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Population dynamics and ecology of the invasive veined rapa whelk, *Rapana venosa* in the southern Black Sea

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ABSTRACT

Spatial and temporal changes in some ecological characteristics (i.e. biomass, abundance, morphometrics, sex-composition, growth parameters and population dynamics) of the invasive veined rapa whelk (*Rapana venosa*) were studied off Sinop Bay, in the southern Black Sea. The whelk specimens were sampled from three depths (15 m, 25 m and 35 m) at monthly intervals between November 2005 and October 2007. Custom-made pots were deployed for the capture of *R. venosa* individuals. Monthly distributions in whelk biomass and abundance peaked in summer (June/July) and mid-autumn (October) and displayed no differences between 2006 and 2007. With the exception of gut weight, all morphometric variables produced three peak periods (January, June and September, respectively) over one year. Densities, morphometrics and sex composition were dictated significantly by bottom depth and monthly variation. Two stages were defined in the ovary and testis index maxima denoting longer spawning and recruitments periods starting as early as in March which is a different finding compared to previous studies from the Black Sea. For the estimation of population growth parameters, of the five morphometric variables analysed, siphon width was the best variable to produce clear size cohorts. Whelk growth in terms of shell length and width oscillated seasonally and ceased during February–March. Maximum age of the veined rapa whelk in the southern Black Sea was determined as 3.5 years corresponding to 7 cohorts. Among the environmental parameters, dissolved oxygen, temperature and salinity appeared to affect whelk densities. Results obtained here are important for better management of the whelk fishery in the Black Sea.

1. Introduction

The veined rapa whelk, *Rapana venosa* (Valenciennes, 1846), originally native to the western Pacific waters, is a voracious invasive species for many other regions of the world, including the Black Sea (Drapkin, 1953). It is an important species mainly because of its high-level-invasion capacity of habitats and widespread predation on bivalves in different marine ecosystems. This whelk species has therefore been the focus of many scientific studies, encompassing its biology (e.g. Chung et al., 1993), population dynamics and predation (Harding et al., 2007a), fisheries (Sağlam et al., 2015a, b), socio-economy of the fishermen (Janssen et al., 2014), by-catch composition (Kalayci and Yeşilçiçek, 2014; Eryaşar et al., 2018), as well as eco-toxicology (Zhelyazkov et al., 2018).

The rapa whelk was accidently introduced to the Black Sea in 1947 around Novorossiysky Bay (Drapkin, 1953) thereafter spreading through the entire Black Sea in less than two decades. This species was once considered a pest for the Black Sea ecosystem where it decimated several native bivalve species (e.g. *Ostrea edulis, Flexopecten glaber, Chamelea gallina*) as well as mussel beds (dominated by *Mytilus galloprovincialis*) in the Black Sea (Janssen et al., 2014).

However, during the last two decades, the rapa whelk fishery in the Black Sea has become very profitable since exporting to Japan, Korea and some other East Asian countries (Sağlam et al., 2009). Annual

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catches of veined rapa whelks in Turkey have varied between 2000 and 14000 tons with an average figure of 8650 tons during the last two decades (TÜİK, 2020). The bulk of veined rapa whelk catches from the Black Sea are landed by Turkey. Veined rapa whelks were exported at a value of 6.6 $ per kilo in 2007 to Japan (Hin and Hoşgör, 2018). Despite its negative impact on the ecosystem, due to the significant commercial value of this invasive species, measures were set to prevent its over-fishing in the Black Sea. The veined rapa whelks are harvested by dredges, pots and manual collection (Kideys et al., 2007), and all types of collection methods, including dredges are permitted from 31st August-15th April (MAF, 2020).

There are a number of studies which evaluate relevant population growth parameters, reproduction period, maturity size and spawning season aimed at optimal fishery management for the veined rapa whelk in the Black Sea (Sağlam et al., 2009, 2015a, b). However, there are still significant gaps in the understanding of ecological characteristics of veined rapa whelks in the Black Sea. For example, the exact timing of reproduction, maximum age, average length of different age classes or growth rate are still unknown for veined rapa whelk in the Black Sea which are essential for the sustainable management of this species. The present study therefore endeavored to determine these parameters using a high number of variables (weights and/or length/width of shell, total tissue, muscle, gut, penis, gonad, aperture and siphon) in addition to determining sex composition, population growth parameters and ecological relationships with some environmental parameters for a depth range of 15–35 m using pot sampling. Therefore, results obtained from this study will be important not only for fishery management but also for better understanding of the ecology of the veined rapa whelk in the Black Sea and worldwide where this species is distributed.

2. Material and methods

Sampling for the present study was conducted at monthly intervals during November 2005–October 2007, covering both open and closed fishing seasons in Sinop Bay, in the southern Black Sea (Fig. 1). Sinop coasts are among the most important fishery areas for the veined rapa whelk in Turkey. The sampling area displays dynamic inter-annual physical environmental characters as reflected by other biological monthly data, e.g. strong inter-annual anomalies in mesozooplankton during 2002–2004 and 2005–2009 (Üstün et al., 2018).

Rapana venosa specimens were collected by three sets of trapping pots (Fig. 1) modified by Kideys et al. (2007) from pots used to sample the common whelk *Buccinum undatum* in the Irish Sea (Kideys, 1991). Numerous holes of about 1 cm were distributed around the perimeter of pots for dispersing the smell of the bait whilst preventing whelks caught larger than this size from escape. Three sets of 10 pots were deployed on the sandy bottom at 3 stations at depths of 15, 25 and 35 m (Fig. 1) from November 2005 to October 2007. Pots were baited with a mixture of Mediterranean mussels (*Mytilus galloprovincialis*) and trash fish or fish offal. Soak time of pot deployment at sea varied between 48 and 192 h depending on a sufficient catch being landed following daily control checks (see Fig. 4b).

Following collection, several biological and morphological measurements were conducted for each specimen at the laboratory (Fig. 1d, Table 1). Weights of all variables were measured after specimens were retained on blotting papers for 2–3 min.

During recovery of pots, physical parameters of seawater (temperature, salinity, pH, dissolved oxygen were measured from surface to bottom using a YSI 6600 Multi Parameter V2 Sonde and optical parameter (Secchi disk depth).

The Gonadosomatic Index (GSI%) was estimated separately for female and male specimens.

