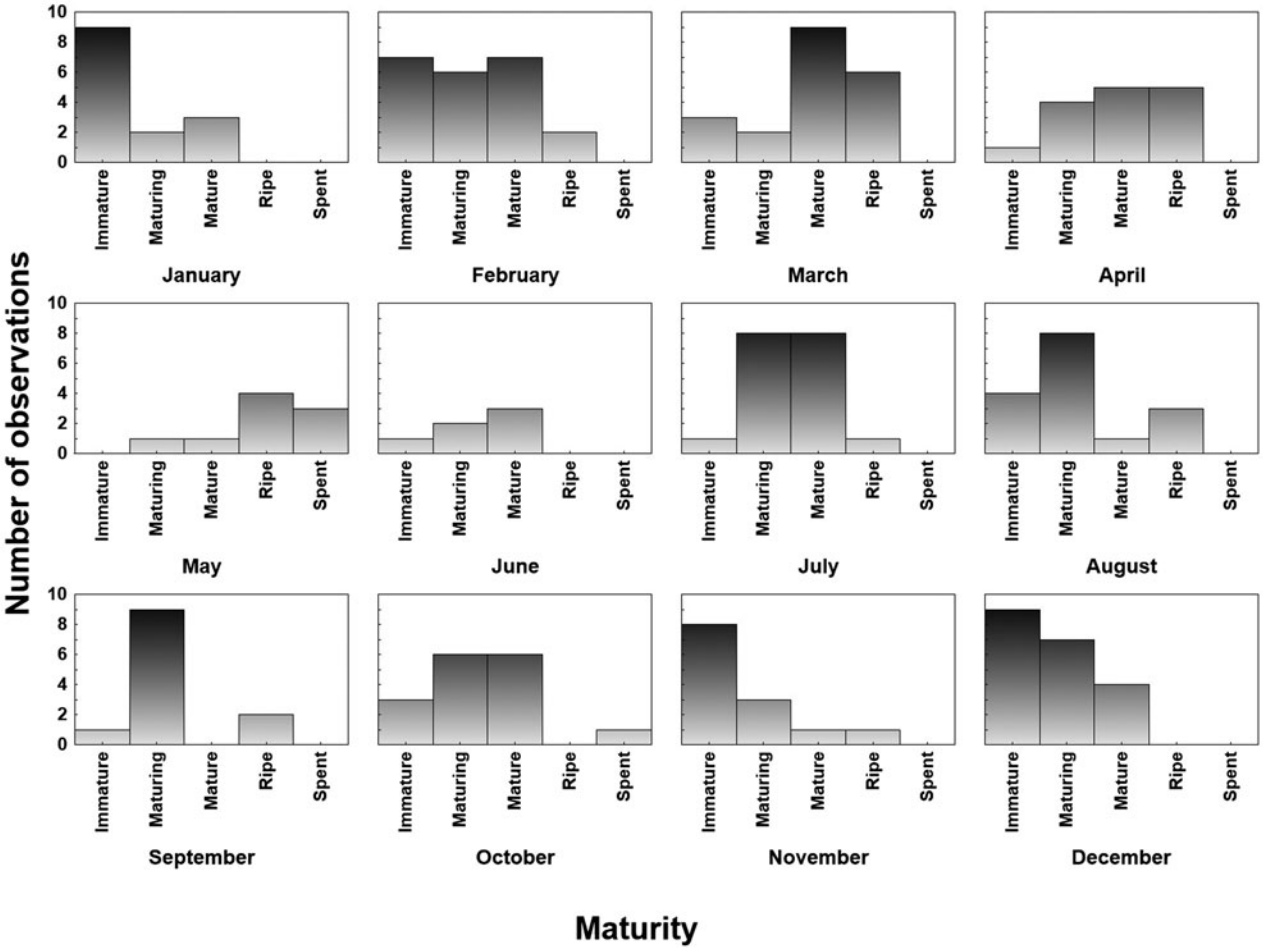

Figure 4. Functional structure of *Lutjanus malabaricus* stock in the waters off Ha Tinh and Nghe An provinces in June 2020–May 2021.

