

# Shift in Growth of an Apex Marine Predator: Bluefish *Pomatomus saltatrix* (L., 1766) (Perciformes: Potamonidae) in Relation to Changes in Feeding

Yoana G. Georgieva & Georgi M. Daskalov

Institute of Biodiversity and Ecosystem Research, Bulgarian Academy of Sciences, 2 Gagarin Street, 1113 Sofia, Bulgaria;  
E-mails: georgieva.ioana@gmail.com; georgi.m.daskalov@gmail.com

**Abstract:** Bluefish *Pomatomus saltatrix* (L., 1766) is known to be one of the most voracious predators and as such is considered very important for the state and functioning of the Black Sea ecosystem. In this study, we explored the current trends in the feeding and growth of bluefish in Bulgarian waters of the Black Sea. We compared bluefish growth parameters between the past (1950s-1970s) and modern periods (2013-2015), based on results from this study and historical data (age-at-length and weight) from the literature. During the autumn of 2013-2015, bluefish showed poor feeding intensity with 75 % of the examined stomachs being empty. Small pelagic fishes, such as horse mackerel, sprat and anchovy were found to be the preferred food of bluefish. The study revealed that sexually mature specimens (age 2 and 3) had significantly lower size and growth rate than those reported in studies from the 1950s-1970s. We hypothesise that this might be due to a combination of factors, such as a shift in the bluefish diet, from which larger fishes (mackerel and bonito) disappeared, and intensive fishing.

**Key words:** Black Sea, bluefish, diet, growth, feeding intensity, food item

## Introduction

Before 1970, the pelagic predatory fish species bonito *Sarda sarda* (Bloch, 1793), bluefish *Pomatomus saltatrix* (L., 1766), Black Sea mackerel *Scomber scombrus* (L., 1758) and the large variety of the horse mackerel *Trachurus mediterraneus* (Steindachner, 1868) (heterosis hybrid, with higher growth rate) were the preferred targets of fisheries in the Black Sea (DASKALOV et al. 2007). By the late 1960s, all of these important fisheries collapsed mainly due to heavy, unregulated fishing (DASKALOV 2002). The bonito and bluefish stocks were severely depleted, while the large variety of horse mackerel and the Black Sea mackerel became extinct in the Black Sea (PRODANOV et al. 1991). The landings of bonito and bluefish increased in the late 1980s and 1990s in Turkey (mostly in the Bosphorus area), but these species never recovered in the Northern and Western Black Sea (PRODANOV et al. 1997). The depletion of

top predators has provoked a system-wide trophic cascade, involving four trophic levels, nutrients and oxygen (DASKALOV et al. 2007). During the regime of high abundance, top predators were controlled mainly by the abundance and availability of their food. Later, they were depleted by heavy fishing, releasing the predation pressure on planktivorous fish, which themselves increased rapidly after 1970. As a response to increased planktivory by fish, zooplankton declined and jellyfish and phytoplankton burgeoned. The excessive catch of immature fish specimens, the competition between small pelagic fish and jellyfish on forage zooplankton, as well as the jellyfish's predation upon fish eggs and larvae led to the collapse of small pelagic fish stocks in the early 1990s. Since then, a partial recovery has taken place mainly due to decreased fishing capacity and improving environmental conditions (DASKALOV et

al. 2007), but this combination of uncontrolled fisheries and eutrophication has caused important alterations in the structure and dynamics of the Black Sea ecosystem (DASKALOV 2002).

Bluefish is targeted by the fisheries over its entire global range but in many cases basic biological, fisheries and stock assessment information is lacking (JUANES et al. 1996). The shortage of information reduces the effectiveness of the stock assessment and management of historically viable bluefish fisheries (IVANOV & BEVERTON 1985, CEYHAN et al. 2007). Bluefish is a marine, pelagic migratory species found in most temperate coastal regions of the world except for the Eastern Pacific (SHEPHERD & PACKER 2006). The species is known to be sensitive to coastal water quality degradation (POTTERN et al. 1989) and occurs in relatively warm waters with sea temperature between 14 and 30°C (FAHAY et al. 1999). Its life cycle, distribution, seasonal migration and spawning are dependent upon variations in sea water temperature (SABATES et al. 2012). A study based on length-at-age data from bluefish populations suggests three groupings with different growth rates and length at first maturity (JUANES et al. 1996). The ‘fast’ growth group includes populations off North-Eastern North America and North-Western Africa and tends to have large sizes at maturity (43–45 cm, TL). The ‘medium’ growth group includes populations in the Black Sea and off Eastern South America and has intermediate sizes at maturity (34–35 cm, TL). The ‘slow’ growth group includes the South African, Mediterranean and Australian populations, with relatively smaller sizes at maturity (25–27 cm, TL) (JUANES et al. 1996).