Several statistical analyses were performed on the measured parameters. Correlations between morphometric and environmental parameters were checked using Spearman's rank correlation. The density as well as biomass (g/pot/d = g/pot/24 h; total weight with shell, total

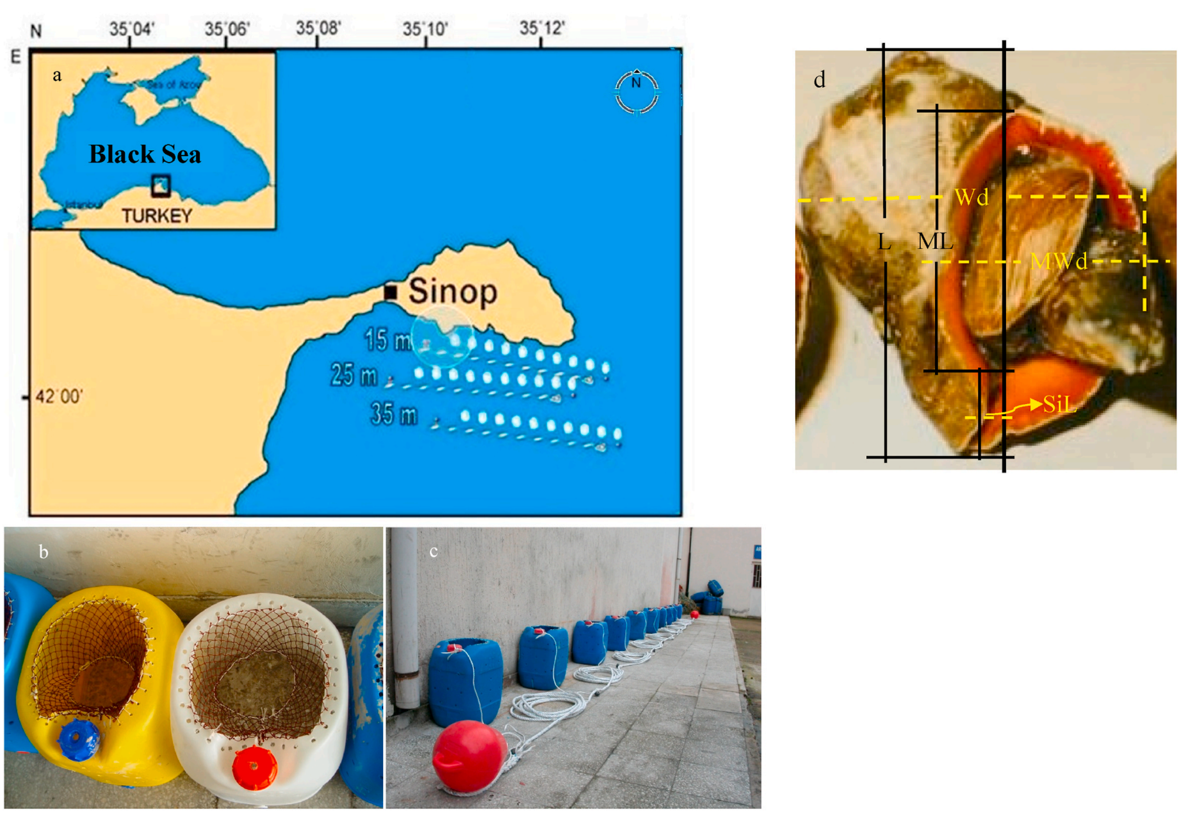

Fig. 1. (a) Sampling area (b) close-up of pots (c) pots ready for deployment at sea, and (d). Morphometric variables measured for veined rapa whelk specimens (see Table 1 for abbreviations).

Table 1
Variables measured for each veined rapa whelk specimen with abbreviations used for statistical analyses.

Variable	Unit	Precision	Abbreviation
Shell length	mm	0.1	L
Shell width	mm	0.1	Wd
Aperture (mouth) length	mm	0.1	ML
Aperture (mouth) width	mm	0.1	MWd
Siphon width	mm	0.1	SiL
Total weight with shell	g	0.01	Bio
Sex	Female or Male	exact	F or M
Total tissue weight	g	0.01	Meat
Muscle weight	g	0.01	Muscle
Gut weight	g	0.01	Gut
Penis weight	g	0.01	Verge
Gonad weight	g	0.01	Gonad
Operculum weight	g	0.01	Oper

tissue weight, muscle weight, gut weight, penis weight, gonad weight and operculum weight) and abundance (ind/pot/d) related parameters of the whelks were tested for monthly and depth variation using two-way ANOVA. Individual density and morphometric variables were also tested for depth, sex and monthly variation using three-way ANOVA. Due to inter-variable dependence in the environmental data and growth of the veined rapa whelk, and to the non-linear effect of environmental data on the biological data, a multivariate analysis, Canonical Correspondence Analyses (CCA) was used to confirm major gradient in a combination of the environmental parameters and the relationships between a matrix set of multivariate data for density, morphometric measurements and environmental parameters (CANOCA ver. 4.5.3).

ELEFAN I, Electronic Length Frequency Analysis of the software FISAT II (ver. 1.2.2) was applied to estimate coefficients of a seasonalized von Bertalanffy Growth Function (S-VBGF) for shell length to yield the cohorts. A model of "length-at-age data" of the software FISAT II was applied to estimate coefficients of a deseasonalized von Bertalanffy Growth Function (VBGF) for appropriate variables (e.g. shell siphon width and shell length). Before estimation of the coefficients, Bhattacharya's method was applied to biometric frequency distribution to separate the overlapped cohorts, and then NORMSEP to normalize the distribution using maximum likelihood method (ML), and a matrix of length-at-age data was formed using a method of "Linkage of means" to the analysis of length-at-age data in the subroutine of FISAT II (Gayanilo and Pauly, 2001). FISAT II recommended that the Bhattacharya is used before the solution of the maximum likelihood function embedded in NORMSEP. Otherwise overlapped the cohorts could not be separated by using directly NORMSEP.

3. Results

3.1. Density (catch rate)

The monthly abundance and biomass distributions of the whelk for the three separate depth layers were statistically not different for the entire sampling period between years 2006 and 2007 (Fig. 2a and b; Paired sample *t*-test, t = 0.0994, p = 0.923, and t = 0.8068, p = 0.441 at 15 m, t = 0.2111, p = 0.838, and t = 0.7440, p = 0.476 at 25 m, and t = −0.3705, p = 0.720, and t = 0.3687, p = 0.721 at 35 m respectively, n = 11 months). A critical water salinity of <14 determined a decrease in density whereby specimens migrated to lower depths (Fig. 2a and b). Water temperatures (>10 °C) accelerated the density synergistically concurrent with above-threshold salinity concentrations, which was more pronounced at the sea surface (Fig. 2a–c). A critical temperature of <8 °C caused a reduced abundance.

3.1.1. Monthly abundance

When the same months were combined (since monthly abundance did not differ significantly between the two sampling years; pairwise *t*-test at p < 0.05) (Fig. 2), whelk abundance varied between 2 ± 2 (X ± SD) ind/pot/day in February and 14 ± 3 ind/pot/day in September (Fig. 3a). Following combining values from the two years, there appeared monthly and depth-wise significant differences in the abundances (two-way ANOVA, p = 0.004 and p = 0.027, respectively) at p < 0.05 (Fig. 3a and b).

There was an increase trend in abundance from January (6 ± 2 ind/pot/d) to June/July (12 ± 2 ind/pot/d) followed by a decrease till December (2 ± 3 ind/pot/d). Two peak periods in abundance were observed: a primary peak in September and a secondary peak in June/July (Fig. 3a).

In contrast to biomass (see below), the abundance was significantly higher at 25 m (8 ± 1 ind/pot/d) than at 15 m (5 ± 1 ind/pot/d) (Fig. 3b), which implies that larger sized and heavier individuals were found at 15 m.

3.1.2. Monthly biomass

Biomass (total weight with shell) varied between 17.4 ± 83.4 (X ± SD) g/pot/d in February and 334.2 ± 83.4 g/pot/d in June/July during one year. No significant difference in biomass was observed between monthly values but a significant difference in biomass did occur for different depths (two-way ANOVA, p = 0.170 and 0.008, respectively). Interaction between months * depths showed that the biomass values were not significantly different (p = 0.562).

