

# Population dynamics of mantis shrimp *Harpiosquilla harpax* and *Oratosquillina* sp. in the waters south of Madura Island, Indonesia

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Manuscript received: 28 November 2019. Revision accepted: 16 March 2020.

**Abstract.** Ekalaturrahmah YAC, Zairion, Wardiatno Y. 2020. Population dynamics of mantis shrimp *Harpiosquilla harpax* and *Oratosquillina* sp. in the waters south of Madura Island, Indonesia. *Biodiversitas* 21: 1458-1466. Mantis shrimps are a potential fishery resource in Indonesia, but information about their population dynamics in the southern waters of Madura is limited. This study aimed to determine the population structure, growth, life span, and rate of exploitation for two taxa of mantis shrimp (*Harpiosquilla harpax* and *Oratosquillina* sp.). The research was conducted from September 2018 to February 2019 in the southern waters of Madura. The results showed that for *H. harpax* the majority of males caught ranged in length between 132.50 and 139.37 mm while the majority of females were between 153.45 and 160.22 mm. For *Oratosquillina* sp., the majority of males caught ranged from 84.70 and 89.60 mm while the majority of females were between 89.85 and 95.30 mm. The Growth Coefficient (K) for *H. harpax* was estimated to be 0.65 per year for males and 0.60 per year for females; while for *Oratosquillina* sp. the estimates were 0.81 and 0.78 per year, respectively. The  $L_{\infty}$  value for *H. harpax* males was 183.00 mm and for females 250.55 mm, while the  $L_{\infty}$  values for *Oratosquillina* sp. were 112.64 mm for males and 137.02 for females. The life span of *H. harpax* was estimated at 5 years, while for *Oratosquillina* sp. it was 4 years. The exploitation rate (E) for *H. harpax* males and females was 0.65 and 0.67 respectively, while for *Oratosquillina* sp. it was 0.54 and 0.58. These estimations indicated overexploitation of the resource, particularly in the case of *H. harpax*.

**Keywords:** Exploitation rate, growth, life span, mantis shrimp, Southern waters of Madura

## INTRODUCTION

Mantis shrimp is so named because its morphology and characteristics are similar to those of terrestrial mantis grasshoppers and praying grasshoppers. Taxonomically, mantis shrimp belongs to the order Stomatopoda within the class Malacostraca. There are 19 Stomatopoda families, grouped into five superfamilies, i.e. Bathysquilloidea, Squilloidea, Erythrosquilloidea, Lysiosquilloidea, and Gonodactyloidea. Altogether, more than 400 species of Stomatopoda have been identified and they are classified under 100 genera (Barber and Erdmann 2000). In the South China Sea, 116 stomatopod species from 51 genera have been identified within 13 families, classified into 4 superfamilies (Moosa 2000). Moreover, a number of new mantis shrimp species have been identified from Indonesian waters. They are *Manningia misool* found in Irian Jaya (Ahyong 1997), *Harpiosquilla raphidea*, and *Oratosquillina gravieri* found in Kuala Tungkal, District of Tanjung Jabung Barat, in the Province of Jambi (Mashar and Wardiatno 2011), and *Haptosquilla glyptocercus*, *Gonodactyllelus annularis*, *Gonodactylus viridis*, *Chorisquilla hystrix* found in the coastal waters of Pemuteran Bali (Pujawan et al. 2012).

Results of studies on the marine crustacean resource of Indonesia, including estimations of mantis shrimp populations, need to be disseminated to the public in order to facilitate sustainable management of these resources; i.e. to manage the harvest and prevent population decline (Hargiyatno et al. 2013). Priatna et al. (2014) argue that one of the requirements for correct fisheries management is data availability, especially accurate and reliable information on the fisheries resources to be utilized.

A review of several previous studies on mantis shrimps in Indonesia and the surrounding waters revealed a body of information on mantis shrimp biology (Wardiatno and Mashar 2010); spatial distribution of two types of mantis shrimps in Kuala Tungkal waters (Mashar and Wardiatno 2011); population dynamics of mantis shrimps in Kuala Tungkal in the Province of Jambi, Indonesia (Wardiatno and Mashar 2011); population dynamics of mantis shrimp *O. gravieri* in Pelabuhan Ratu Bay Waters (Ambarsari et al. 2016); and last but not least, on growth aspects of the giant mantis shrimp *H. raphidea* Fabricius, 1798 in Banten Bay, in the Province of Banten (Mulyono et al. 2016). On the other hand, for the southern waters of Madura, there has never before been a formal investigation of the presence of mantis shrimps and of their population dynamics, even though previous studies have shown that mantis shrimp

represents 14.8% of the total bottom trawl catch in those waters. The relatively large contribution of mantis shrimps in the catch of local fishermen emphasized the need for the investigation reported here. As such, the objective of this study was to analyze the population structure, growth rate, life-span, and exploitation level of mantis shrimps *Harpisquilla harpax* and *Oratosquilla* sp. found in the southern Madura waters, and ultimately to provide a core of empirical data on which to base further studies for the sustainable management of these mantis shrimp resources.

## MATERIALS AND METHODS

### Study area

The study was conducted in the southern waters of Madura, in the Province of East Java, Indonesia. The observation sites consisted of three locations: i.e. station 1 located in the sub-district of Pangarengan and Mandangin Island in Sampang District; station 2 in the sub-district of Pademawu in Pamekasan District; and station 3 located in the sub-district of Bluto in Sumenep District (Figure 1). Monthly sampling of mantis shrimps was conducted from September 2018 to February 2019 in those three sampling areas.