The bluefish caught in the Aegean, Marmara and Western Black Seas is considered to belong to the same unit stock (IVANOV & BEVERTON 1985, TURAN et al. 2006). Bluefish is not a primary target of the Bulgarian commercial fishery but as a piscivore it is a significant component of the pelagic food web (PRODANOV et al. 1997). It enters the Black Sea in spring for feeding and spawning and moves back to the Sea of Marmara in winter (PRODANOV et al. 1997). In the Black Sea adult bluefish is dominantly piscivorous and feeds mainly on horse mackerel, anchovy, mackerel and other fish species (STOYANOV et al. 1963). On rare occasions, in the absence of fish it consumes bottom invertebrates. Bluefish juveniles feed on zooplankton, such as molluscan larvae, copepods and mysids, but when the individuals reach 6–8 cm of body length, they switch to a diet dominated by fish (STOYANOV et al. 1963, SCHILLING et al. 2017, LAWSON et al. 2018). Bluefish is reported to exert a pronounced selectivity of prey and their sizes (JUANES & CONOVER 1994). During summer

and early autumn, the juvenile bluefish grow faster, due to high piscivore feeding rates (JUANES & CONOVER 1994), and may have significant impact on prey fish populations (BUCKEL et al. 1999, LAWSON et al. 2018). In the Black Sea, the predatory impact of bluefish strongly affects other commercial stocks (PRODANOV et al. 1991) and is thought to have contributed to the expiration of the Black Sea mackerel (IVANOV & BEVERTON 1985, PRODANOV et al. 1991).

A literature review shows little information about bluefish biology in the Black Sea basin. The available studies refer to: bluefish age–size structure; growth and feeding (VINOGRADOV 1949, 1960, TURGAN 1959, STOIANOV 1962, KOLAROV 1963, 1964, 1970, SVETOVIDOV 1964, TARANENKO 1973, PRODANOV et al. 1997, IVANOV & BEVERTON 1985); bluefish reproductive areas (IVANOV & BEVERTON 1985, GORDINA & KLIMOVA 1996) and genetic and morphological variation of bluefish populations throughout the Black, Marmara, Aegean and Eastern Mediterranean Seas (TURAN et al. 2006).

The aim of the present study was to explore bluefish diet and feeding intensity, as well as data on age, size and growth rate. We performed comparisons between the results of this study (2013–2015) and bluefish growth model derived from historical studies (1959–1971) conducted in the Black Sea (TURKAN 1959, STOYANOV et al. 1963, KOLAROV 1964, TARANENKO 1973).