Biomass values were generally lower during the cold period (February–May; 17.4 ± 83.4–55.5 ± 83.4 g/pot/d) compared to warm water months (July–October; 160.9 ± 83.4–262.0 ± 59.0 g/pot/d). The biomass in June was particularly notable compared to cold water months. Whelk biomasses peaked twice yearly; a primary peak in June/July and a secondary peak in October.

Biomass values were significantly higher at 15 m (281.3 ± 40.4 g/pot/d) than at 25 (91.3 ± 40.4 g/pot/d) and 35 m (115.4 ± 40.4 g/pot/d) respectively, whereas the two latter depths displayed no significant difference.

Males exhibited a significantly larger edible meat mass (10.7 ± 0.1 g) than females (8.7 ± 0.2 g) at p < 0.05.

3.2. Morphometric parameters

3.2.1. Shell length

Shell lengths varied between 15.9 mm and 119.2 mm throughout the study. The average shell length varied between 64.0 ± 0.5 mm in July and 79.9 ± 1.2 mm in January (Fig. 4a). Shell lengths were significantly different between months, sampling depths and sexes (Three-way ANOVA, p < 0.000X, p < 0.000X and p < 0.000X, respectively). Interaction of months * bottom depths altered shell length significantly (p = 0.0002) whereas combinations of both month * sex and depth * sex did not (p = 0.218 and p = 0.992, respectively).

Following a post-hoc test, Least Significant Difference (LSD) showed that the shell length was significantly higher in January (<75.0 mm) than for most other months of the year excepting June/July (78.2 ± 0.8 mm) and December (77.9 ± 1.7 mm) (Fig. 4a). The average shell length increased from February (69.1 ± 2.6 mm) till June/July, with a sudden decrease occurring in July (64.0 ± 0.5 mm) and thereafter increasing again till September. After a decrease in October, it increased again during November to December (Fig. 4a).

The larger shells occurred at 35 m depth. The average length at this depth (76.1 ± 0.5 mm) was significantly different than those at 15 m (68.7 ± 0.2 mm) and 25 m (67.4 ± 0.5 mm) (Fig. 4b).

Male individuals were significantly longer (70.3 ± 0.2 mm) than females (68.5 ± 0.4 mm) (Fig. 4c).

3.2.2. Gonad weight and gonadosomatic index (GSI)

Ovary weights varied between 0.18 ± 0.04 g in April and 0.49 ± 0.04 g in January. Ovary weight was significantly different among the

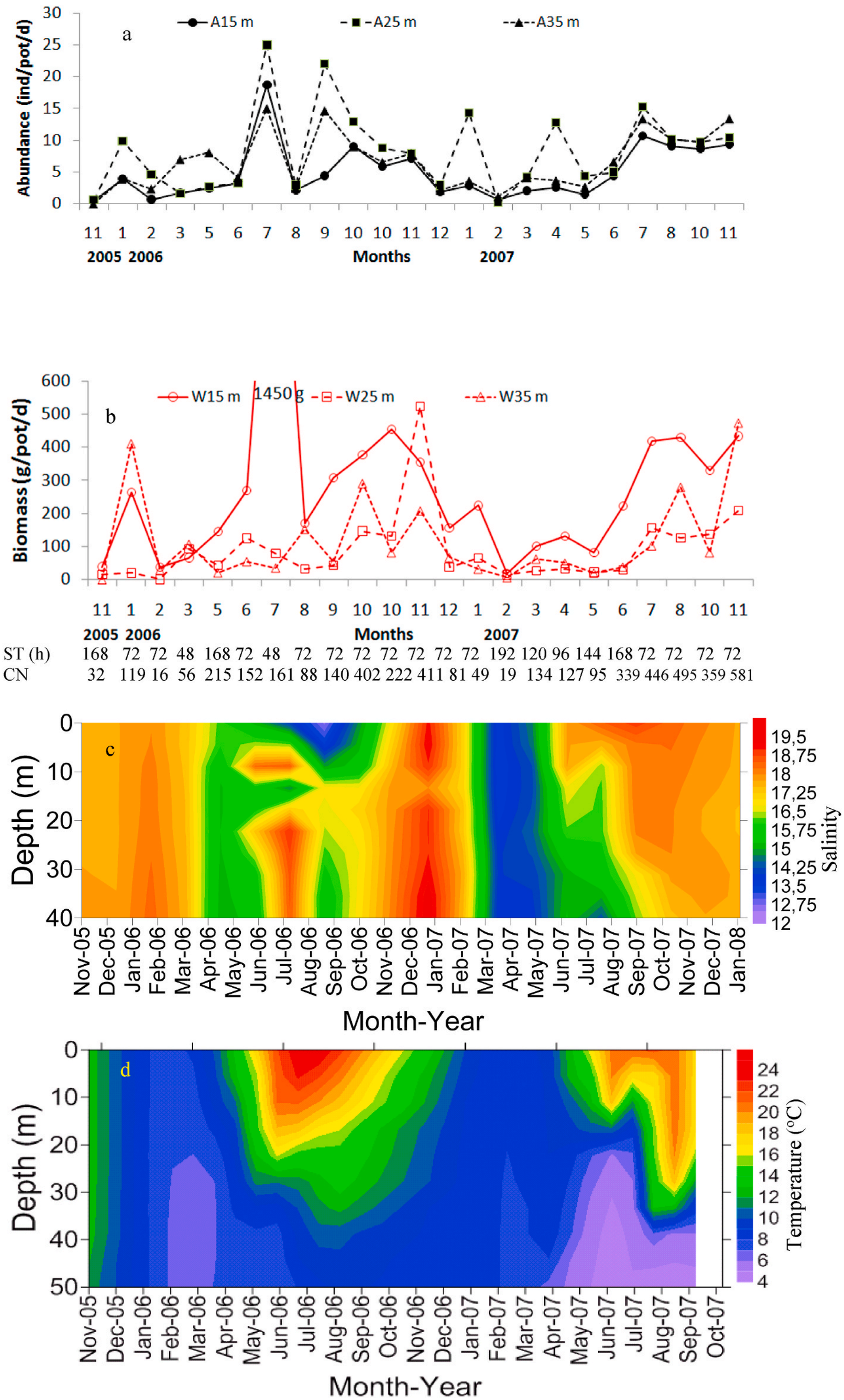

Fig. 2. Monthly abundance (a) and biomass (b) of the veined rapa whelk (ST is soak time of pot deployment in h, and CN is total number of individuals captured), water salinity (c) and temperature (d) at the sampling area during the sampling period from 2005 to 2007.

months and bottom depths (Two-way ANOVA, $p < 0.000X$ and $<0.000X$, respectively) at $p < 0.05$. The ovary weight decreased from January to April, and then increased by May (0.29 ± 0.03 g) remaining at the same value of 0.22 ± 0.01 g till October, then increased slightly to a secondary peak value of 0.42 ± 0.04 g in December. Ovary weight increased from 0.18 ± 0.01 g at 15 m to 0.44 ± 0.01 g at 35 m.