### Procedures

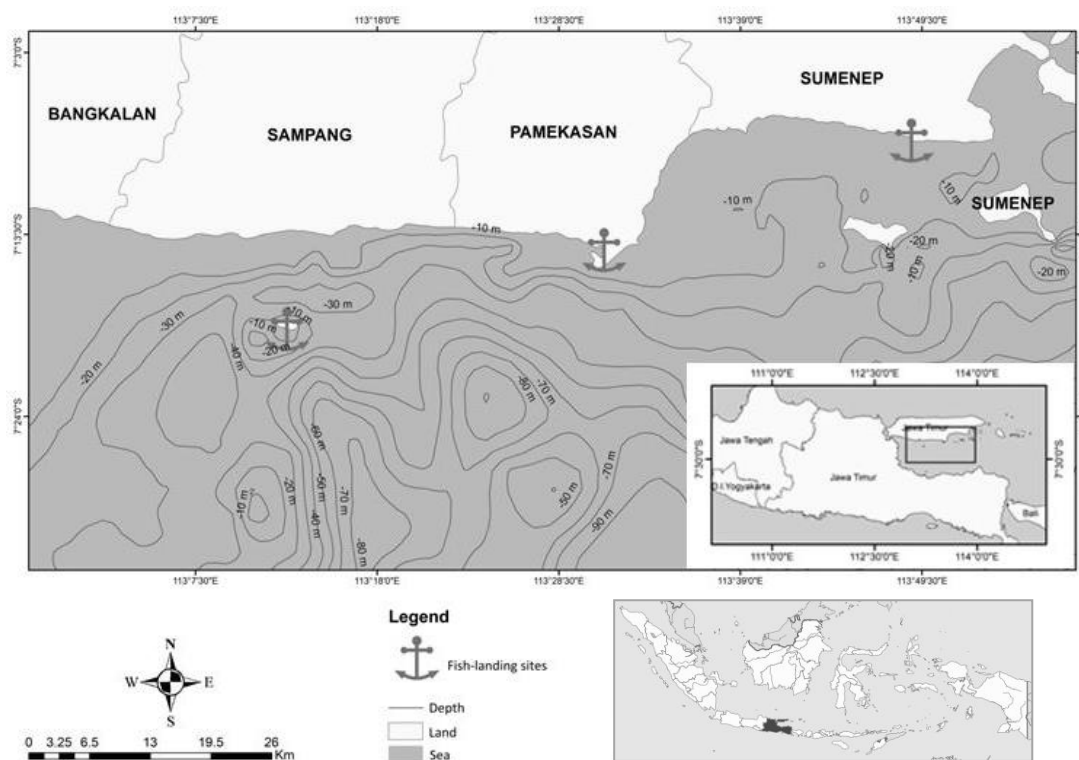
Both primary and secondary data were collected in the present study.

Primary data were collected from a field survey of the crop of mantis shrimps caught by local fishermen using a bottom trawl device in the southern waters of Madura. The samples were collected from 2-3 different fishermen in each location, and the entire harvest of mantis shrimps caught in the bottom trawls were subject to classification and measurement.

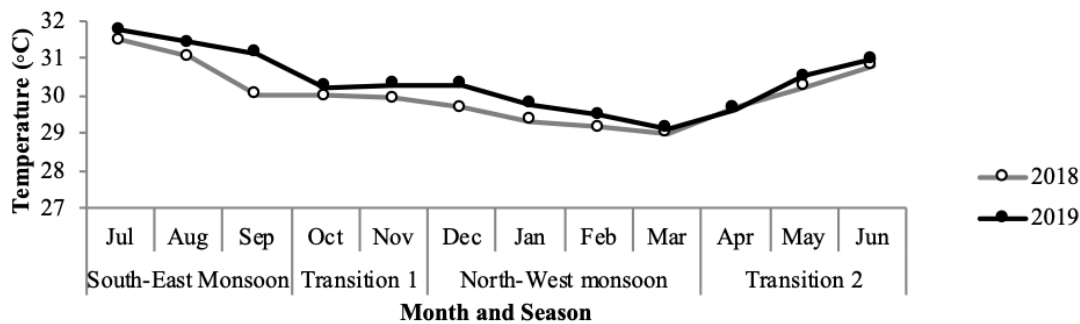
The main secondary data gathered in the investigation were estimates of sea surface temperatures obtained from [Oceancolor.gsfc.nasa.gov](http://Oceancolor.gsfc.nasa.gov), processed using Aqua MODIS Imagery. This temperature data was incorporated in algorithms used to estimate natural mortality rate of the mantis shrimps. Sea surface temperature over the study period ranged from 29.48 to 31.76°C, with an average temperature over the past two years of 30.21°C. The average temperature was used in calculations of the shrimp natural mortality rates.

Sampling of mantis shrimp was representative of three different seasons; namely the South-East monsoon (September 2018); the first transition (October to November 2018); and the North-West monsoon (December 2018 to February 2019) (Figure 2).

The total number of mantis shrimps collected in the study was 1102; consisting of 690 *H. harpax* individuals and 412 *Oratosquilla* sp. individuals. The dimension and weight of each individual in the sample were measured and recorded. The shrimp length was measured using a caliper capable of measuring to the nearest 0.01 mm, while the weight was measured using a digital scale capable of measuring to the nearest 0.01 grams.