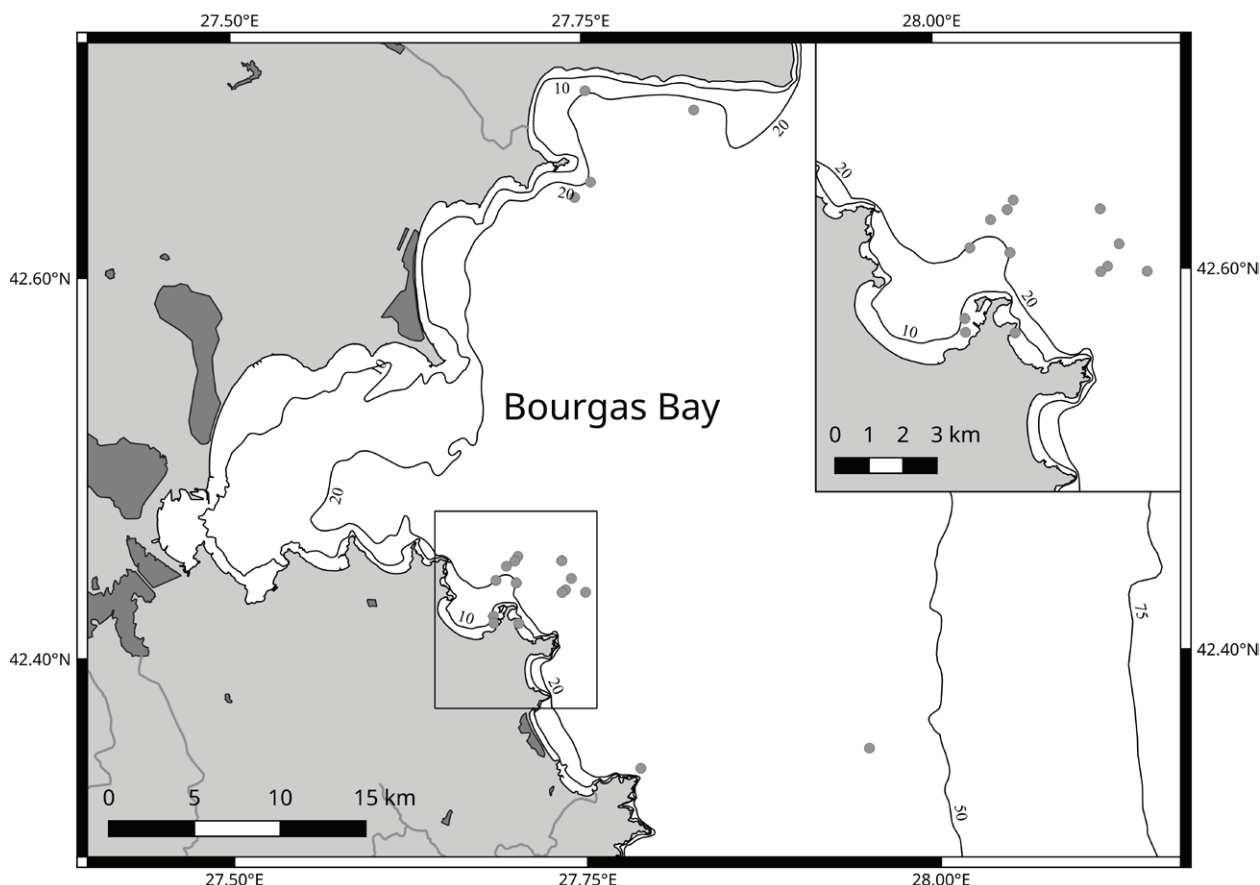
## Materials and Methods

### Sampling

Totally, 974 bluefish specimens were collected using gill nets in September–November 2013–2015 from commercial trawl vessels and artisanal fishing vessels, operating in the Bourgas Bay fishing area (South-Western Black Sea, Fig. 1). The samples were chilled on ice and further processed in the laboratory.

### Age and growth

Individual total length (TL) was measured to the nearest 0.1 cm and individual body weight (W) was measured to the nearest 0.1 g. Age was determined by reading 933 sagittal otoliths. The extracted otoliths were soaked in distilled water and examined, using a reflected light microscope. The von Bertalanffy growth model (VBGM) was applied to relate fish length to age, following the equation:  $L_{(t)} = L_{\infty} [1 - \exp^{-k(t-t_0)}]$ , where  $L_{(t)}$  is length-at-age;  $L_{\infty}$  is asymptotic length;  $k$  is growth curvature parameter and  $t_0$  is the point in time when fish has length zero. The GULLAND & HOLT (1959) and VON



**Fig. 1.** Map showing the area of bluefish samples in the South-Western Black Sea, Bourgas Bay.

BERTALANFFY (1934) (SPARRE & VENEMA 1998) plots were used for estimating the growth parameters  $k$ ,  $t_0$  and  $L_\infty$ . Because of the lack of specimens older than 3 years in our samples, the VBGM was fitted only to pooled historical data from 1959-1971 (TURGAN 1959, STOYANOV et al. 1963, KOLAROV 1964, TARANENKO 1973; Appendix 1). We then compared the present and historical periods based on VBGM, growth performance index (MUNRO & PAULY 1984):  $\phi' = \text{Log}(K) + 2\text{Log}(L_\infty)$ , population parameters data (body length and weight) and weight-length relationship ( $W = a \times TL^b$ , where  $a$  and  $b$  are parameters) derived from the literature (TURGAN 1959, STOYANOV et al. 1963, KOLAROV 1964, TARANENKO 1973, CEYHAN et al. 2007). Student's  $t$ -test was used to compare population parameters between 1959-1971 and 2013-2015. In order to transform fork length (FL) from previous studies to total length (TL), we used a linear regression model ( $TL = 1.1363FL - 0.7094$ ), based on 295 specimens ( $R^2 = 0.98$ ).