The gonadosomatic index (GSI), calculated based on the total weight of females ranged between 0.34 ± 0.07 in June and 0.61 ± 0.06 in December (Fig. 5a, e). There were two peak GSI periods (GSI>0.5); from July to September and from December to February (Fig. 5a, e). The GSI was more pronounced in winter compared with the summer. The index was also significantly different among the months and bottom depths (Two-way ANOVA, $p < 0.000X$ and $<0.000X$). The gonadosomatic index increased significantly from the shallowest depth (0.36 ± 0.01) through

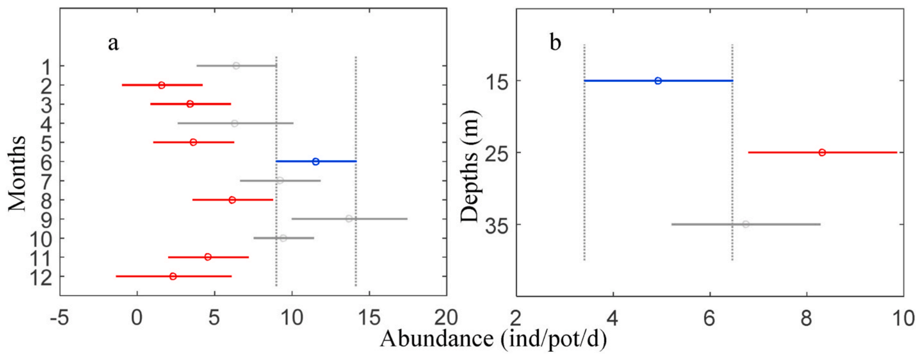

Fig. 3. Mean values ± SD of *Rapana venosa* abundance in ind/pot/d by (a) months (b) bottom depths and pair-wise test results (Least Significant Difference, LSD) of differences in biomass among sampling months and bottom depths (circle: mean, horizontal bar: standard deviation, blue symbols; to be tested among the months or depths, red symbols: significantly different, grey symbols: not significantly different from that coinciding between vertical discrete grey lines). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

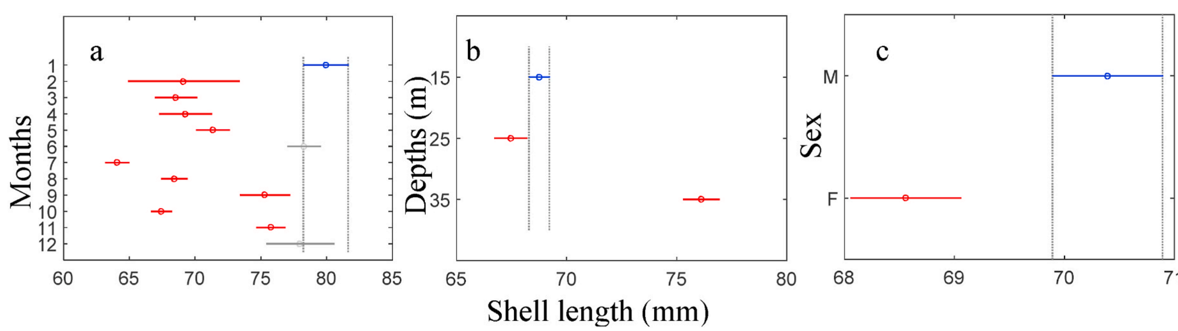

Fig. 4. 95% confidence limits (Mean values ± SD) of individual shell lengths in mm of *Rapana venosa* between (a) months, (b) bottom depths, and (c) sexes and pair-wise test (Least Significant Difference, LSD) of differences in the individual shell length between sampling months, bottom depths and sexes.

mid-range depths (0.51 ± 0.02) to the greatest depth (0.66 ± 0.02) at $p < 0.05$ (Fig. 5b, e).

Individual testis weights varied between 0.14 ± 0.01 g in October and 0.36 ± 0.02 g June/July in one year. Testis weight decreased from January (0.29 ± 0.02 g) to March (0.14 ± 0.01 g), followed by an increase reaching a peak value of 0.36 ± 0.02 g in June/July. Thereafter, an abrupt decrease occurred in August to 0.18 ± 0.01 g. This latter weight remained until a further increase by September (0.25 ± 0.02 g), dropping to a minimum value of 0.14 ± 0.01 g in October. Testis weight started to increase by November (0.26 ± 0.02 g), and reached the value of January in December (0.29 ± 0.02 g). The weight was significantly different amongst months and bottom depths (Two-way ANOVA, $p <$ 0.000X and 0.022, respectively) at $p < 0.05$. Individual testis weight was significantly higher at 35 m (0.27 ± 0.01 g) than at 15 m (0.17 ± 0.01 g) or 25 m (0.18 ± 0.01 g) at $p < 0.05$.

The gonadosomatic index based on total weight of males varied 0.23 ± 0.02 in April and 0.37 ± 0.02 in December over a one year period (Fig. 5c). Similar to females, there were two peak GSI periods for the males (GSI>0.3); from June to August, (just one month earlier than that of females), and from December to February) (Fig. 5c, f). Occurrence of males having high GSI values suggested that the fertilizing took place at the greatest depth where the lowest temperature values occurred, which were more pronounced in the second GSI period (June–August) (Fig. 5c–d, f). The GSI was more pronounced and higher in 2006 than that in 2007 depending on the shell length (Fig. 5e and f). The index was significantly different amongst months (Two-way ANOVA, $p <$ 0.000X) and depths ($p <$ 0.000X). The index was significantly higher at 35 m (0.35 ± 0.01) than at 15 m (0.27 ± 0.01) and 25 m (0.28 ± 0.01) at $p < 0.05$ (Fig. 5d).

The high GSI period was shorter (1–2 months) under the typical salinity concentration (i.e. 18psi) for the Black Sea than for low-salinity conditions (Figs. 2d and 5e-f). For the onset of the GSI periods, the minimum shell length was 40 mm both for females and males. Regardless of year, the GSI showed the same two periods of the highest values for male and female specimens. The GSI was significantly higher at 35 m (February–March and September–November) than that at 15 m or 25 m.

3.3. Female:Male ratio

During the entire sampling period, the overall female:male ratio was close to unity (i.e. 0.96). Sex ratios decreased from January (1.2 ± 0.3) to April (0.7 ± 0.5), and then increased to a value of two annual peaks in May (1.45 ± 0.31). The ratios then decreased again till August (0.7 ± 0.3), after which secondary peak values occurred in September (1.59 ± 0.45), and then decreased till November (0.5 ± 0.3)-December (0.6 ± 0.5) over the year. Ratios significantly changed between months (Two-way ANOVA, $p = 0.002$), depths ($p = < 0.000$) and their interaction ($p = < 0.000$) at $p < 0.05$.

The sex ratios imply that males dominated the shallowest waters (0.4 ± 0.1), males and females accounted for a fifty-fifty share of the population at 25 m (0.8 ± 0.1), with females dominating the deepest waters significantly (1.5 ± 0.1) at $p < 0.05$ (two-way ANOVA).

3.4. Population dynamics

3.4.1. Shell length

The theoretical maximum shell length was estimated as 126.5 mm, K 0.5, C (amplitude of oscillation in growth) 0.4 and WP (winter point) 0.4 (February–April) by ELEFAN I (Fig. 6a).