**Figure 1.** Mantis shrimp research locations in the southern waters of Madura, Indonesia



**Figure 2.** Sea Surface Temperature (SST) in the southern waters of Madura. Source: Aqua Modis Imagery

### Data analysis

Sex ratio is the number of male shrimps divided by the number of female mantis shrimps collected from the catch. It was calculated using the following formula:

$$NK = \frac{\sum J}{\sum B}$$

Where, NK is the sex ratio,  $\sum J$  is the number of male mantis shrimps, and  $\sum B$  is the number of female mantis shrimps.

Sex ratio balance tests (i.e. whether the ratios differed significantly from 1:1) were performed using the chi-square test ( $\alpha=0.05$ ).

The relationship between shrimps' weights and their lengths was determined using linear regression analysis on the logarithmically transformed data, according to the following formula:

$$\log W = \log a + b \log L$$

Where,  $a$  is the intercept and  $b$  is the slope.

Estimation of the mantis shrimps' growth parameters (i.e. the growth coefficient  $K$ , and the asymptotic length  $L_{\infty}$ ) was obtained using the ELEFAN (Electronic Length-Frequency Analysis) I in the FiSAT program (FAO-ICLARM Fish Stock Assessment Tools) II version 1.2.2. This was based on the von Bertalanffy's growth model (Sparre and Venema 1999) as follows:

$$L_t = L_{\infty} [1 - e^{-K(t-t_0)}]$$

Where,  $L_t$  is the length of a mantis shrimp (mm) at the age of  $t$ ,  $L_{\infty}$  is the theoretical maximum length or asymptotic length of a shrimp (mm),  $K$  is the growth coefficient (mm/unit time), and  $t_0$  is the theoretical age (month) when the shrimp's length (mm) is zero.

The value of  $t_0$  was estimated using Pauly's equation as stated in Sparre and Venema (1999) as follows:

$$\log (-t_0) = -0.3922 - 0.2752 (\log L_{\infty}) - 1.038 (\log K)$$

The estimated maximum age of a mantis shrimp was calculated using the following formula (Pauly 1983; Pradeep 2016):

$$t_{\max} = (3/K) + t_0$$

Mantis shrimp mortality rates and exploitation levels were analyzed using the length-converted catch curve in FiSAT II package (Pauly 1983; Sparre and Venema 1999). Firstly, the rate of total mortality ( $Z$ ) was estimated from the result of  $K$  estimation using von Bertalanffy's growth equation. Subsequently, the natural mortality rate ( $M$ ) was estimated from the relationship between  $M$  and  $L_{\infty}$ ,  $K$  and the annual mean sea surface temperature  $T$  ( $^{\circ}\text{C}$ ), in accordance with Pauly's empirical equation (1980) as follows:

$$\log (M) = -0.0066 - 0.2795 \log (L_{\infty}) + 0.6543 \log (K) + 0.4634 \log (T)$$

Fishing mortality ( $F$ ) was determined by subtracting natural mortality ( $M$ ) from the total mortality ( $Z$ ); i.e.  $F = Z - M$ . Finally, exploitation level ( $E$ ) was calculated as the ratio of the fishing mortality ( $F$ ) to the total mortality ( $Z$ ); i.e.  $E = F/Z$  (Pauly 1983). The level of exploitation obtained was then compared to the optimum level; i.e. 0.5, according to Gulland (1971) in Pauly (1983).

## RESULTS AND DISCUSSION

### Sex ratio

The sex ratio of mantis shrimps *H. harpax* and *Oratosquilla* sp. caught in the southern waters of Madura varied from month to month throughout the study (Table 1). Based on monthly chi-square tests ( $\alpha=0.05$ ), we can see that the sex ratio for *H. harpax* was in a balanced state; i.e. in no month did the sex ratio differs significantly from 1:1. However, for *Oratosquilla* sp. in the month of January, the M:F sex ratio reached 1:1.66, and the chi-square test performed across all months indicated that there was a significant preponderance of females over males. The overall sex ratio in the current study was 1:0.98 and 1:1.26

for *H. harpax* and *Oratosquillina* sp., respectively. In general, we can say that the sex ratio of mantis shrimp *H. harpax* was balanced, whereas the sex ratio of *Oratosquillina* sp. was unbalanced.

Differences in the sex ratios for the mantis shrimp from month to month can be caused by seasonal factors, spawning patterns, and behavior. Sea surface temperatures in the southern waters of Madura monthly fluctuated over the two years 2018-2019 (Figure 2). The average temperature for 2 years was 30.21°C; during the study period the water temperature ranged from 29.22-31.76°C. Water temperature greatly affects the life of mantis shrimp.

**Body length-frequency distribution**

The frequency distribution for body length of *H. harpax* was unimodal, ranging from 55.31 mm to 237.56 mm (Figure 3). Classification of the data according to sex, showed that male mantis shrimps *H. harpax* ranged between 69.11 mm and 180.99 mm in length, while the females measured between 61.32 mm and 237.39 mm in length. Based on our classification of shrimp length into 26 classes, the modal class for male *H. harpax* was between 132.50 mm and 139.37 mm, while the modal class for females was between 153.45 mm and 160.22 mm in length.