### Stomach content analysis

The stomachs of all 974 bluefish specimens were examined. The total weight of the stomach contents was measured to the nearest 0.01 g, and the food items (measured to the nearest 0.001 g) were identified to

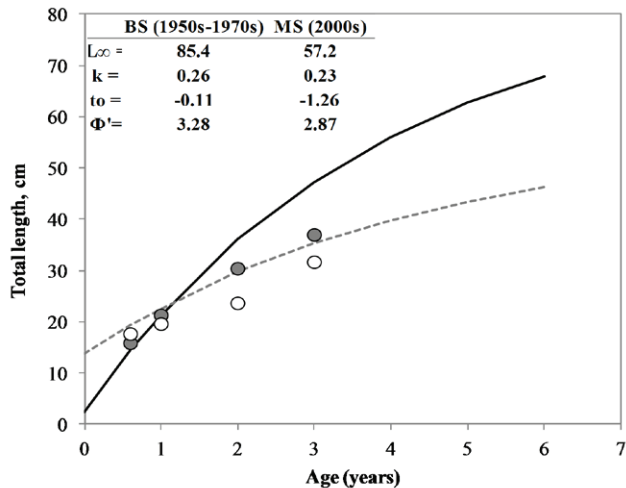
the lowest possible taxonomic level. The importance of the different prey types in the bluefish's diet were assessed using the Index of Relative Importance,  $IRI = (\%Cn + \%Cw)\%F$  (PINKAS et al. 1971), modified on a percentage basis  $\%IRI = (IRI / \sum IRI) 100$  (CORTESE 1997), where  $\%Cn$  is the percentage of the number of each food item divided by the total number of the food items in all stomachs,  $\%Cw$  is the percentage of the wet weight of each prey item divided by the total weight of stomach contents. Bluefish feeding intensity (or food consumption) was quantified using the Gastro-Somatic index,  $Ga.SI = 100(\text{total stomach content weight} / \text{total fish weight})$  (DESAI 1970) and the Vacuity index,  $VI = 100(\text{number of empty stomachs} / \text{number of examined stomachs})$  (BERG 1979).

The length groups in the samples had different numbers of specimens. To explore the variation of food intake as a function of body size, we calculated individual consumption as the average number of ingested prey items CN and the average ingested biomass CW, which were defined as the total number and, respectively, the total biomass of food items found in all stomachs of length group  $L_{(m)}$  divided by the total number of individuals in that length group.

A correlation analysis between the following pairs of parameters was performed: weekly mean

**Table 1.** Numbers N (%), length TL (cm ± standard deviation) and weight (g ± standard deviation) at-age of bluefish in Bulgarian bluefish landings, autumn, 2013-2015. Values are mean (± standard deviation).

Age group	N	N (%)	TL, cm (SD)	W, g (SD)
0	559	51.2	17.3 (±0.9)	56.6 (±9.1)
1	379	42.8	19.7 (±0.6)	76.3 (±8.8)
2	25	2.4	23.8 (±3.5)	141.3 (±78.1)
3	10	3.6	31.8 (±0.6)	312.6 (±19.2)