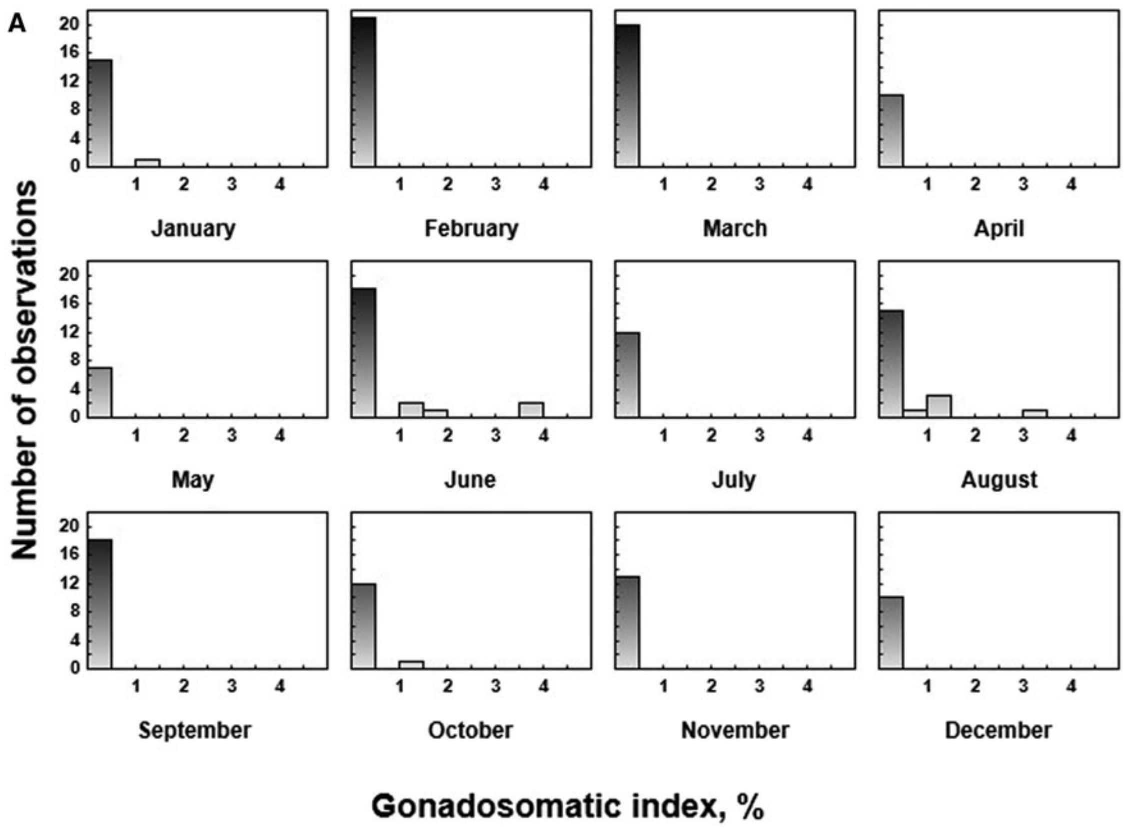

Figure 5. Gonadosomatic index of *Lutjanus malabaricus* stock ((A) males, (B) females) in the waters off Ha Tinh and Nghe An provinces in June 2020–May 2021.

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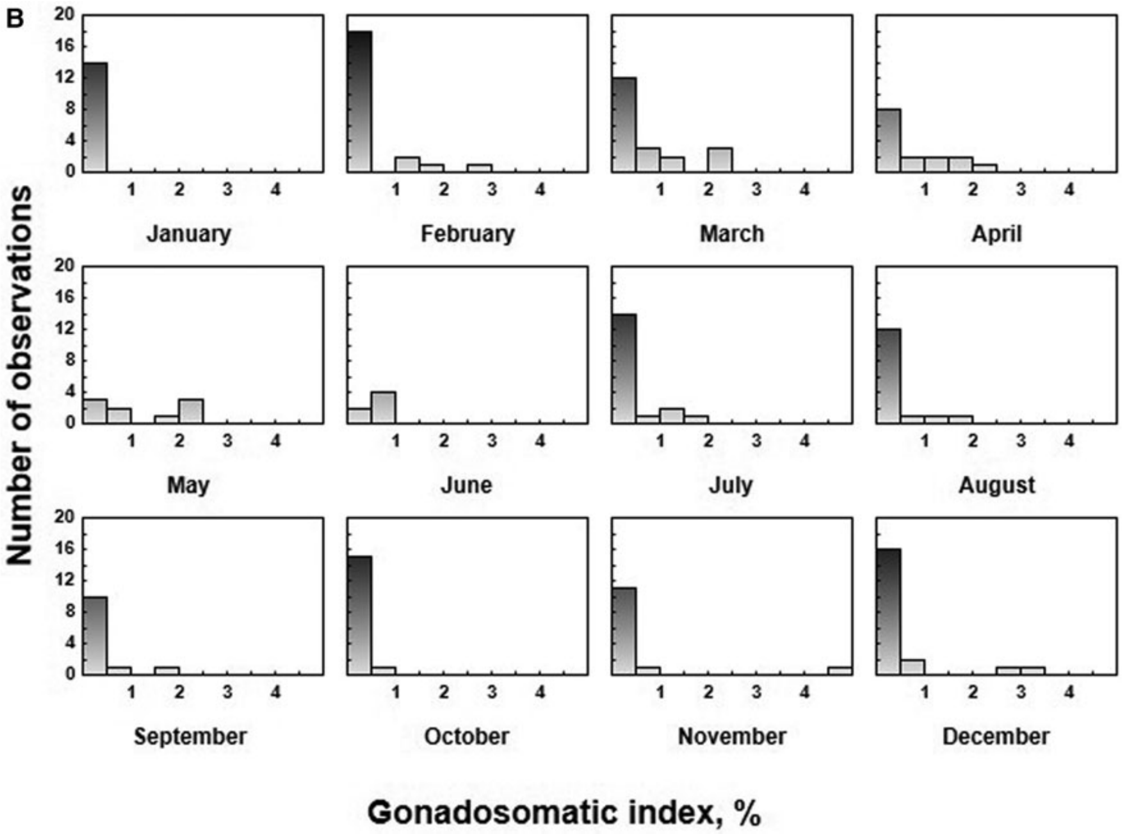

