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# Fishery biology of purpleback squid, Sthenoteuthis oualaniensis, in the northwest Indian Ocean

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| Abstract                                  |  |  |  |
| The paper introduc<br>Ocean, which partly | es the fishery biology of <i>Sthenoteuthis oualaniensis</i> in the northwest Indian<br>y had the squid fishing in September–November, 2003, in SIOFA Area. |  |  |

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# Fishery biology of purpleback squid, *Sthenoteuthis oualaniensis*, in the northwest Indian Ocean

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#### Abstract

Three surveys of purpleback squid (*Sthenoteuthis oualaniensis*) resource were carried out by Chinese squid jigging boats in the waters of  $4^{\circ}N-21^{\circ}N$ ,  $58^{\circ}E-65^{\circ}E$  in the northwestern Indian Ocean during September and November 2003, and from September 2004 to April 2005. The daily catch ranged from 0.1 t/days to 36.0 t/days, with majority of the catch from areas defined by  $15^{\circ}N-18^{\circ}N$  and  $60^{\circ}E-62^{\circ}E$ , and by  $18^{\circ}30'N-20^{\circ}N$  and  $62^{\circ}30'E-64^{\circ}E$ . The sex ratio (M:F) for the total catch was 1:30.5. The mean mantle length (ML) was 299 mm for males (range 106–462 mm) and 352 mm for females (range 106–612 mm). Three separate groups with different sizes were identified: those larger than 400 mm ML located in the north of  $18^{\circ}N$ ; squid ranging 300–400 mm ML in the area from  $12^{\circ}N$  to  $18^{\circ}N$ , and those shorter than 300 mm ML in the south of  $12^{\circ}N$ . There was no systematic difference in squid size along the longitude direction. The relationship between body weight (BW, g) and mantle length (mm) was quantified by BW =  $40.64348 \text{ ML}^{2.9115}$  and BW =  $45.78507 \text{ ML}^{2.5842}$  for females and males, respectively. In the waters south of  $16^{\circ}N$ , more than 70% of females were immature, while in the area north of  $18^{\circ}N$ , more than 48% were mature. Squid in the same maturity stage varied greatly in size, suggesting that *S. oualaniensis* may spawn all year around. The oldest squid from September 2004 to April 2005 were slightly younger than 1 year old, suggesting that all the examined individuals were hatched during January and November 2004. The peak spawning time is from March to May. Most of the stomachs analyzed had food remains and only 8% were empty. The stomachs contained three major groups: fish, cephalopods and crustaceans, mainly *Cypselurus spp* and *S. oualaniensis*. More than 60% of the stomachs had evidence of cannibalism for the squid larger than 400 mm ML.

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# 1. Introduction

The purpleback squid (*Sthenoteuthis oualaniensis*; Lesson, 1830), is widely distributed in the equatorial and tropical waters of Indo-Pacific ocean (Zuev and Nesis, 1971; Voss, 1973; Nesis, 1977). It is most abundant in the south China Sea and northwestern Indian Ocean. The squid is of special interest from the view point of effective and rational use of the world ocean's biological resources (Trotsenko and Pinchukov, 1994). Since the 1970s, investigations of squid resources were made by the former USSR and Japan in the Northwest Indian ocean (Chesalin, 1994; Yatsu, 1997; Chesalin and Zuyev, 2002). The maximum mantle length (ML) of *S. oualaniensis* was up to 690 mm, and the life span about 0.5–1 year (Trotsenko and Pinchukov, 1994).

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Three populations with distinguishable size ranges were identified (Yatsu, 1997; Yatsu et al., 1998). Russian scientists, however, showed that *S. oualaniensis* had complicated population structures with five forms of distinguishable sizes (Nesis, 1993; Zuyev et al., 2002). Squid are often highly fecund with more than 0.5 million eggs (Trotsenko and Pinchukov, 1994; Zuyev et al., 2002). The potential fecundity of the giant form of squid ranged between 2 million and 5 million eggs and the holding capacity of the oviducts was approximately 300,000 eggs (Snyder, 1998). Indirect evidences suggested that *S. oualaniensis* might be a multiple spawner (Harman et al., 1989; Snyder, 1998).