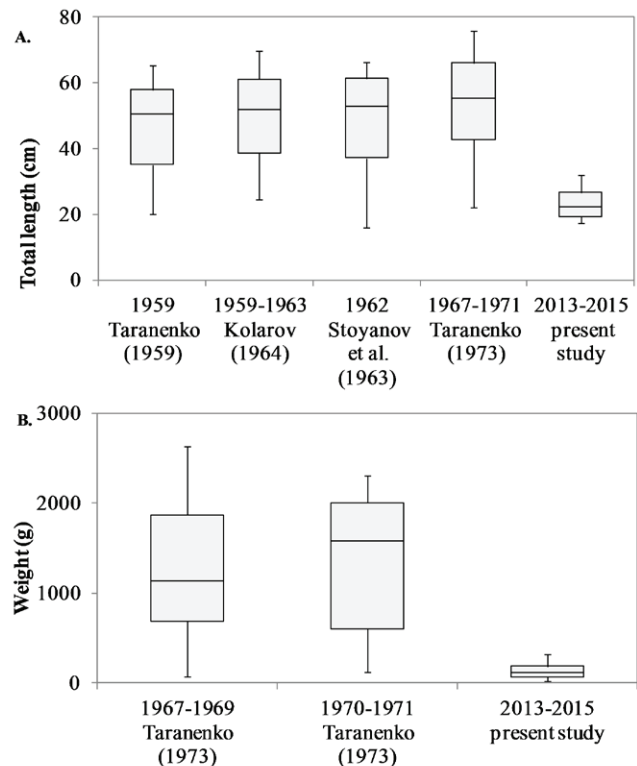
**Fig. 2.** Bluefish growth curves estimated by the VBGM based on age-at-length observation data in the Black Sea for 1959-1971 (black line) (TURGAN 1959, STOIANOV et al. 1963, KOLAROV 1964, TARANENKO 1973) and for the Marmara Sea for 2003-2004 (grey dash line) (CEYHAN et al. 2007). Interposed are age-at-length data from the Marmara region for 2003-2004 (grey circles) (CEYHAN et al. 2007) and from the Bulgarian Black Sea for 2013-2015 (white circles).

values of sea water temperature (SST) and Ga.SI; SST-VI; TL-Ga.SI; TL-VI; TL-CN; TL-CW. SST data (September, October and November of 2013-2015) were obtained from [www.stringmeteo.com](http://www.stringmeteo.com) and from the Laboratory of Marine Ecology in Sozopol ([www.iber.bas.bg](http://www.iber.bas.bg)). The nutritive values of the main bluefish food items in terms of crude protein and total lipid content were calculated (g per g fish body weight) using data from [www.FISHBASE.ORG](http://www.FISHBASE.ORG), [WWW.FAO.ORG](http://WWW.FAO.ORG), [WWW.NDB.NAL.USDA.GOV](http://WWW.NDB.NAL.USDA.GOV), MERDJANOVA (2014).

## Results

### Age-size and growth parameters

In 2013-2015, four age groups (0-3) were found in the samples (Table 1). The young individuals of age 0 years (51%) and 1 year (42%) were the most abundant in the bluefish landings, while 2- and 3-year-old specimens contributed with less than 10% to the catches.

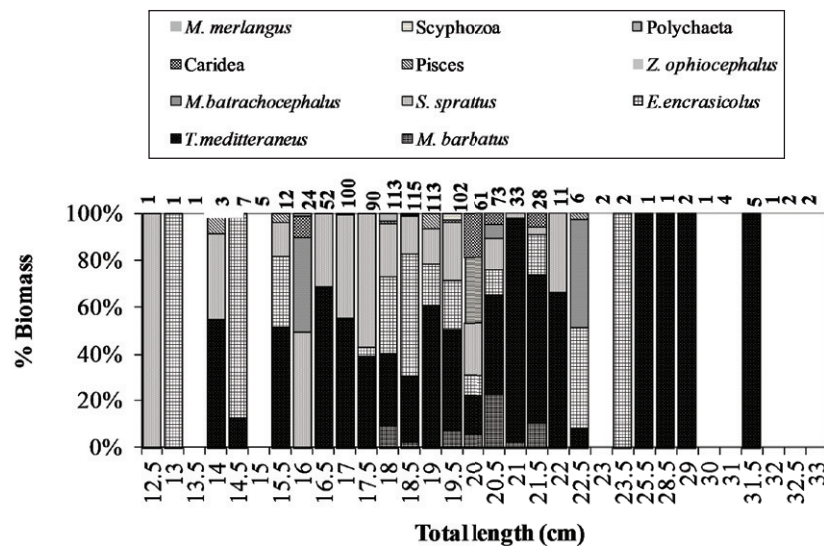
**Fig. 3.** Boxplots of average body length (a) and weight (b) values in bluefish landings determined by different authors in the Black Sea. Two-sample t-test analyses showed that the average body lengths ( $p < 0.0001$ ) and weights ( $p < 0.0001$ ) at age 2 and 3 in the modern period differed significantly from historical studies.

In the period 1959-1971, specimens aged 2-7 years were dominant (87.9%) in the landings, and age class 0 was absent. The estimated von Bertalanffy growth parameters (1959-1971) were  $L_{\infty} = 85.4$  cm,  $k = 0.26$ ,  $t_0 = -0.11$  (Fig. 2).