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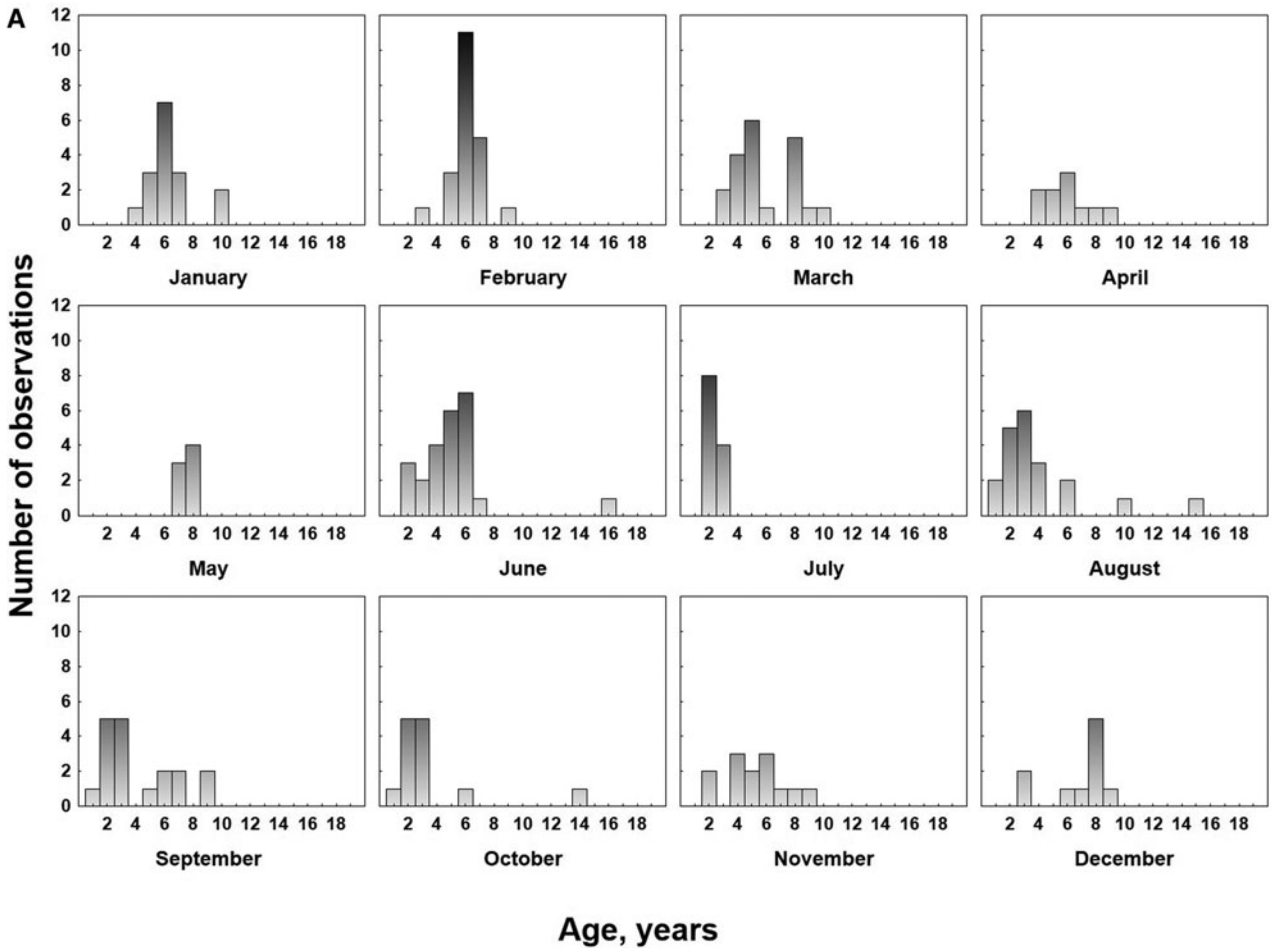

Figure 6. Age structure of *Lutjanus malabaricus* stock ((A) males, (B) females) in the waters off Ha Tinh and Nghe An provinces in June 2020–May 2021.