The squid is characterized by a wide ecological amplitude, complex intraspecific structure, high fecundity, short life cycle, high natural mortality, high growth rate and significant production (Zuev and Nesis, 1971; Nesis, 1977; Zuev et al., 1985). All these features make purpleback squid an interesting species in theoretical and applied studies.

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| Table 1            |             |               |       |
|--------------------|-------------|---------------|-------|
| The key parameters | of research | squid jigging | boats |

| Boat name      | New Century No. 57         | New Century No. 61        | New Century No. 18         | Dai Yunyu No. 807  |
|----------------|----------------------------|---------------------------|----------------------------|--------------------|
| Total length   | 68.06                      | 49.66                     | 67.7 m                     | 54.3 m             |
| GRT            | 851                        | 581                       | 976                        | 432                |
| Single machine | 45                         | 37                        | 45                         | 38                 |
| Fishing light  | $160 \times 2 \mathrm{kW}$ | $120 \times 2  \text{kW}$ | $160 \times 2 \mathrm{kW}$ | $130 \times 1  kW$ |

Table 2

Summary of survey areas and sample collection of S. oualaniensis between September 2003 and April 2005

| Data                         | Boat name                                 | Survey area            | Planned stations | Fishing stations | Collected sample | Range (ML, mm) |
|------------------------------|---|------------------------|------------------|------------------|------------------|----------------|
| September–November 2003      | New Century No. 57;<br>New Century No. 61 | 58°E–66°E<br>2°N–18°N  | 102              | 128              | 1270             | 130–355        |
| September 2004–February 2005 | New Century No. 18<br>Dai Yunyu No. 807   | 12°N–21°N<br>58°E–69°E | 158              | 291              | 1430             | 142–612        |
| March–April 2005             | Dai Yunyu No. 807                         | 6°N-12°N<br>58°E-65°E  | 56               | 72               | 292              | 127–590        |

In the north Indian Ocean, the density of purpleback squid generally ranges from 50 kg km<sup>-2</sup> to 75 kg km<sup>-2</sup>, and high concentration is mainly found in the Arabian Sea (Zuev et al., 1985). Previous studies indicated that *S. oualaniensis* dominated the epipelagial zone of the Arabian Sea both in number and biomass and that the mean biomass was estimated as  $4.5 \text{ t km}^{-2}$  (Chesalin and Zuyev, 2002). The squid density in the area from 20°N to 22°N reached  $6.5 \text{ t km}^{-2}$ , and the area between 14°N and 15°N even reached up to 12–42 t km<sup>-2</sup> (Nesis, 1993). Based on the Japanese survey, the biomass of *S. oualaniensis* was estimated to be 2 million t (Yatsu, 1997). These studies suggest that the squid could sustain higher exploitation levels in the future.

Little information is available on the fishery biology of the purpleback squid in the high sea of northwestern Indian Ocean. Thus, there is a need for collecting more information on the distribution and fishery biology of purpleback squid prior to the development of a commercial fishery for the species. This study describes the biological features derived from the data collected during three scientific surveys for *S. oualaniensis* undertaken by the Chinese squid jigger vessels during September and November 2003, and from September 2004 to April 2005 in the high sea of northwestern Indian Ocean.

#### 2. Materials and methods

The survey was carried out by the four Chinese squid jiggers *New Century* No. 57, *New Century* No. 61, *New Century* No. 18 and *Dai Yunyu* No. 807 (Table 1). The survey area is described in Table 2. Fishing stations were pre-selected and defined by  $1^{\circ} \times 1^{\circ}$  longitude and latitude before the survey. The final fishing positions were defined as the actual sites where squid were caught (Fig. 1). Samples were randomly taken from the catch and 2992 specimens of both sexes were measured in dorsal mantle length (to 1 mm) and weighed to 10 g. Data on sex and maturity stage on a scale of *I–V* (Lipinski, 1979) were recorded. The number of specimens analyzed per station varied depending on the catch rate. Fishing position, sea surface temperature (SST),



Fig. 1. The three survey areas covered by the Chinese squid jigger vessels in the northwest Indian Ocean. The left panel is for the survey made during September and November 2003, the middle for September 2004 and February 2005, and the right for during March and April 2005.

number of jig lines in use (eight jiggers per line), fishing depth, time at the beginning and end of each drift, and total catch were recorded.