Based on the "length-at-age" model, the theoretical maximum shell length was estimated to be 164.1 mm, K 0.39, and t_0 -0.10 (Fig. 6b). The shell length produced about 7 annual cohort or growth curves, implying that maximum age of the veined rapa whelk in the Black Sea was about 3.5 years accounting for the number of cohorts and cohort age (Fig. 6b).

3.4.2. Siphon width

One of the best measurements producing clear cohorts was siphon width in the estimation of growth parameters for the whelks. While other morphometric variables were seen to be interdependent, siphon

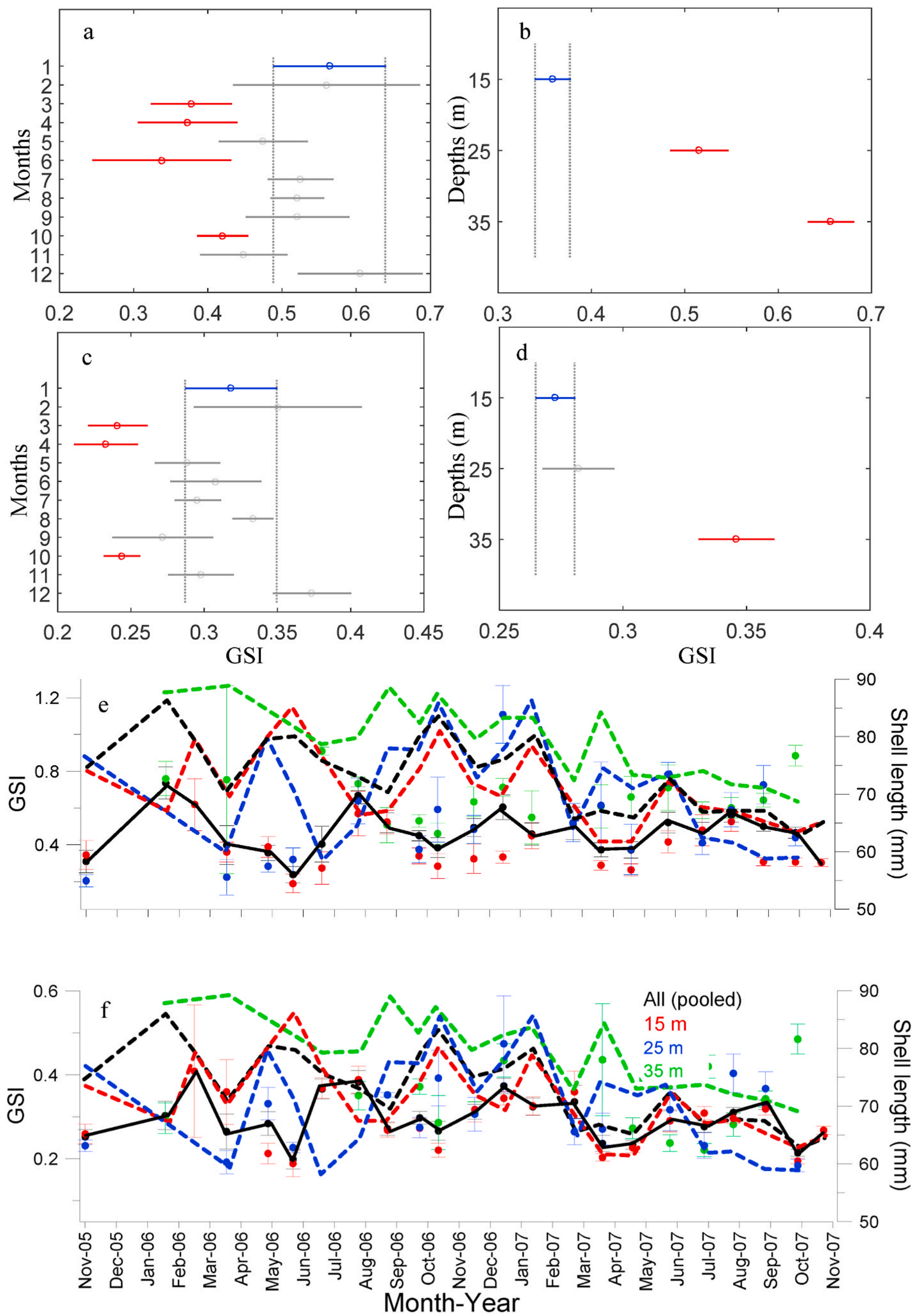

Fig. 5. 95% confidence limits (mean values ± SD) of gonadosomatic index (GSI) based on the total weight for the females (a–b) of *Rapana venosa* and the gonadosomatic index for the males (c–d) and pair-wise test (Least Significant Difference, LSD) of differences in the indices among the sampling months and bottom depths. Monthly GSI (X ± standard error and continuous line is mean GSI only for pooled data) and mean shell length (dashed lines) of females (e), and males (f) from years 2005/2006 to 2007.

width was observed as an independent growth variable (Fig. 8c). Siphon width measurements produced neither C (amplitude of seasonal oscillation in growth) nor WP (winter point when the growth ceased) values.

Siphon width measurements were subjected to length-at-age analysis decomposed by the NORMSEP and mean linkage. However, the siphon width showed a deseasonalized VBGF. The age of the veined rapa whelk was then estimated to be 3.5 years similar to that for the shell length. The theoretical maximum siphon width was estimated to be 12.36 mm, K 0.47, and t_0 -0.10.

3.5. Correlations with environmental parameters

Ecological aspects of the veined rapa whelk were resolved for density and morphometric measurements separately, using the Spearman correlation.

Bottom depth overall correlated negatively with density but positively with the morphometrics of shell size. Temperature positively correlated with biomass, abundance, sexual and reproductive traits (penis biomass and gonad biomass) at $p < 0.05$. Dissolved oxygen concentrations correlated negatively with siphon width and shell length and positively with the GSI at $p < 0.05$. Sea surface salinity did not correlate significantly with any of the traits.

3.5.1. Density

The density (catch rate) variables comprised all variables weighed and converted to biomass (g/pot/d) and abundance (ind/pot/day). Density correlated primarily with the bottom depth (Eigen value: 0.462) and near-bottom temperature (−0.420) and secondarily with dissolved oxygen concentration of the near bottom (0.280) and surface waters (0.291) (Fig. 7). This discrimination occurred over the CCA axis 1 with a percentage variance of 77.7% for the bottom depth and months (Fig. 7a and b). Biomasses of the variables were positively correlated with the