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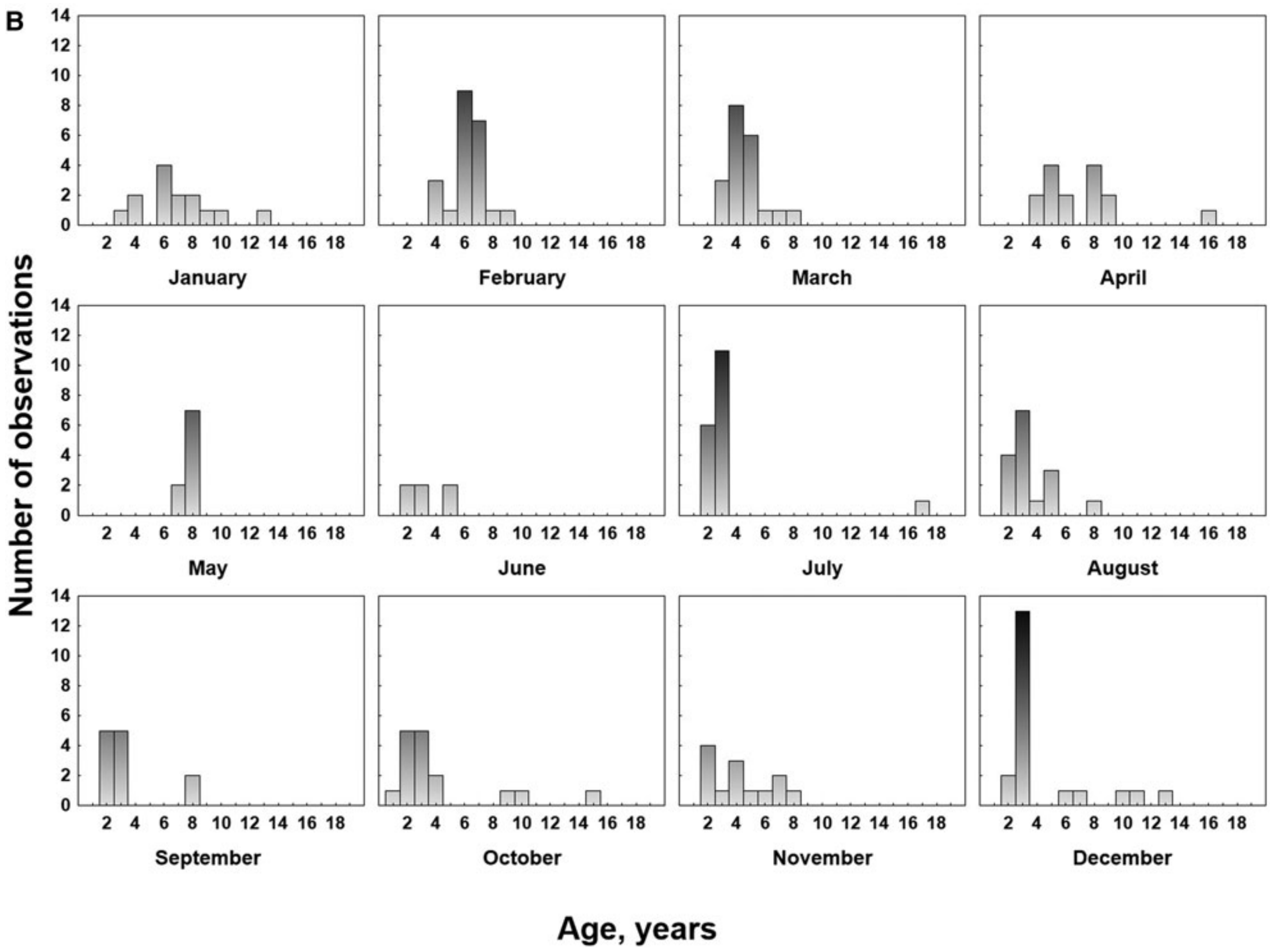

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Growth and weight gain

In order to reconstruct the growth, standard length and age data were pooled by sex. Since the seasonal differences in length-at-age were insignificant (Mann–Whitney *U* test, *Z* value = −0.9, *P* = 0.3916 in males; *Z* value = −0.7, *P* = 0.48 in females), no separation by the seasonal group was introduced.

In case of males, the von Bertalanffy function fitted to the standard length-at-age data was as follows: $L_t = 76.2\ (1 - \exp\ (-0.077\ (t + 2.26)))$, $R^2 = 0.747$, and the proportion of variance accounted for was 0.56 (Figure 7A).

Residual values ranged from 0.01 to 27.48 cm, and the mean residual was 5.71 cm.