Statoliths were dissected from the sampled squid in the field and stored in 90% alcohol for age and growth analyses. There were 104 specimens of females in total with ML from 142 mm to 575 mm. Methods of ageing followed those described by Gonzalez et al. (1997). An image analysis system (WT-Tiger 3000) was used for counting rings on both sides of statoliths. The hatching date was estimated from age derived in the ageing study and the date when the squid were caught.

Mantle lengths of the specimens used for diet analyses ranged from 156 mm to 610 mm. Major prey in the stomach contents were identified based on undissolved tissues in the stomach. The degree of stomach fullness was recorded on five scales as follows: 0, stomach empty; 1, little content; 2, stomach less than half full; 3, stomach more than half full; and 4, full stomach.

ML–weight data were fitted to the following equation: BW = aML<sup>b</sup>, where BW is body weight, and a and b are two parameters to be estimated. Log transformation was applied to the equation and parameters a and b were estimated with the linear least squares method (Ricker, 1975).

#### 3. Results

#### 3.1. Catch data

The daily catch ranged from 0.1 t/days to 36.0 t/days. The catch totaled 1570 t in the three surveys, and the average daily catch reached 4.4 t/days. The number of fishing days when the daily catch was lower than 1 t/days only consisted of 6.6% of the total fishing days, and the number of days when daily catch was more than 5 t/days consisted of 42.5% of the total fishing days (Fig. 2). During the three surveys, the catch mainly came from the areas defined by  $15^{\circ}N-18^{\circ}N$  and  $60^{\circ}E-62^{\circ}E$  and by  $18^{\circ}30'N-20^{\circ}N$  and  $62^{\circ}30'E-64^{\circ}E$  (Fig. 3), which are located on the edge of upwelling area. No other squid species were caught in the surveys.

#### 3.2. Population structure

Altogether 2897 females and 95 males *S. oualaniensis* were randomly sampled and examined. The sex ratio (M:F)



Fig. 2. The composition of *S. oualaniensis* catch per day during the three surveys in the northwest Indian Ocean.



Fig. 3. The spatial distribution of accumulative catch of *S. oualaniensis* in the  $0.5^{\circ} \times 0.5^{\circ}$  latitude and longitude in the northwest Indian Ocean.

for the catch was 1:30.5. The mean ML was 299 mm for males (range 106–462 mm) and 352 mm for females (range 106–612 mm). The mean body weight was 891 g for males (range 50–2390 g) and 1654 g for females (range 35–8300 g). There was a clear mode from 260 mm to 300 mm ML for males, but for females, the observed distribution was likely to represent two or more modes at 300–360 mm ML and 480–540 mm ML (Fig. 4).

Two-degree longitude and  $2^{\circ}$  latitude were used as the spatial unit for calculating catch statistics. The mean ML and its standard deviation for each spatial unit were summarized in Table 3. Squid size showed large spatial difference, especially along the latitude. Three groups might exist: large squid of over 400 mm ML mainly located in the north of 18°N, medium squid ranging 300–400 mm ML mainly distributed in the area from 12°N to 18°N, and small squid of under 300 mm ML mainly in the south of 12°N. There was no such spatial pattern in size distribution along the longitude.

Table 3

The mean mantle length (mm) of S. oualaniensis by  $2^\circ$  latitude and  $2^\circ$  longitude in the northwest Indian Ocean