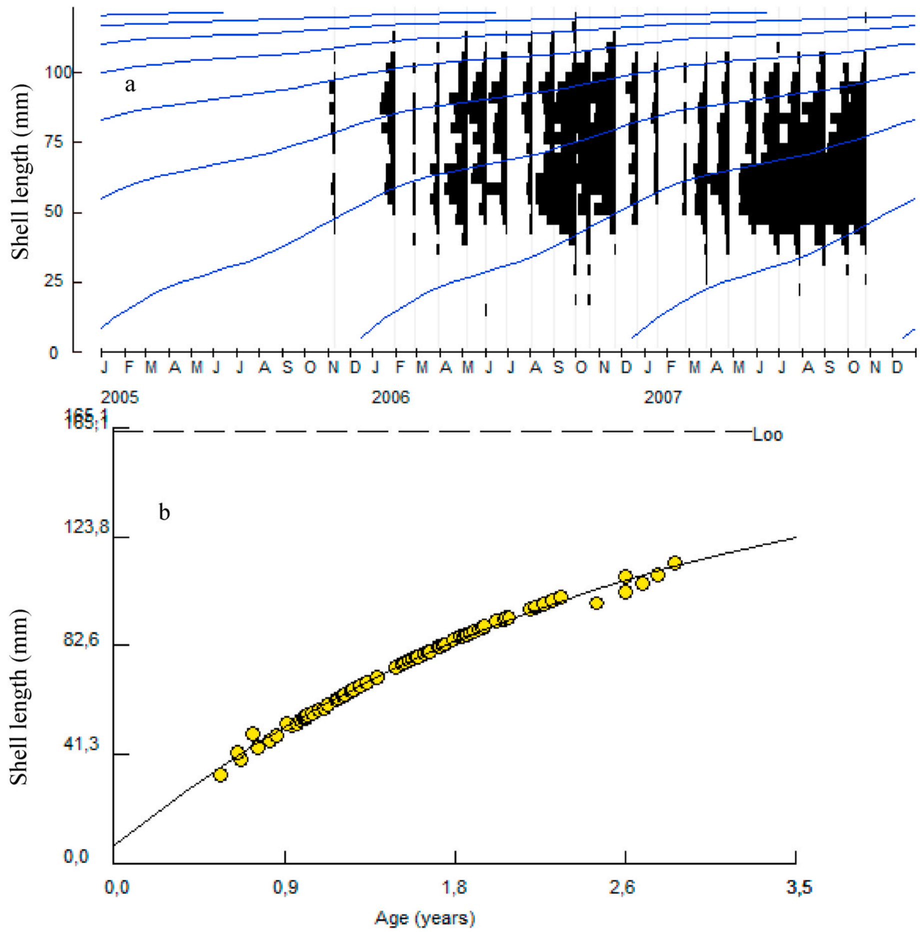

Fig. 6. ELEFAN I response surface solution to estimate the growth parameters for the shell length (mm) of the veined rapa whelk and the growth curves (a) and growth parameters (b) estimated by the analysis of "length-at-age" for the shell length (mm) of the veined rapa whelk.

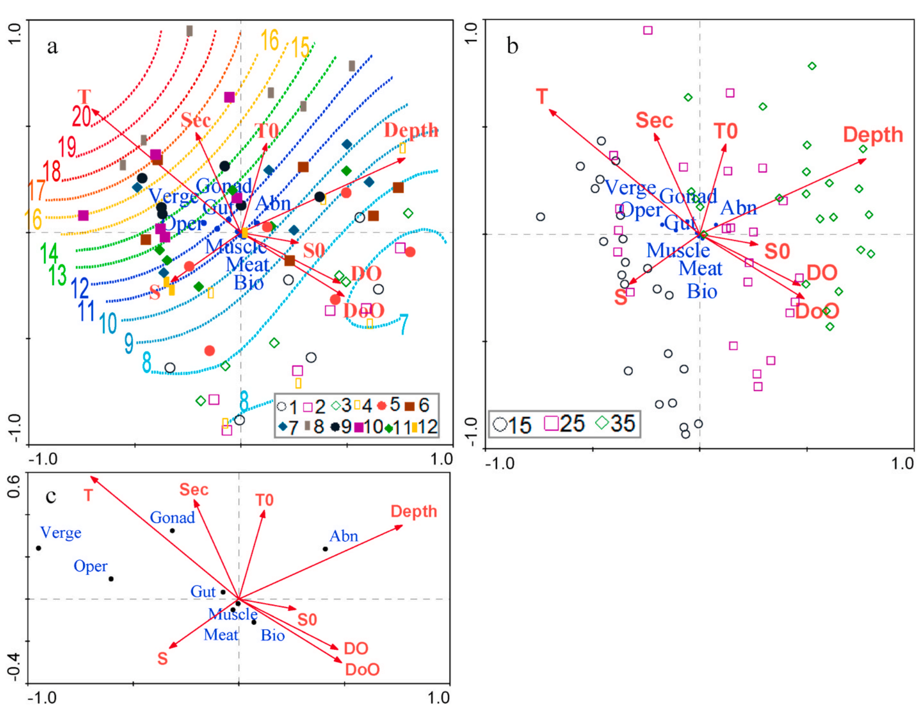

Fig. 7. Triplot of CCA for the density variables (Abn; abundance of ind/pot/d, Bio; biomass, Meat; flesh biomass, Muscle; muscle biomass; Gut; gut tissue biomass, Verge; penis biomass, Gonad; gonad biomass and Oper; Operculum biomass in g/pot/d) in relation with the environmental parameters (Depth; depth, DO; dissolved oxygen, T; temperature, S; salinity of the near-bottom water and of sea surface water; X0; suffix is 0; sea surface, and Sec; Secchi disk depth) by the months overlapped by near-bottom isotherms, °C (a) and depths (b). Biplot of CCA for the density and environmental parameters without sample plots (c).