In the case of females, the function with fitted coefficients was: $L_t = 56.9\ (1 - \exp\ (-0.176\ (t + 0.48)))$, $R^2 = 0.782$, and the proportion of variance accounted for reached 0.61 (Figure 7B).

Residual values ranged from 0.005 to 21.99 cm, and the mean residual was 5.83 cm.

Following the same approach, the weight gain pattern was reconstructed. Data were pooled by sex, and no seasonal separation was introduced. Coefficients of the von Bertalanffy function for weight growth were fitted to gutted weight-at-age data.

In males, the function with the fitted coefficients was: $W_t = 6498\ (1 - \exp\ (-0.1(t + 1.96)))^3$, $R^2 = 0.685$, and the proportion of variance accounted for was 0.47 (Figure 8A).

Residual values ranged from 0.7 to 4602.3 g and increased with weight, although the mean residual value was 408.2 g.

In females, the function with the fitted coefficients was: $W_t = 8317\ (1 - \exp\ (-0.1(t + 1.31)))^3$, $R^2 = 0.801$, and the proportion of variance accounted for was 0.64 (Figure 8B).

Residual values varied between 1 and 4047.2 g and followed the same pattern of increase with weight, as in the case of males. The mean residual value in females was 384.1 g.

In modelling length–weight relationship, the standard length and gutted weight were used as a measure of length and weight, respectively. Similarly to describing growth and weight gain, the data were pooled by sex.

In males, the function with fitted coefficients was: $GW_{SL} = 0.079\ SL^{2.63}$, $R^2 = 0.898$, and the proportion of variance accounted for was 0.81 (Figure 9A).

In females, the function was: $GW_{SL} = 0.055\ SL^{2.72}$, $R^2 = 0.892$, and the proportion of variance accounted for was 0.80 (Figure 9B).

Residual values ranged from 0.4 to 2306.2 g (mean – 209.7 g) in males and from 0.9 to 3057.1 g (mean – 269.8 g) in females.

Since estimated growth coefficients *b* in both sexes were below 3 (*b* = 2.63 in males and *b* = 2.72 in females), we assume that both sexes were characterized by negative allometric growth (Raeisi *et al*., 2011; Mazumder *et al*., 2016).

Discussion

Despite the wide distribution and significant ecological and economical value of snappers, knowledge of the local patterns of life-history traits of species inhabiting Vietnamese waters is very scarce. The present study represents the first attempt to describe the life-history traits of intensively exploited *L. malabaricus* and their seasonal variation in the waters off northern Vietnam.

It was found that the stock of Malabar blood snapper in Nghe An and Ha Tinh provinces is in a sex-balanced condition (i.e. the

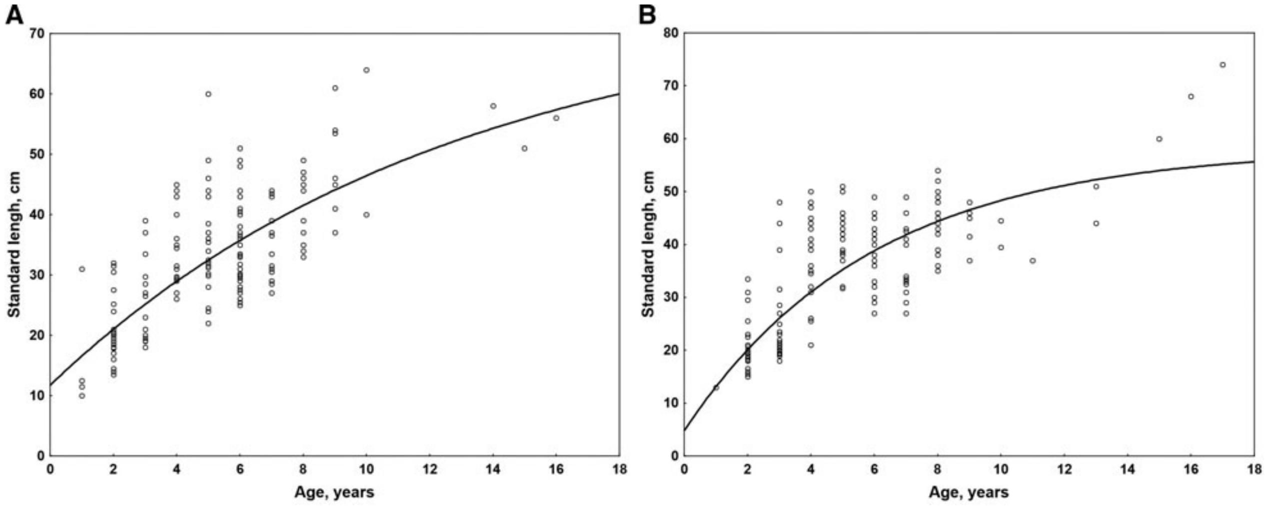

Figure 7. Growth pattern of male (A) and female (B) *Lutjanus malabaricus* in the waters off Ha Tinh and Nghe An provinces in June 2020–May 2021.