Figure 4 shows the frequency distribution of body length for *Oratosquillina* sp., wherein the shrimps' lengths ranged between 29.2 mm and 139.39 mm. Classification of the shrimps lengths according to sex shows that the male

mantis shrimps ranged between 29.2 mm and 104.51 mm in length, while the females ranged between 33.02 mm and 134.77 mm. Based on our classification of shrimp length into 20 classes, the modal class for male *Oratosquillina* sp was between 84.70 and 89.60 mm, while the modal class for females was between 89.85 and 95.30 mm in length.

**Length-weight relationship**

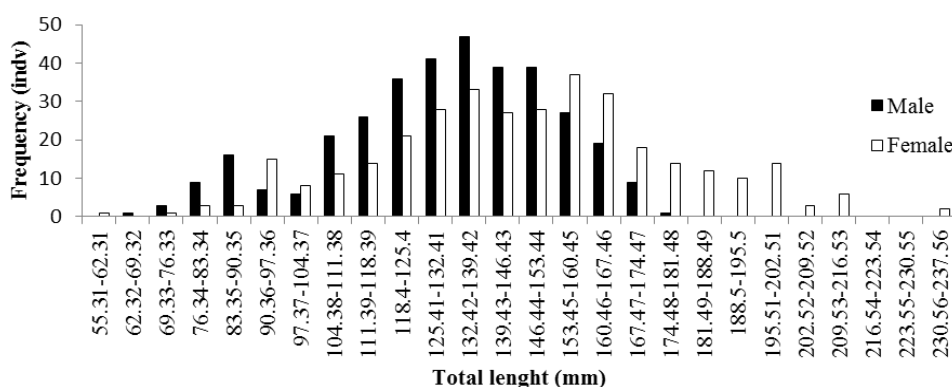
The entire sample of 1102 shrimps caught in the investigation, consisted of 690 *H. harpax* individuals and 412 *Oratosquillina* sp. individuals. The relationship between body length and weight measured on *H. harpax* shrimps is shown in Figure 5 in separate graphs, (i) for the 347 males and (ii) for the 343 females. For the *Oratosquillina* sp. shrimps, the relationships for 182 males and 230 females are shown in Figure 6.A and 6.B respectively.

The Mantis shrimp growth patterns could be determined from the value of *b*, the slope's value in the linear regression equation of the logarithmic relationship between body length and weight. For *H. harpax*, the equation of best fit for the length-weight relationship was  $W=0.0210L^{2.3057}$  for the male shrimps and  $W=0.0163L^{2.4302}$  for the female shrimps (Figure 5). Likewise, from the analysis of the length-weight relationship of the *Oratosquillina* sp. shrimps, we obtained equations of best fit of  $W=0.0405L^{2.3090}$  for the males and  $W=0.0365L^{2.4970}$  for the females (Figure 6).

**Table 1.** Sex ratio of mantis shrimps (*Harpiosquilla harpax* and *Oratosquillina* sp.) for each month throughout the study

Sampling period	<i>Harpiosquilla harpax</i>					<i>Oratosquillina</i> sp.				
	N	Male	Female	Sex ratio (M:F)	$\chi^2$	N	Male	Female	Sex ratio (M:F)	$\chi^2$
September 2018	56	21	35	1:1.66	TS	79	35	44	1:1.25	TS
October 2018	59	29	30	1:1.03	TS	63	28	35	1:1.25	TS
November 2018	192	107	85	1:0.79	TS	48	23	25	1:1.08	TS
December 2018	160	83	77	1:0.92	TS	57	26	31	1:1.19	TS
January 2019	122	65	57	1:0.87	TS	64	24	40	1:1.66	S
February 2019	101	42	59	1:1.40	TS	101	46	55	1:1.19	TS
Total	690	347	343	1: 0.98	TS	412	182	230	1:1.26	S

Note: N: number of samples; M: male; F: female; S: significantly different; TS: Not significantly different



**Figure 3.** Length frequency distribution of mantis shrimp *Harpiosquilla harpax* caught in the southern waters of Madura, Indonesia

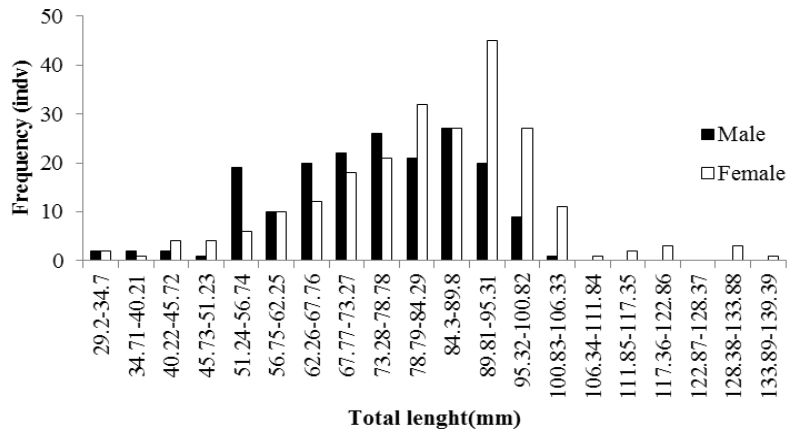


Figure 4. Length frequency distribution of mantis shrimp *Oratosquilla* sp. caught in the southern waters of Madura, Indonesia