|                           | 58°E-60°E      | 60°E-62°E      | 62°E64°E      | 64°E–66°E      |
|---------------------------|----------------|----------------|---------------|----------------|
| 4°N−6°N                   |                |                |               | 177 ± 33.1     |
| $6^{\circ}N-8^{\circ}N$   |                |                | $234\pm35.0$  | $192\pm18.5$   |
| $8^{\circ}N-10^{\circ}N$  | $130 \pm 14.2$ | $167 \pm 50.3$ |               | $220 \pm 37.7$ |
| $10^{\circ}N-12^{\circ}N$ | $250 \pm 55.1$ |                |               |                |
| $12^{\circ}N-14^{\circ}N$ | $319 \pm 77.7$ | $303 \pm 76.7$ | $369\pm58.7$  | $337 \pm 41.4$ |
| 14°N–16°N                 | $347 \pm 92.5$ | $328\pm 64.5$  | $395\pm75.7$  | $312 \pm 39.5$ |
| 16°N−18°N                 |                | $436\pm85.6$   | $319\pm 61.5$ | $316\pm 64.6$  |
| $18^{\circ}N-20^{\circ}N$ |                |                | $409\pm96.6$  | $446 \pm 68.5$ |
| $20^{\circ}N-22^{\circ}N$ |                |                |               | $414\pm71.3$   |
|                           |                |                |               |                |



Fig. 4. The mantle length composition of female and male squid S. oualaniensis during the three surveys in the northwest Indian Ocean.

#### 3.3. ML-weight relationships

Overall ML (mm)–weight (g) relationships (Fig. 5) were estimated for the samples collected as

BW = 40.64 ML<sup>2.9115</sup>, r = 0.91, N = 2897 for females, and BW = 45.79 ML<sup>2.5842</sup>, r = 0.94, N = 95 for males.

The ML-weight equations differed significantly between sexes (p < 0.05, ANCOVA).

# 3.4. Maturity

Maturity status differed between sexes (Fig. 6). Eighty-eight percent of males were in the preparatory stage (II), maturing stage (III) and mature stage (IV). For females, only 20% were in the mature stage or fully mature stage (IV or V), but the majority were immature (I and II).

There were differences in female maturities along the latitude (Table 4). In the fishing area north to  $16^{\circ}N$ , more than 70% of



Fig. 5. The relationship between body weight and mantle length for female and male squid *S. oualaniensis* in the northwest Indian Ocean.

females were immature (stages I and II), while in the area north to  $18^{\circ}$ N, more than 48% of females were in the mature or fully mature stage (IV or V).

Female squid of the same maturity stage tended to have large variations in ML ranges. For the immature female squid (stage I), the sizes varied from 163 mm and 438 mm ML. The smallest and largest fully mature females (stage V) had the ML of 244 mm and 513 mm, respectively. Mature squid were present throughout the three surveys.

#### 3.5. Age

The ages of squid that were sampled for ageing ranged from 88 days to 363 days (Fig. 7a). All the specimens hatched during January and November 2004 (Fig. 7b), with the majority (57.8%)



Fig. 6. The frequency of different maturity stages of squid *S. oualaniensis* in the northwest Indian Ocean.

Table 4

The maturity stage of female *S. oualaniensis* in different latitudes during the survey period

| Latitude (N)                  | Stage I | Stage II | Stage III | Stage IV | Stage V |
|-------------------------------|---------|----------|-----------|----------|---------|
| <12°N                         | 57.17   | 25.46    | 7.80      | 4.56     | 5.01    |
| $12^{\circ}N$ – $14^{\circ}N$ | 50.44   | 23.16    | 12.35     | 6.18     | 7.87    |
| $14^{\circ}N$ – $16^{\circ}N$ | 43.86   | 28.47    | 6.34      | 13.81    | 7.52    |
| 16°N-18°N                     | 19.89   | 49.42    | 8.30      | 8.30     | 14.09   |
| 18°N-20°N                     | 13.08   | 31.23    | 4.55      | 22.60    | 28.54   |
| >20°N                         | 10.20   | 29.20    | 5.02      | 25.58    | 30.00   |



Fig. 7. The composition of age (a) and hatching date (b) of squid *S. oualaniensis* in the northwest Indian Ocean.

of hatching occurring from March to May. The oldest squid in the sample grew to the size of 575 mm ML and weighted at 5564 g.

# 3.6. Diet

Most of the stomachs analyzed had food remains and only 8% were empty. The stomachs contained three major groups: fish, cephalopods and crustaceans, representing 56%, 36% and 8% of the stomach contents by weight, respectively. All the species remains in the stomach were identified as *Cypselurus spp* and *S. oualaniensis*, and more than 60% of the stomachs showed the evidence of cannibalism.