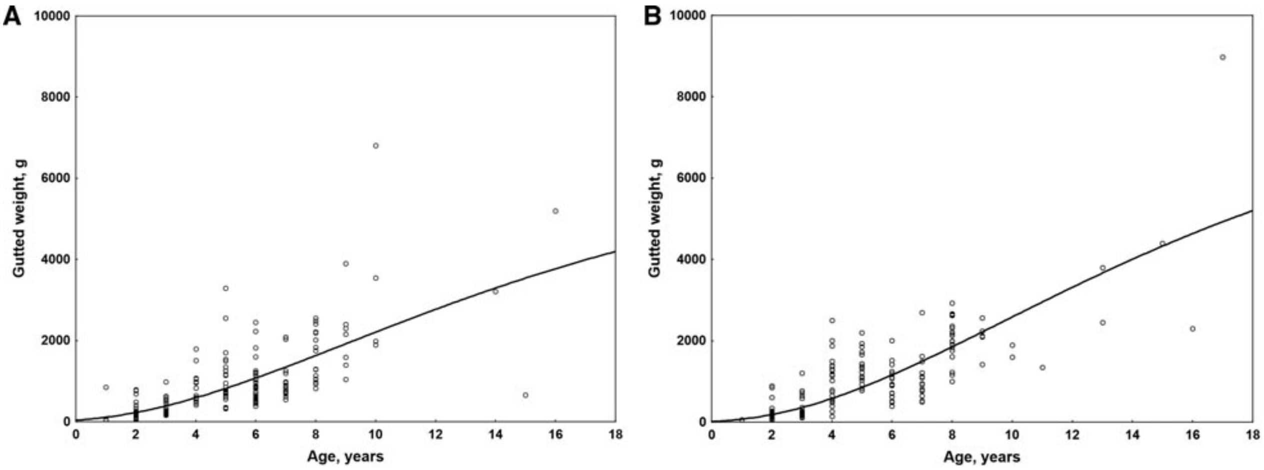

Figure 8. Weight gain of male (A) and female (B) *Lutjanus malabaricus* in the waters off Ha Tinh and Nghe An provinces in June 2020–May 2021.

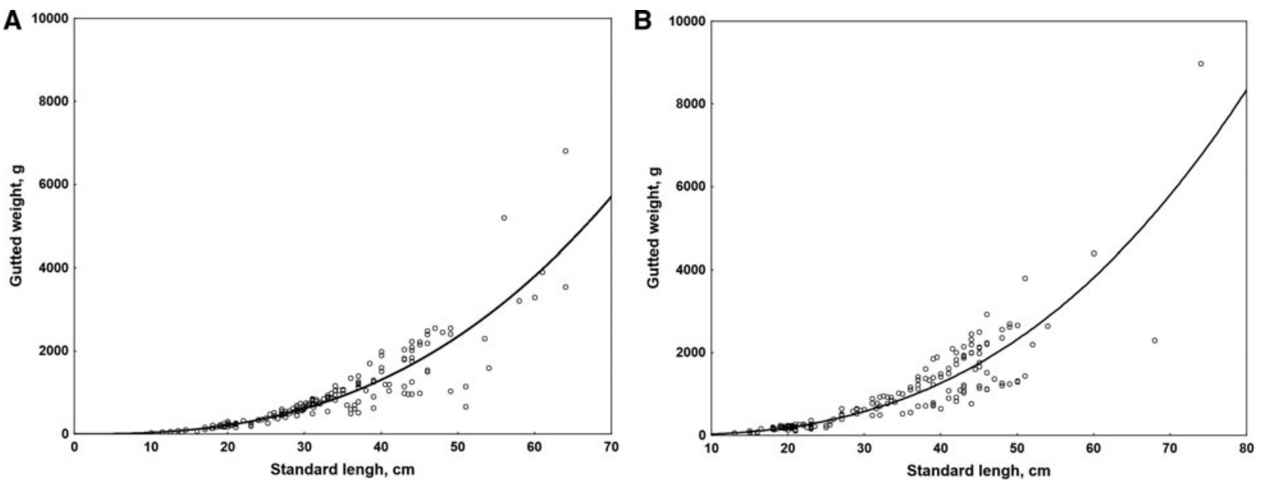

Figure 9. Length–weight relationship of male (A) and female (B) *Lutjanus malabaricus* in the waters off Ha Tinh and Nghe An provinces in June 2020–May 2021.

amount of males is equal to the amount of females) during the whole year, which is in agreement with observations performed in Pinrang waters (Rapi *et al*., 2020). Even though a statistically significant prevalence of males was observed in June, we tend to assume that it was an artefact of sampling. Such a sex ratio is not typical for snapper stocks; usually, they are characterized by a clear predomination of one sex (Shimose and Tachihara, 2005; Fry *et al*., 2009). Although these findings also could be due to sampling artefacts, because in cases when the sample size exceeded 100 individuals and specialized fishing gear was used, the sex ratio of *L. malabaricus* was close to 1:1 (Fry *et al.*, 2009; Rapi *et al.*, 2020).