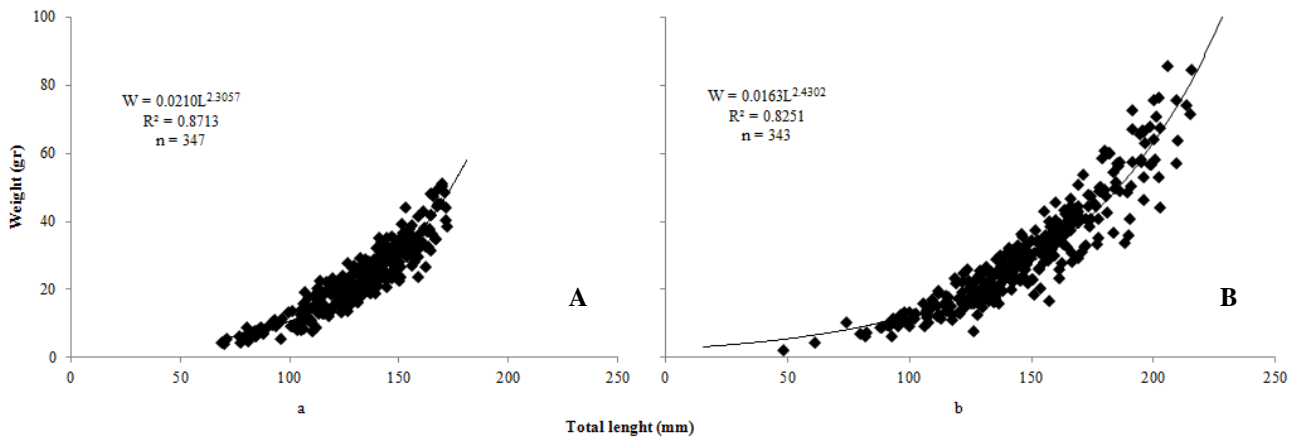


Figure 5. Length-weight relationship of mantis shrimp *Harpiosquilla harpax* caught in the southern waters of Madura, Indonesia: A. Male, B. Female

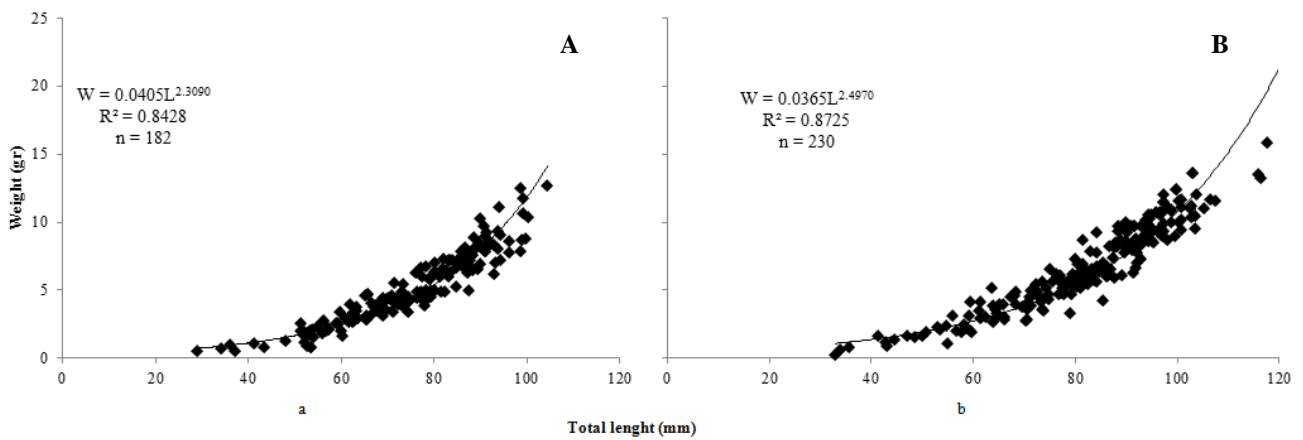


Figure 6. Length-weight relationship of mantis shrimp *Oratosquilla* sp. caught in the southern waters of Madura, Indonesia: A. Male, B. Female

**Estimation of growth parameters**

Estimation of growth parameters encompasses calculation of the growth coefficient (K); asymptotic length ( $L_{\infty}$ ); and theoretical age of mantis shrimps when their total length is zero ( $t_0$ ). Results of the analysis (in Table 2) revealed that male *H. harpax* shrimps had a higher growth coefficient (K) but a lower asymptotic length ( $L_{\infty}$ ) than the female shrimps.

This implies that the female *H. harpax* shrimps needed more time than the males to reach their asymptotic length ( $L_{\infty}$ ). Analysis of the *Oratosquillina* sp. growth parameters revealed similar results.

The von Bertalanfy's growth equation model determined for male *H. harpax* mantis shrimps was  $L_t = 183 (1 - e^{[-0.65 (t + 0.0377)]})$  while for females it was  $L_t = 250.55 (1 - e^{[-0.6 (t + 0.0362)]})$ . The relationship between the age of *H. harpax* shrimps and their total length is illustrated both for males and for females in Figure 7, in which, at the age of 0 years, the males were estimated to be 4.25 mm in length, while the females were 5.20 mm. The life expectancy of a male *H. harpax* was estimated at around 54 months, while a female could be expected to live to 59 months.