About 70% of the stomachs were less than half full, and the fullness of stages I and II consisted of 30% and 32% of the total samples, respectively.

# 4. Discussion

#### 4.1. Squid distribution

The purpleback squid was widely distributed in the survey area, but the majority of catch was located in the areas defined by  $15^{\circ}N-18^{\circ}N$  and  $60^{\circ}E-62^{\circ}E$  and by  $18^{\circ}30'N-20^{\circ}N$  and  $62^{\circ}30'E-64^{\circ}E$ . This is consistent with previous studies (Nesis, 1993; Yatsu, 1997). These areas were characterized with the upper quasi-homogeneous layer, which is concentrated in the areas of large scale cyclonic gyres, especially in the Somali upwelling region (Trotsenko and Pinchukov, 1994; Zuyev et al., 2002). The squid distribution is also closely related to sea surface temperature and the optimal SST for the squid appears to range from 25 °C to 28 °C (Chen and Ye, 2005).

#### 4.2. Population structure

The dominant group observed in the surveys was the squid of 240–300 mm ML for males (38.9% of the total male catch) and 280–380 mm ML for females (42.9%). All the squid in the catch had a dorsal photophore. Based on Japanese research surveys, three populations with different ML existed in the Arabian sea (Yatsu, 1997). Our results are consistent with the previous results.

The squid caught in the northwestern Indian Ocean from the former USSR tended to be smaller than those caught in this study. In summer the ML was mainly in the range of 90–180 mm and 180–270 mm, and in winter mainly ranged from 90 mm to 180 mm ML (Trotsenko and Pinchukov, 1994). The squid in the high sea was obviously larger than that in the Yemen inshore waters, where the squid was regarded as bycatch in the Chinese trawling boats and its size ranges were from 74 mm to 321 mm ML, with the dominant group being in the 110–250 mm ML (Yang, 2002).

Nesis (1993) described a complex population structure for S. oualaniensis that incorporates three major and two minor forms. Researchers disagreed on whether or not the dwarf form is a distinct species (Clarke, 1965; Wormuth, 1976; Nesis, 1993). Roeleveld (from http://swr.nmfs.noaa.gov/pir/feis/ Appendix%20B.pdf) considered the dwarf form to be a separate species that could only be identified as an adult. Snyder (1998) suggested that the giant form resulted from a plastic phenotype in the species. Based on the squid ML composition and maturity from the samples in this study, we conclude that several groups of different sizes may exist in addition to the above three forms. A new study based on Random Amplified Polymorphic DNA (RAPD) analysis is being done in the Marine Biological Laboratory of College of Marine Science and Technology of Shanghai Fisheries University, and preliminary findings suggest a large variation in biology among the groups. The dwarf form (without the dorsal photophore) described by Nesis (1993) was absent in the survey because they may be too small to be caught by the commercial jiggers.

#### 4.3. Maturity and sex ratio

Of the sample collected in this survey, there are many more females than males. This might be caused by the fishing gear and fishing methods. In the survey, the big squid jigger with three lines of 1.6 mm diameter was used. As a result, the small size of squid, mostly males, might have less likelihood to be caught compared with large individuals. Thus, the observed skewed sex ratio may result from the selectivity of fishing gear. According to the results of the former USSR research in the northwest Indian ocean (Trotsenko and Pinchukov, 1994), the sex ratio had a seasonal variation, and the ratio (F:M) was 1:0.24 in summer, but changed to 1:0.52 in winter.

The maturation of females has a clear spatial variation along the latitude. In the area south to 16°N, most of the squid were in the maturity stages I and II, but the squid of large sizes were in the maturity stage III or above. In the area north to 16°N the squid were generally in the maturity stages III to V. This is



consistent with the size distribution of populations. This study also suggests that *S. oualaniensis* may spawn all year round based on the ML composition and maturation stage. This may result from the suitable habitat conditions, i.e. tropical waters with SST being higher than 20 °C throughout the year. The peak spawning took place in March to May, which confirmed the conclusion by Chesalin (1994).