Fish, examined within the framework of this study, were markedly smaller than one caught in Pakistani waters (Masood and Farooq, 2011), or than one found in catches of Indonesian deep-slope demersal fishery (Wibisono *et al.*, 2019). In particular, in the first case, the maximum reported length was 100 cm Masood and Farooq, 2011), and in the second one, this parameter reached 95 cm (Wibisono *et al.*, 2019). On the other hand, the fish found in the shallower waters usually have lengths similar to Vietnamese stock. In the Persian Gulf, it reached 58.5 cm (Raeisi *et al.*, 2011); in coastal waters off Indonesia, this parameter varied from 57 to 74 cm (Fry and Milton, 2009; Rapi *et al.*, 2019); and in waters off the Australian coast, maximum length varied between 68 and 80 cm, depending on the location of capture and depth (Newman, 2002; Northern Territory Government, 2016).

Similar variation may be found in weight: in Indonesian waters, the maximum weight reaches 2.5 kg, according to Rapi *et al.* (2019), while in Australian waters, it exceeded 8 kg (Newman, 2002). It should be mentioned that Fry *et al.* (2009) reported that the mean weight of fish ranges from 768 to 3203 g in waters off Indonesia and New Guinea and from 1224 to 2088 g in Australian waters. The maximum weight of snappers caught in Vietnamese waters was significantly higher than one of the fish studied in Indonesian waters (Rapi *et al.*, 2019) and similar to Australian values (Newman, 2002), while the modal weights were comparable with the mean weights reported by Fry *et al.* (2009) for Bali, Ambon region in Indonesia, Arafura Sea and West and East Gulf off Australia.

We tend to believe that this is the result of the spatial and depth distribution of individuals belonging to different size cohorts, generally typical for snappers (Arreguín-Sánchez *et al.*, 1996; Masood and Farooq, 2011).

Moreover, the fish studied in the framework of this research were markedly younger than in other regions. The maximum age of *L. malabaricus* was 45 years in the Persian Gulf (Ben-Hasan *et al.*, 2021), 10–33 years in Indonesian waters (Fry and Milton, 2009; Ernawati and Budiarti, 2019) and 19–48 years in Australian waters (Milton *et al.*, 1995; Newman, 2002; Fry and Milton, 2009; Northern Territory Government, 2016), while in our sample, the maximum age reached just 17 years. Considering this and the calculated growth parameters, we assume that the size of the older individuals should be similar to the one reported for Australian waters.

Regarding growth parameters, our estimation of constants of the von Bertalanffy equation is close to the ones for Australian waters and southern Indonesia (Edwards, 1985; Newman, 2002; Fry and Milton, 2009) and to waters off Pakistan (Masood and Farooq, 2011). According to the literature data, there is a general trend in the increase of growth coefficients and asymptotic length in the equatorial area (Wahyuningsih *et al.*, 2016; Tirtadanu and Sadhotomo, 2018; Nurulludin *et al.*, 2019). For example, the asymptotic length varied between 55.3 and 97.7 cm in Indonesian waters (Fry and Milton, 2009; Wahyuningsih *et al.*, 2016; Ernawati and Budiarti, 2019) and from 45.9 to 70.7 cm in Australian waters, depending on the sex and area of research (Edwards, 1985; Newman, 2002; Fry and Milton, 2009).

Even though on some occasions this difference was raised from the differences in methodological approaches (some authors, in particular (Tirtadanu and Sadhotomo, 2018), used total length for growth modelling), we tend to assume that lower values of growth constants are characteristic of higher latitudes. The only exception from this rule was observed in the waters off Kuwait, where the growth coefficient was even higher than in Indonesian waters (Ben-Hasan *et al.*, 2021).

Another growth parameter, growth allometry, was addressed in several studies, performed both in the wild and in the aquaculture conditions. These studies showed that the growth of *L. malabaricus* is characterized by slightly negative allometry (Edwards, 1985; Newman, 2002; Mazumder *et al.*, 2016; Tirtadanu and Sadhotomo, 2018; Rapi *et al.*, 2019), and the regression coefficient of the length–weight relationship of *L. malabaricus* varies between 2.10 and 3.20 in aquaculture conditions (Mazumder *et al.*, 2016) and from 2.32 to 3.0 (Tirtadanu and Sadhotomo, 2018; Rapi *et al.*, 2019) in the wild. Aquaculture study clearly showed that the length–weight relationship is affected by the ambient temperature and the diet of fish (Mazumder *et al.*, 2016), thus regional variation of these parameters may explain the differences in the relationship. We do believe that in the wild, the estimated length–weight relationship may also be affected by the season, fishing gear used (Fry *et al.*, 2009; Rapi *et al.*, 2019) and the location of capture (i.e. foraging conditions). This assumption explains why in some studies, regression coefficients differed significantly, even though the fish were sampled in adjacent or even the same region (Edwards, 1985; Newman, 2002; Fry *et al.*, 2009; Tirtadanu and Sadhotomo, 2018; Rapi *et al.*, 2019).