The length at age 0.6 years (14.4 cm TL), predicted by the VBGM (the approximate age of bluefish juveniles), was lower than the average value registered in this study (17.3 cm, TL, Fig. 2). The von Bertalanffy growth parameters reported in the recent period in the Marmara Sea (CEYHAN et al. 2007) are lower than those estimated based on the data from 1959-1971 (Fig. 2). The average body lengths and weights at age in the recent period differed significantly from historical data (Table 2, Figs. 2, 3A, B).

**Table 2.** Results of two-sample t-test based on population data (total body length TL at age, weight W at age) from 2013-2015 (this study) and 1959-1971 based on data from TURGAN (1959), STOIANOV et al. (1963), KOLAROV (1964) and TARANENKO (1973).

Age group	1 year	2 years	3 years
TL at age, cm (2013-2015; 1959-1971)	19.7; 21.9	23.8; 35.7	31.8; 47.2
Observations (2013-2015; 1959-1971)	25; 10	12; 12	4; 12
Df	9	22	13
T Stat	1.94	8.67	18.04
P(T<=t) two-tail	0.08	< 0.0001	< 0.0001
T Critical two-tail	2.26	2.07	2.16
Age group	1 year	2 year	3 year
W at age, g (2013-2015; 1959-1971)	76.3; 105	141.3; 557.4	312.6; 942.2
Observations (2013-2015; 1959-1971)	25; 3	12; 5	4; 5
df	2	6	6
T Stat	0.90	7.70	29.41
P(T<=t) two-tail	0.46	< 0.0001	< 0.0001
T Critical two-tail	4.30	2.45	2.45



**Fig. 4.** Bluefish prey consumption expressed as food item proportion (biomass) by bluefish size category in autumn 2013-2015, Bulgarian landings. The white colour marks the absence of food items in these length classes. The total number of bluefish specimens in each length group for the sampling period is shown above each bar.

These differences were especially pronounced in specimens at age 2 and 3 years, where length and weight were, respectively, 30% and 70% lower in the current study than the historical data. The weight-length relationship calculated for 0-3-year-old individuals showed that in 2013-2015 the bluefish had positive allometric growth ( $a=0.007$ ;  $b=3.093$ ), whereas in 1967-1971, it had negative allometric growth ( $a=0.025$ ;  $b=2.735$ ).

#### Diet and feeding intensity

During the study period (2013-2015) most of the examined bluefish stomachs were empty; food items were found in only 25% of the analysed stomachs.

Representatives of six families of bony fishes were found in bluefish stomachs: Clupeidae (*Sprattus sprattus* (Linnaeus, 1758)), Engraulidae (*Engraulis encrasicolus* (Linnaeus, 1758)), Carangidae (*Trachurus mediterraneus* (Steindachner, 1868)), Gadidae (*Merlangius merlangus* (Linnaeus, 1758)), Mullidae (*Mullus barbatus* (Linnaeus, 1758)) and Gobidae (*Mesogobius batrachocephalus* (Pallas, 1814) and *Zosterisessor ophiocephalus* (Pallas, 1814)) (Appendix 2). A caridean shrimp, polychaetes and a scyphozoan medusa were also found in the stomach content. The most important food items in the bluefish's diet were the horse mackerel (%IRI=58) and the Black Sea sprat (mostly early

juveniles; %IRI=36). The horse mackerel was the preferred food, while the sprat was the most numerically abundant prey in the analysed bluefish stomachs (%Cn=53) – almost twice as numerous as the horse mackerel (%Cn=28). The Black Sea anchovy was found to be a prey of secondary importance (%IRI=5, %Cn=9) and all the other registered prey species were rare in the bluefish diet. In the stomachs of the largest bluefish (TL>23.5 cm), the only registered victim was the horse mackerel, while in the stomachs of the smallest bluefish groups (12.5-16 cm TL), mostly sprat and anchovy were found (Fig. 4).