The size at which *S. oualaniensis* become mature differed among different areas. In Hawaiian waters, *S. oualaniensis* females mature between 158 mm and 205 mm ML with 90% mature at 200 mm ML (maximum size is 335 mm ML, 1.6 kg). Most males become mature by 140 mm ML (maximum size is 210 mm ML; Suzuki et al., 1986; Young and Hirota, 1998). In the north Indian Ocean, however, the females reach maturity between 215 mm and 560 mm ML with most individuals becoming mature in 420–540 mm ML.

#### 4.4. Age

The oldest mature squid was 363 days old with its size reaching 575 mm ML and body weight of 5560 g. The smallest immature squid was 88 days old with a size of 142 mm ML and body weight of 99 g. *S. oualaniensis* is thought to have life span of less than 1 year (Dong, 1991; Trotsenko and Pinchukov, 1994). The age group in the sample was dominated by individuals ranging from 180 days and 270 days old (81.3%). These female squids reached the adult stage. While the squid younger than 180 days only made of 10.3% of the total catch. The squid is a fast-growing animal that can reach ML 550–600 mm at the age of 300 days (Zuyev et al., 2002). The ML–weight relationships differ slightly from what is described in Chesalin (1994) and Zuyev et al. (2002). This may result from differences in sampling time and locations, survey methods and population structure among different studies.

# 4.5. Diet

*S. oualaniensis* is a predator-opportunist, whose feeding spectrum varies with sizes and regions (Dong, 1991). For example, in the eastern tropical Pacific Shchetinnikov (1992) found that *S. oualaniensis* fed heavily on crustaceans (up to 50% of the volume of the diet) and fish larvae between 40 mm and 100 mm ML. In this study, for the northwestern Indian Ocean, the squid of larger than 200 mm ML fed mainly on the small fish *Cypselurus spp.* As the size of squid increased, the smaller squids *S. oualaniensis* became progressively more important in the diet and by 400 mm ML squids comprised more than 50% of the diet. This could be observed at night around the drifting vessel. In the stages of paralarvae and early juveniles, the squid mainly predate on crustaceans (Zuyev et al., 2002).