Considering these limitations, we believe that the data collected in the framework of the present research support the findings of Mazumder *et al.* (2016). In the waters off north-western Australia, regressions coefficients of the length–weight relationship were markedly higher (Newman, 2002), which may be explained by the markedly lower temperatures during the season of capture. At the same time, in the study, methodologically similar to the present research, performed in Indonesian waters, regression coefficient values were equally lower (Rapi *et al.*, 2019).

Monthly observations revealed the seasonal variation of the structure of the stock in the coastal waters. As was mentioned above, during the spring months (February–May), the stock was predominated by a larger fish (length more than 40 cm, weight more than 1 kg); in autumn, the greatest share of the stock was smaller (less than 35 cm and 1 kg, respectively); while in other months, these groups were mixing. An increase in the size, observed in spring months, may be the result of spawning migrations of larger fish to the coastal waters. In this case, in spring, large individuals migrate closer inshore mixing with the local resident individuals of smaller size. Indeed, in the late spring, especially in May, the stock was represented mostly by spawning individuals, while in autumn, the majority of studied fish was either immature or maturing. Spawning migrations may be found in some species of Lutjanidae (Arreguín-Sánchez *et al.*, 1996) but have never been observed in *L. malabaricus*. We believe that these migrations are the consequence of bottom morphology in the area of research; the continental shelf there is relatively wide, therefore the area preferred by large individuals for foraging is located offshore at the distance from the fishing grounds. Thus, during most of the year, these individuals inhabit forage in the offshore area moving inshore to the coastal waters only during the spawning season.

In addition to these unusual migrations, the season of spawning in Vietnamese waters differs from other regions. According to Fry *et al.* (2009) in northern Australia and eastern Indonesia fish spawn year-round, up to 30% of females and up to 80% of males are in a mature or breeding state for most of the year. The peak of spawning occurs from September to March in Australia (Fry *et al.*, 2009), and in Indonesian waters, seasonality of spawning has a more complex and region-dependent pattern. Fry and Milton (2009) identified an extended spawning season with multiple broad peaks throughout the year (January–March and October, according to Fry *et al.*, 2009) in the waters off Eastern Indonesia; on the other hand, Rapi *et al.* (2019) have found

https://doi.org/10.1017/S0025315423000346 Published online by Cambridge University Press

that in the waters off Sulawesi, there i's only one peak of spawning which takes place in June.

Summing up, even though the results of the present study are largely preliminary, it is possible to draw some conclusions. We would like to highlight that the life-history traits of the Vietnamese stock of Malabar blood snapper have a lot of similarities with the north-eastern Australian one. Both stocks are characterized by generally larger representatives, lower growth rates and potentially greater longevity of individuals (Milton *et al.*, 1995; Newman, 2002; Fry and Milton, 2009). Highly likely, the similarities and differences in the general stock structure we described here reflect both the peculiar properties of local oceanographic conditions and large-scale geographic variability.

At the same time, the seasonal spawning migrations we described here were never observed before. A combination of these traits makes the Vietnamese stock unique and demands precautious exploitation. Precautious exploitation of the Vietnamese stock of *L. malabaricus*, in turn, requires discrimination of the populations, identifying their ranges, and further studies on the reproductive biology, longevity and growth of the species.

Acknowledgements. The present study was performed in a framework of the collaborative research project of Vietnam – Russia Joint Tropical Science and Technology Research Center, Ecolan E-3.1 'Conservation, restoration and sustainable use of marine coastal ecosystems based on research of their structural and functional organization', Task 16: 'The study of reproductive biology of Malabar blood snapper (*Lutjanus malabaricus*) in the coastal waters of central Vietnam for the conservation, reproduction and sustainable use'. The authors would like to thank Nguyen Van Luc for providing ideas on the design of the study. The authors sincerely thank all anonymous reviewers for their valuable contribution to this article.

Author contributions. Conceptualization, methodology, data curation, writing – original draft and visualization, Y. H. T. D. and F. V. L.; software, writing – review and editing and supervision, F. V. L.; formal analysis and investigation and resources, Y. H. T. D. and N. H. L.; funding acquisition, Y. H. T. D.

Financial support. Not applicable.

Competing interests. None.

Ethical standards. Not applicable.

Data availability. The data that support the findings of this study are available from the corresponding author, Fedor Lishchenko, upon reasonable request.

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