The von Bertalanfy's growth equations determined for *Oratosquillina* sp. shrimps were  $L_t = 112.64 (1 - e^{[-0.81 (t + 0.0733)]})$  for the males and  $L_t = 137.02 (1 - e^{[-0.78 (t + 0.0790)]})$  for the females. The relationship between age and the total length of male and female *Oratosquillina* sp. is illustrated in Figure 8, where at the age of 0 years, the males were estimated to be 6.49 mm in length, while the females were estimated at 8.19 mm in length. Life expectancy of a male *Oratosquillina* sp. was estimated to be around 43 months, while a female could be expected to live to 45 months.

The growth curves in Figures 7 and 8 show that female *H. harpax* and *Oratosquillina* sp. shrimps need more time before they reach their asymptotic length ( $L_{\infty}$ ) than the males. This is a result of *H. harpax* females having a smaller growth coefficient (K), thus reaching their  $L_{\infty}$  later than the males. Moreover, energy obtained from food consumed by female mantis shrimps is prioritized for the formation and maturation of their gonads rather than for their own growth.

**Mortality rate and exploitation level**

The values for total mortality (Z), fishing mortality (F), and natural mortality (M) of mantis shrimps *H. harpax* and *Oratosquillina* sp. are presented in Table 3. Fishing mortality (F) of *H. harpax* is higher than that of *Oratosquillina* sp. both for the males and the females. Furthermore, the exploitation level (E) of *H. harpax* was estimated at 0.65 per year for males and 0.67 per year for females, or 30-33% above the theoretical optimum level; whereas for *Oratosquillina* sp., the exploitation level (E) was only 0.54 per year for males and 0.58 per year for females, i.e. 9-17% above the optimum level.

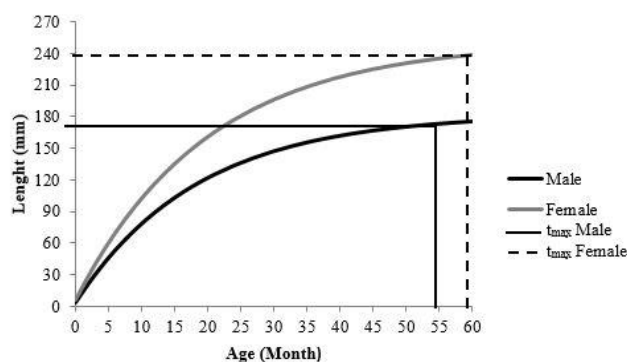
The rate of fishing mortality (F) of *H. harpax* for both the male and female was higher than the natural mortality rate (M). Furthermore, for male *H. harpax* the total mortality (Z) was higher than for females; this suggests that the male mantis shrimp stock is more susceptible to death than the female.

**Table 2.** Estimation of mantis shrimp growth parameters

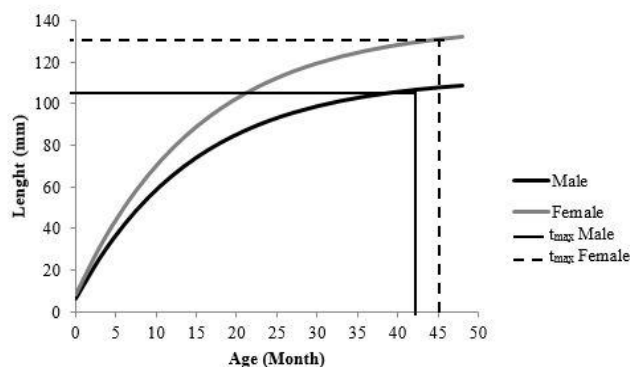
Growth parameter	<i>Harpiosquilla harpax</i>		<i>Oratosquillina</i> sp.	
	Male	Female	Male	Female
K (year <sup>-1</sup> )	0.65	0.60	0.81	0.78
$L_{\infty}$ (mm)	183.00	250.55	112.64	137.02
$t_0$ (year)	-0.0377	-0.0362	-0.0733	-0.0790
$t_{max}$ (month)	54	59	43	45

**Table 3.** Mortality rates and exploitation level of mantis shrimps (*Harpiosquilla harpax* and *Oratosquillina* sp.) in the southern waters of Madura

Parameter	Mortality rates (year <sup>-1</sup> )			
	<i>Harpiosquilla harpax</i>		<i>Oratosquillina</i> sp.	
	Male	Female	Male	Female
Natural mortality (M)	0.84	0.73	1.11	1.03
Fishing mortality (F)	1.57	1.47	1.33	1.44
Total mortality (Z)	2.41	2.20	2.44	2.47
Exploitation (E)	0.65	0.67	0.54	0.58



**Figure 7.** Relationship between the age and total length of *Harpiosquilla harpax* males and females in the southern waters of Madura based on the von Bertalanfy's growth equation



**Figure 8.** Relationship between the age and total length of *Oratosquillina* sp. males and females in the southern waters of Madura based on the von Bertalanfy's growth equation

Similarly, the fishing mortality rate of mantis shrimps *Oratosquillina* sp. for both the males and females was higher than their natural mortality rate, but not as high as for *H. harpax*. The total mortality rate ( $Z$ ) of male *Oratosquillina* sp. mantis shrimps was the same as that of the females.