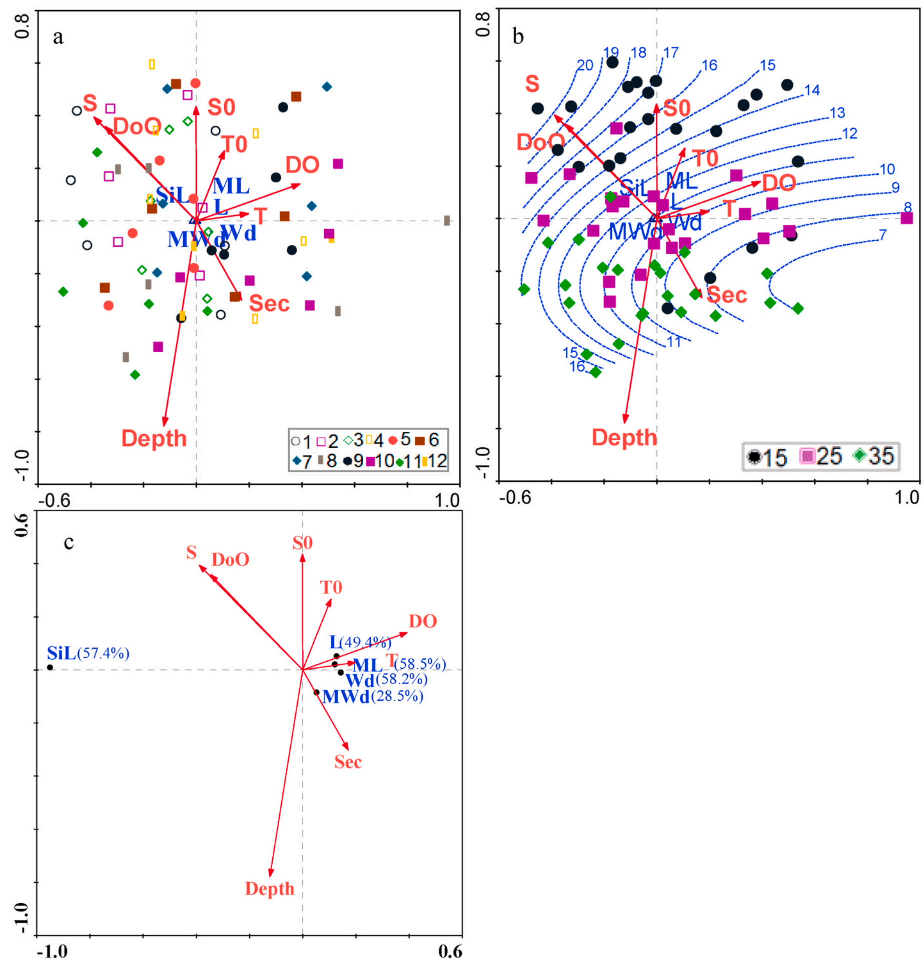

Fig. 8. Triplot of CCA for the morphometrical variables (L; shell length, Wd; shell width, ML; aperture length, MWd; aperture width and SiL; siphon width in mm) in relation with the environmental parameters by (a) months and (b) depths overlapped by near-bottom water isohalines. Biplot of CCA for the morphometrical variables (as percentage variances) and environmental parameters without sample plots (c).

physical parameters with the exception of sea surface temperature and partially with salinity (Fig. 7c). Abundance positively correlated with depth and dissolved oxygen concentration and slightly correlated with the sea surface temperature and salinity (Fig. 7). Additionally, penis and gonad and operculum biomasses were higher for shallower waters than at greater depths where the rest of the variables increased with the bottom depths (Fig. 7b and c). On CCA axis 2, the near-bottom water temperature correlated with sexual and reproductive biomasses and operculum biomass with a cumulative percentage variance of 96.1% (Fig. 7c). Both CCA axes were verified significantly for the discriminations by the Monte-Carlo test ($F = 11.317$, $p = 0.012$ and $F = 1.924$, $p = 0.014$, respectively) since the cumulative percentage variance was highly significant among the variable discrimination (15.9% by CCA1 and 19.6% by CCA2). The entire CCA discrimination was explained mostly by percentage variances of the penis (50.1%) and operculum biomass (46.9%), followed by total biomass (20.6%), gonad biomasses (16.4%), abundance (14.6%) and flesh biomass (8.3%) (Fig. 7c).

3.5.2. Morphometry

Morphometry of the veined rapa whelk was characterized by shell length, shell width, aperture length, aperture width and in mm for the CCA solution (Fig. 8). The variables were separated according to dissolved oxygen and near-bottom water salinity, followed by near-bottom temperature on the CCA axis 1 (Fig. 8a and b). While shell length, shell width, aperture length, and aperture width displayed negative correlation with salinity, the reverse was true for siphon width values which positively correlated with salinity (Fig. 8c). Dissolved oxygen concentrations (DO) of near-bottom waters positively correlated with the CCA1, but negatively correlated with sea surface water values (Fig. 8). The CCA1 explained the correlation with a percentage variance of 97.8% while the CCA2 explained with a cumulative variance of 99.8% of the total variance. Therefore, a variance of 2.0% was attributed to the bottom depth explaining the discrimination on CCA axis 2 (Fig. 8b and c). Both axes were significantly proofed by the Monte Carlo test ($F = 69.21$, $p = 0.002$ and $F = 9.08$, $p = 0.002$, respectively) at $p < 0.05$ since the cumulative explained percent variance was high only for the variable discrimination (53.6% by CCA1 and 54.6% by CCA2) compared with density. This implies that siphon width was a distinguished variable characterizing independent growth from the other variables of the veined rapa whelk. Aperture width and shell width correlated positively with the bottom depths whereas shell length and aperture length negatively correlated with bottom depths but siphon width did not (Fig. 8b and c). The sampling months were not effective in discriminating the variables (Fig. 8a).

4. Discussion

The total average biomass including shell varied between 0.21 ± 0.04 kg/pot/d (8 ± 1 ind/pot/d) and 0.62 ± 0.08 kg/pot/d (24 ± 3 ind/pot/d) at the Trabzon coasts, located in the southeastern Black Sea (Sağlam et al., 2017), which are much higher values compared with the results of the present study (0.0174 ± 0.0834 kg/pot/d with 1.59 ± 1.81

ind/pot/day and 0.3342 ± 0.0834 kg/pot/d with 13.68 ± 2.56 ind/pot/day). On the Trabzon coasts, the highest biomasses were found in the spring-summer period and the lowest in autumn – winter (Sağlam et al., 2017). The highest abundance was found in autumn (October) and the lowest abundance was in spring (April) at depths shallower than 16 m at the Turkish Black Sea coast where no sampling was carried out in June/July (Culha et al., 2009). The catch of the veined rapa whelk peaked generally in spring during 1998–2009 in Chesapeake Bay, but this shifted annually to winter, early spring during 1999–2000 and a secondary minor peak occurred in October–December of some years (Harding and Mann, 2016).

Rapana venosa extended to a depth of 36 m and was dominant between 10 m and 36 m in the Uruguayan shelf (Carranza et al., 2008). In Chesapeake Bay, the veined rapa whelk moved to greater depths during cold seasons (Harding and Mann, 2016). Abundance was observed to decrease towards the bottom depths from <16 m to >30 m for the eastern Turkish Black Sea coasts (Kalayci and Yeşilçiçek, 2014). During September–December and April, the catch per unit effort (CPUE) of a commercial dredge was estimated to be higher (103 ind/min) in shallow waters (7–18 m) than at greater depths (69 ind/min; 19–26 m) (Eryaşar et al., 2018). Whelk abundance was found to increase by depths of 1 m through 5 m and 10 m–15 m on the central Turkish Black Sea coast (i.e. Sinop area) (Culha et al., 2009). Similarly, abundance increased greatly from depths >20 m (3 ind/m^2) to 2–10 m (120 ind/m^2) in the productive region off the Danube delta on the northwestern shelf of the Black Sea where abundance is considerably higher than the Turkish Black Sea (Snigirov et al., 2013).

Maximum shell lengths were reported higher in studies of some other seas compared to measurements from the Black Sea in this study (140 mm in Choi and Ryu, 2009 for Korean waters; 195 mm in Harding and Mann, 2016 for Chesapeake Bay). The range in shell length was 15.9 mm–119.2 mm in our study. Sağlam et al. (2015b) measured a minimum length of 7.9 mm and a maximum length of 116.1 mm on the Trabzon and Samsun coasts of Turkey from the fisheries data during mid 2006 - early 2007. Kaykaç et al. (2018) reported a range of 25–115 mm off Samsun at depths <11 m in July 2014. Total shell lengths of specimens sampled off Samsun ranged from 43.5 to 109.5 mm during December 2014–November 2015 (Bayraklı et al., 2016). On Romanian coasts, shell length varied between 36 mm and 109 mm in February (Sereanu et al., 2016), which was similar to the present study with the lengths ranging from 40 mm (February 2006) and 51 mm (February 2007) to 101 mm for both years. Snigirov et al. (2013) measured the minimum size class as 28–38 mm corresponding to age group 2 in the population of the northwestern Black Sea. This illustrated that the population included specimens with a minimum age of 2 years old as we observed the minimum dominant corresponding size groups with the exception of a few specimens having shell length <30 mm corresponding to age 1. Three peak periods occurred for the shell-sized dimensional traits; February/March - to June – to July (min - to max – to min), July - to September – to October, and October – to December/January – to February.