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### References

- Chen, X.J., Ye, X.C., 2005. Preliminary study on the relationship between fishing ground of *S. oualaniensis* and environmental factors in northwestern Indian Ocean. J. Shanghai Fisheries Univ. 14 (1), 55–60 (in Chinese).
- Chesalin, M.V., 1994. Distribution and biology of the squid *Sthenoteuthis oualaniensis* in the Arabian Sea. Hydrobiol. J. 30 (2), 61–73.
- Chesalin, M.V., Zuyev, G.V., 2002. Pelagic cephalopods of the Arabian Sea with an emphasis on *Sthenoteuthis oualaniensis*. Bull. Mar. Sci. 71 (1), 209–221.
- Clarke, M.R., 1965. Large light organs on the dorsal surfaces of the squids Ommastrephes pteropus, Symplectoteuthis oualaniensis and Dosidicus gigas. Proc. Malacol. Soc. Lond. 36, 319–321.
- Dong, Z.Z., 1991. The Biology of Oceanic Economic Cephalopod in the World. Shangdong Science Press, Jinan, pp. 17–19, 94 (in Chinese).
- Harman, R.F., Young, R.E., Reid, S.B., Mangold, K.M., Suzuki, T., Hixon, R.F., 1989. Evidence for multiple spawning in the tropical oceanic squid *Stenoteuthis oualaniensis* (Teuthoidea: Ommastrephidae). Mar. Biol. 101, 513–519.
- Gonzalez, A.F., Rodhouse, P.G., Trathan, P.N., Yau, C., 1997. Interactions between oceanography, ecology and fisheries of ommastrephid squids on the southern Patagonian shelf. Mar. Ecol. Prog. Ser. 152, 205–215.
- Lipinski, M., 1979. Universal maturity scale for the commercially important squids. The results of maturity classification of the *Illex illecebrosus* population for the years 1973–1977. International Commission for the North Atlantic Fisheries Res Doc 70/2/38, Ser 5364, Canada.
- Nesis, K.N., 1977. Population structure in the squid *Sthenoteuthis oualanienses* (Lessonn 1930) (Ommastrephidae) in the Western Tropical Pacific. In: Proceedings of the Academy of Science USSR, Shirsch Inst. Oceanol., vol. 107, pp. 15–29.
- Nesis, K.N., 1993. Population structure of oceanic Ommastrephids, with particular reference to *Sthenoteuthis oualaniensis*: a review. In: Okutani, T., O'Dor, R.K., Kubodera, T. (Eds.), Population structure of oceanic Ommastrephids, with particular reference to *Sthenoteuthis oualaniensis*: a review. Recent Advances in Fisheries Biology. Takai University Press, Tokyo, pp. 375–383.
- Ricker, W.E., 1975. Computation and interpretation of biological statistics of fish populations. Bull. Fish. Res. B Can. 191, 382.
- Shchetinnikov, A.S., 1992. Feeding spectrum of squid Sthenoteuthis oualaniensis (Oegopsida) in the eastern Pacific. J. Mar. Biol. Assoc. United Kingdom 72, 849–860.
- Snyder, R., 1998. Aspects of the biology of the giant form of *Sthenoteuthis oualaniensis* (Cephalopoda: Ommastrephidae) from the Arabian Sea. J. Mollus. Stud. 64, 21–34.
- Suzuki, T., Yamamoto, S., Ishii, K., Matsumoto, W.M., 1986. On the flying squid *Sthenoteuthis oualaniensis* (Lesson) in Hawaiian waters. Bull. Fac. Fish. Hokkaido Univ. 37 (2), 111–123.
- Trotsenko, B.G., Pinchukov, M.A., 1994. Mesoscale distribution features of the purpleblack squid *Sthenoteuthis oualaniensis* with reference to the structure of the upper quasi-homogeneous layer in the West India Ocean. Oceanology 34 (3), 380–385.
- Voss, G.L., 1973. Cephalopod resources of the world. FAO Fish. Circ. 10, 75.
- Wormuth, J.H., 1976. The biogeography and numerical taxonomy of the Oegopsid Squid Family Ommastrephidae in the Pacific Ocean. Bull. Scripps Inst. Oceanogr. 23, 1–89.
- Yang, D.K., 2002. The resources and its exploitation and utilization of two species of squid. J. Shanghai Fisheries Univ. 11 (2), 176–179 (in Chinese).
- Yatsu, A., 1997. The biology of *Sthenoteuthis oualaniensis* and exploitation of the new squid resources. Bull. Far-Sea Fishery 101, 6–9 (in Japanese).
- Yatsu, A., Katto, F., Kakizoe, F., Yamanaka, K., Mizuno, K., 1998. Distribution and biology of *Sthenoteuthis oualaniensis* in the Indian Ocean—preliminary results from the research cruise of the R/V Shoyo-Maru in 1995. In: Okutani, T. (Ed.), Distribution and biology of *Sthenoteuthis oualaniensis* in the Indian

Ocean—preliminary results from the research cruise of the R/V Shoyo-Maru in 1995. Contributed papers to 1st International Symposium on Large Pelagic Squids. JAMARC, Tokyo, pp. 145–153.

- Young, R.E., Hirota, J., 1998. Review of the ecology of Sthenoteuthis oualaniensis near the Hawaiian Archipelago. In: Okutani, T. (Ed.), Review of the ecology of Sthenoteuthis oualaniensis near the Hawaiian Archipelago. Contributed Papers to International Symposium on Large Pelagic Squids. Japan Marine Fishery Resources Research Center, Tokyo, pp. 131– 143.
- Zuev, G.V., Nesis, K.N., 1971. Kal'mary (Biologiya I Promysel) (Squids [Biology and Fsihery]). Pishchevaya Promyshlennost, Moscow, p. 360.
- Zuev, G.V., Nigmatullin, Ch.M., Nikol'skii, V.N., 1985. Nektonnye Okeanicheskie kal'mary (Nectonic Oceanic Squids). Agropromizdat, Moscow, p. 224.
- Zuyev, G., Nigmatullin, C., Chesalin, M., Nesis, K.N., 2002. Main results of long-term worldwide studies on tropical nektonic oceanic squid genus *Sthenoteuthis*: an overview of the Soviet investigations. Bull. Mar. Sci. 71 (2), 1019–1060.