### Discussion

Sex ratio is the ratio between male aquatic biota and female aquatic biota in a population. A ratio of 1:1, i.e. 50% males and 50% females, is seen as the ideal condition for species perpetuation (Bal and Rao 1984; Effendie 2002). From our calculations on the mantis shrimp catch in the southern waters of Madura, we obtained a sex ratio of 1: 0.98 for *H. harpax* and 1: 1.26 for *Oratosquillina* sp. The chi-square tests revealed that the sex ratio value of *H. harpax* mantis shrimps was in a balanced state, whereas for *Oratosquillina* sp. the sex ratio was unbalanced. This result is in line with previous studies by Djuwito et al. (2013) and Ambarsari et al. (2016) on mantis shrimps *Oratosquilla oratoria* in Cilacap and *Oratosquilla gravieri* in Pelabuhan Ratu Bay, which reported unbalanced sex ratios among the shrimps, of 1: 1.28 and 1: 1.57 respectively.

The population of harvested mantis shrimps *H. harpax* consisted of slightly more males than females (Table 1), and this is in line with the findings in a number of other studies that show the harvested crop of shrimps is mostly male shrimps (Wardiatno and Mashar 2011; Rao et al. 2015; Mulyono et al. 2016). On the other hand, the harvest of *Oratosquillina* sp. shrimps comprised significantly more females than males (Table 1); this is in line with the finding in a study by Kim et al. (2017) on *O. oratoria* in the coastal area of Tangyeong in Korea where most of the mantis shrimps caught were females.

Differences in the abundance of male and female mantis shrimp are influenced by seasons. This inference is supported by results of the study by Yan et al. (2015) on *H. harpax* in the Beibu Gulf of the South China Sea and by Kim et al. (2017) on *O. oratoria* in the coastal region of Tangyeong Korea. In those two pieces of research, male mantis shrimp were more common in the summer, while there were mostly female mantis shrimp in the winter. These results are explained by the fact that summer is a spawning period during which female mantis shrimps live in burrows to incubate their eggs (Hamano and Matsuura 1984).

According to Ahyong et al. (2008), mantis shrimp reach the maturity stage at a length of 10-30 cm. On the other hand, Nakajima et al. (2010) reported that for *Oratosquilla oratoria*, maturity started from 10 cm. The sex ratio of the two species of mantis shrimp differed, which may be related to differences in the behavioral pattern of spawning. The genus *Harpisquilla* spawns inside the nest, then the males leave the nest while the females stay in nest to incubate the eggs. Conversely, *Oratosquilla* spawns outside the nest and the males leave the nest to fertilize other females. The expectation is that the sex ratios for both mantis are in a balanced state. However, it is also preferred that female numbers are not less than or even more than

males so that the populations in the wild can be maintained.

The difference in the number of shrimps in specific waters may be related to growth patterns, migration, and changes brought in by new shrimp species appearing among the existing populations. Moreover, Bal and Rao (1984) argue that imbalances in numbers of fish are related to their eating habits, spawning, or migration of particular types of fish. Simanjuntak et al. (2008) maintain that sexual patterns and sexual ratios vary quite a lot in a tropical region such as Indonesia. Unbalanced sex ratios are influenced by numerous factors including differences in behavior patterns, mortality rates, and growth rates (Effendie 2002).

With regard to the frequency distribution for body length, the modal class for *H. harpax* fell between 132.42 mm and 139.42 mm (Figure 3), while the modal class for *Oratosquillina* sp. fell between 89.81 mm and 95.31 mm (Figure 4). Mashar and Wardiatno (2011) reported that in their study the majority of mantis shrimps *Oratosquilla garvieri* were between 79 mm and 103 mm in length, presumably, because shrimps of that particular size had successfully adapted themselves to the environment.

According to Table 1, our collection of mantis shrimps traversed three different seasons namely the South-East Monsoon (September), First Transition (October-November), and North-West Monsoon (December-February). The majority of mantis shrimps gathered from the September catch were smaller than the catch from the other months. This result was related to recruitment periods in the preceding months. Nakajima et al. (2010) reported that in the period of May-July the lengths of *Oratosquilla* mantis shrimps were < 10 cm in length, while in August the *Oratosquilla* were bigger (i.e. >10 cm in length). This change in size presumably reflected changes in response to the spawning periods of Mantis shrimps (Kim et al. 2017).

The growth pattern of Mantis shrimps is referred to as negative allometric growth ( $b < 3$ ). Analysis of the length-weight relationship of mantis shrimps *H. harpax* and *Oratosquillina* sp. in our study shows that the growth patterns for these mantis shrimps, for both males and females, conformed to this negative allometric model. The similar growth patterns for the two types of mantis were presumably a consequence of resemblances in the characteristics of their environments (e.g. food supply and habitat).

Generally speaking, a negative allometric growth pattern in aquatic biotas is the result of overfishing, competition, and trophic potential (Mashar 2011; Arshad et al. 2015). Incidentally, the values of  $b$  obtained from the current study differed from the value obtained in the study by Muzammil (2010) on mantis shrimp *O. gravieri*. Different  $b$  values for the same fish species may be the results of different growth rates; age differences and stages of gonad development; food; sampling time; and water conditions (temperature and salinity) (Froese 2006; Tarkan et al. 2006; Jennings et al. 2001; Rahman et al. 2012).