Conversely, Bayraklı et al. (2016) estimated meat yields ranging from 9.08% to 46.27% with a mean of 29.32 ± 0.29, with the highest values in January (36.45%) and the lowest in September (23.30%). Total weights were measured as ranging from 2.18 g to 119.34 g on the Romanian coasts in February (Sereanu et al., 2016) which was lighter than 56.1 ± 6.6 g confidence-limited estimates for the present study, and the weight range from 12 to 144 g in February 2006 and 20 g–175 g in February 2007.

Sound estimation of the GSI seasonality and spawning period/s is important in determining the optimum season of fishery ban for this species. Similar to our results, Sağlam et al. (2009) also found that the minimum shell length of mature females and males was 40 mm in the southern Black Sea. They estimated the lowest ovary index in January and the highest in June (7.52) with a slight decrease towards August whereas the testis index peaked in June–July. However, their GSI analysis indicated only one short spawning period which was between July and early August during the entire year, similar to the findings for Chesapeake Bay (Harding et al., 2007b). Şahin et al. (2009) also reported the spawning period for this whelk as confined to summer (June–July) in the eastern Black Sea of Turkey. These results contrast with two GSI peaks (December–February and July–September) and the accompanying earlier onset of the spawning period (starting in March) in one year, findings in our study. Recent observations from an ongoing project on population dynamics of the veined rapa whelk in the Black Sea, egg capsules also began to be observed by March (personal communication with Prof Nuri Başusta, Fırat University, Fisheries Faculty, Elazığ, Turkey) which supports our results. Similarly, spawning periods of the veined rapa whelk were reported to be from April to late July (Chung et al., 1993) or May to July (Choi and Ryu, 2009) both in Korean waters. The reason for this discrepancy between our and other studies performed in the Black Sea could be that our sampling covered depths greater than 15 m, whilst the other two studies were in shallow waters and hence reproductive migration may have caused bias in results. Similar to Sağlam et al. (2017), we also suggest that the spawning occurs in the shallower waters and specimens with spent ovaries then return back to greater depths in the southern Black Sea. Further study is needed to analyze gonad tissue and to observe the mature egg capsules with determination of their stages.

In the Cheasapekae Bay, the peak of egg capsule deposition was observed in each of years 2001 and 2002 when the veined rapa whelk deposited egg capsules depending on critical temperature (18 °C) (Harding et al., 2008). Similar temperature thresholds for the onset of egg capsule deposition in its native habitat were 18–19 °C in Korea (Chung et al., 1993; Wei et al., 1999) and 19 °C in Japan (Amio, 1963) when the GSI increased with the shell length. In our study, two GSI peaks occurred in winter (when temperature was about 10 °C), and summer, followed by declining GSI during the next two months when egg capsules were deposited. Gönener and Özsandıkçı (2017) also observed overwintering veined rapa whelk to become active at temperatures above 10 °C.

The female (F): male (M) ratios varied between 0.5 and 0.6 in November–December and 1.45–1.59 in May and September in the present study area, and were close to unity on annual average for the entire study period. Our female to male sex ratio was similar in Samsun Bay but different in Trabzon waters (F:M = 1:6) during 2006–2007 in Sağlam et al. (2015b)'s study.

During the CCA analysis of the present study, the siphon width was found a distinguished variable from the other variables, which has not been considered in the previous studies for estimation of population dynamic parameters (Şahin et al., 2009; Sağlam et al., 2015a). The growth parameters of de-seasonalized VBGF were estimated for shell length as $L\infty = 103.9$ mm, $K = 0.345$, and $t_0 = -0.310$ by Şahin et al. (2009) and $L\infty = 112.4$ mm, $K = 0.310$, and $t_0 = -0.486$ by Sağlam et al. (2015a). Infinitive shell length of 164.1 mm estimated in the present study was comparatively overestimated excepting t_0 and K. Similarly, the K and t_0 values were low (0.104 and −2.478 respectively) whilst the $L\infty$ value was high (199.7 mm) in relation to the de-seasonalized model of the West Sea, Korea (Choi and Ryu, 2009). We estimated $t_0 = -0.10$ corresponding to 36.5 days for shell length and siphon width. It is known that the development in the capsule takes place about 20 days after egg fertilization (Uyan and Aral, 2003). The hatching time displayed an inverse correlation with the water temperature (34 d at 16 °C, 15 d at 22 °C, and 13-12 d at 25–34 °C at salinity 30). Salinity has been observed to affect the hatching time; the longest incubation time was 25 d at salinity 10 and 21 d at salinity 40, and the shortest time was 15d at salinity 25, when all whelks were kept at 25 °C (Shaojun et al., 2014). The hatching time was estimated longer for *Rapana venosa* in the Black Sea as 15–27 d at salinity 15–18 at a constant temperature of 25 °C (Sağlam and Düzgüneş, 2007). Growth rate of the veined rapa whelk is slower (K = ~0.20) in Chesapeake Bay (resulting in greater longevity and shell length, Harding and Mann, 2016) than for the southern Black Sea.

Primarily, the bottom depths governed the densities of the veined rapa whelk. Throughout the year, a positive correlation was evident between dissolved oxygen levels and density distribution. Temperature and salinity were found to be negatively correlated with density. We determined a critical lower salinity value of 14, and temperature of 8 °C in the Black Sea. Harding and Mann (2016) estimated a critical minimum temperature threshold of 10–12 °C for *Rapana venosa* to feed actively on epifauna in Chesapeake Bay. *Rapana venosa* survived in waters with a salinity range from 12.39 to 28.24 (average value of 19.94) with a minimum critical threshold of 14.98 and at temperatures ranging from 18.12 °C to 22.04 °C (20.43 °C on average) in the Uruguayan shelf (Carranza et al., 2008). Onset of spawning occurred at 18 °C and continued up to 28 °C in Chesapeake Bay (Harding et al., 2008). These ranges show a slight correlation between density and temperature, as well as salinity in the Black Sea. Salinity values were paramount factors correlating negatively with the morphometrical variables of the veined rapa whelk during the year. Dissolved oxygen levels partially affected most of the variables with a positive correlation. In addition, lower depths were negatively related to size of the veined rapa whelks.

Our detailed results, though obtained more than a decade ago, will be important in the management of whelk fisheries and for a better understanding of the ecological characteristics of this species in the Black Sea.

CRediT authorship contribution statement

Erhan Mutlu: Conceptualization, Formal analysis, Funding acquisition, Methodology, Supervision, Software, Project administration, Validation, Writing – review & editing, Writing – original draft, Visualization. **Ahmet E. Kideys:** Conceptualization, Methodology, Supervision, Writing – review & editing. **Fatih Şahin:** Data curation, Resources, Investigation. **Gökhan Erik:** Data curation, Investigation, Resources. **Hakan Aksu:** Resources, Investigation, Data curation. **Ercan Erdem:** Data curation, Investigation, Resources. **Sedat Karayücel:** Resources, Investigation, Data curation. **Levent Bat:** Data curation, Investigation, Resources.

Declaration of competing interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Erhan Mutlu reports financial support was provided by State Planning Organization, Turkey.

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