**Table 4.** Mantis shrimp growth parameters obtained in several studies in Indonesian and neighboring waters

Species	Growth coefficient (year)	Asymptotic length (mm)	Location	Author (s)
<i>Harpiosquilla harpax</i>	0.65 (M); 0.60 (F)	183 (M); 250.55 (F)	Southern waters of Madura	Present study
<i>Harpiosquilla harpax</i>	1.10 (M); 0.75 (F)	183.8 (M); 215.3 (F)	Perak, Peninsular Malaysia	Arshad et al. (2015)
<i>Harpiosquilla harpax</i>	0.89 (M,F)	210 (M,F)	Vietnam	Dinh et al. (2010)
<i>Harpiosquilla raphidea</i>	1.68 (M); 1.32 (F)	381.68 (M,F)	Kuala Tungkal, Jambi	Wardiatno and Mashar (2011)
<i>Oratosquilla gravieri</i>	0.23 (M); 0.37 (F)	192 (M); 182.50 (F)	Palabuhanratu Bay waters	Ambarsari (2016)
<i>Oratosquilla oratoria</i>	0.82 (M); 0.72 (F)	183.75 (M); 184.8 (F)	Tongyeong, Korea	Kim et al. (2017)
<i>Oratosquilla oratoria</i>	0.75 (M,F)	191 (M,F)	Pesisir Hongkong	Pitcher et al. (1998)
<i>Oratosquillina</i> sp.	0.81 (M); 0.78 (F)	112.64 (M); 137.02 (F)	Southern waters of Madura	Present study
<i>Squilla mantis</i>	1.6 (M); 1.3 (F)	200 (M,F)	Ebro Delta	Abello and Martin (1993)

Note: M: male; F: female

Figures 7 and 8 show that mantis shrimps with different body length to age relationships have different  $L_{\infty}$  and K values. Table 4 lists growth coefficients (K) and asymptotic lengths ( $L_{\infty}$ ) for species of mantis shrimps obtained in a number of studies around Indonesian and neighboring waters. Different  $L_{\infty}$  and K values may be caused by intrinsic factors such as heredity, parasites, or diseases (Knaepkens et al. 2002) and/or by external factors such as temperature and food availability (Effendie 2002). Mantis shrimps with a smaller growth coefficient in Figures 7 and 8 are delayed in reaching their asymptotic length ( $L_{\infty}$ ). Growth parameters estimated for a fish caught are influenced by the composition of the fish samples and by the analysis method (Widodo 1988). Moreover, growth parameters ( $L_{\infty}$  and K) of the same fish resources obtained from different locations may have different values. This can be caused by environmental conditions in the water at each location including food availability, water temperature, and oxygen saturation (Przybylski 1996; Tsoumani et al. 2006), as well as by fish size and gonad maturity (Merta 1992).

Life expectancy (lifespan) of mantis shrimps *H. harpax* and *Oratosquillina* sp. in this study was estimated based on the values of K and  $t_0$ . Taylor (1958) in Pauly (1983) explains that lifespan is the age when the shrimp's length ( $L_t$ ) reaches 95% of its estimated asymptotic length ( $L_{\infty}$ ). Results of the lifespan calculations (Figures 6 and 7) show that the estimated life expectancy of *H. harpax* is less than 5 years, while *Oratosquillina* sp. will not exceed 4 years. Life expectancy for males is lower than for females (Table 2). The expected lifespans of mantis shrimps *H. harpax* and *Oratosquillina* sp. are not that much different from lifespans determined for other mantis shrimp species; for example, *Squilla mantis* may reach 1.5 years (Abello and Martin 1993), *Oratosquillina* sp. 3.0 to 3.5 years (Hamano et al. 1987), *Oratosquilla stephensoni* around 2.5 years (Dell and Sumpton 1999), and *H. raphidea* from 6.7 to 8.5 years (Mashar 2011).

The rate of fishing mortality (F) of mantis shrimps *H. harpax* was estimated at 1.57 year<sup>-1</sup> for males and 1.47 year<sup>-1</sup> for females. For *Oratosquillina* sp. shrimps, the males (1.33 year<sup>-1</sup>) had lower fishing mortality than the females (1.44 year<sup>-1</sup>). The fishing mortality figure for *H. harpax* was 1.86 and 2.01 times higher than the natural mortality rate for males and females respectively; whereas

for *Oratosquillina* sp. fishing mortality was 1.19 and 1.40 times higher than natural mortality for males and for females respectively. These figures indicate that in the southern waters of Madura more mantis shrimps *H. harpax* and *Oratosquillina* sp. die in fishing activities than as a result of natural causes.

According to Gulland (1971) in Pauly (1983), the optimum exploitation level (E) of fishery resources is 0.5, which means that the natural mortality rate should be the same as the fishing mortality. A value of E greater than 0.5 indicates overexploitation of the particular resource. Exploitation level (E) of mantis shrimps *H. harpax* male was estimated at 0.65 year<sup>-1</sup> for males and 0.67 year<sup>-1</sup> for females and for *Oratosquillina* sp. it was 0.54 year<sup>-1</sup> in males and 0.58 year<sup>-1</sup> in females. The measured exploitation levels (E) of mantis shrimps exceeded optimum exploitation levels by 30% and 33% for *H. harpax* male and females respectively, and by 9% and 17% for *Oratosquillina* sp. male and females respectively. These figures clearly indicate that mantis shrimps in the southern waters of Madura are overexploited. Overexploitation of *H. harpax* could lead to "recruitment overfishing" as the majority of mantis shrimp were in mature stages of development. On the other hand, the possible overexploitation of *Oratosquillina* sp. is "growth overfishing" as most of the shrimps sampled in this study were small, with a preponderance of females.

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