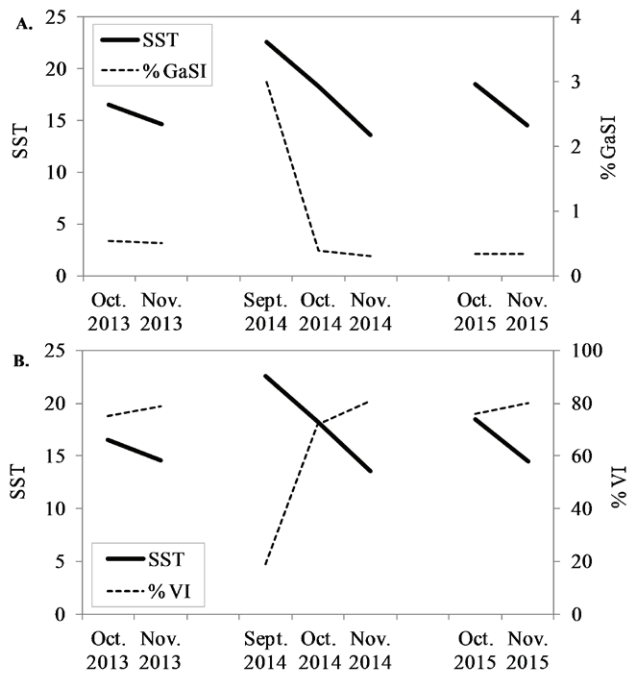
During 2013-2015, there were strong positive correlations between SST and Ga.SI values (0.795 – Pearson correlation; 0.679 – Spearman correlation), strong negative correlations between SST–VI values (-0.863 – Pearson correlation; -0.893 – Spearman correlation; 0 (Figs. 5A, B) and medium to weak negative correlation between TL– Ga.SI (-0.359 – Pearson correlation; -0.402– Spearman correlation) and TL–VI values (-0.263 – Pearson correlation; -0.203 – Spearman correlation).

The bluefish feeding intensity (indicated by the VI and Ga.SI) tended to decrease with the cooling of the sea water and when fish grew (as indicated by the decrease of the Ga.SI and increase of the VI in the larger length classes, Figs. 6A, B). An exception was 2015, when higher Ga.SI values in the biggest size group (23.5 cm TL) were recorded. However, in this year's samples, no specimens greater than 23.5 cm were found. By contrast, in 2013 and 2014, the fish in the largest groups (>29 cm TL) mainly had empty stomachs. The individual food consumption (CN and CW) with respect to body length showed a tendency of decrease in the largest fish, as the number (CN) of ingested food items decreased more sharply (-0.492 – Pearson correlation; -0.381– Spearman correlation) than the biomass (CW) intake (-0.225 – Pearson correlation; -0.198 – Spearman correlation (Fig. 7).

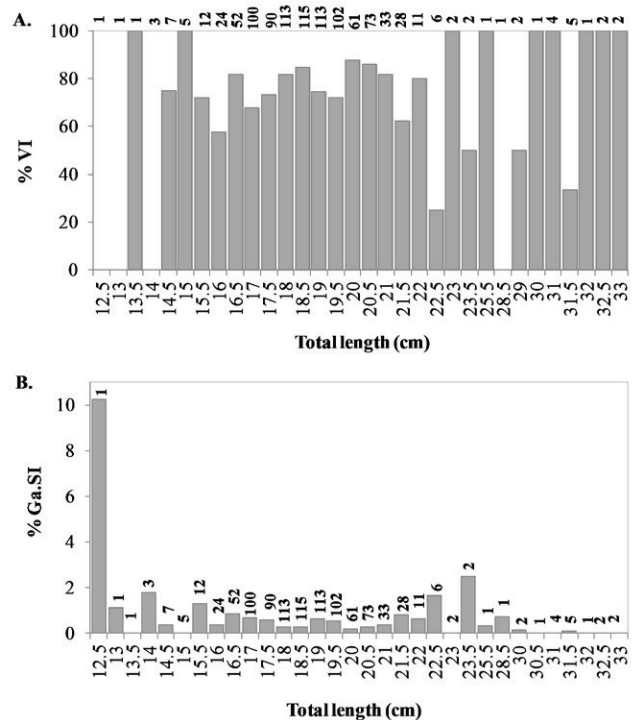
As a high rank predator, bluefish had high crude body protein and lipid contents (Table 3).

## Discussion

The body size of bluefish during the study period (2013-2015) differed significantly from the body sizes reported in previous decades. The length-weight relationship indicated that in 2013-2015, the bluefish grew faster in weight than in length, whereas in 1967-1971, it grew faster in length than in weight. Turkish studies from the Black and Marmara Seas have also reported lower sizes than those measured in the 1959-1971 period (TURAN et al. 2006, CEYHAN et al. 2007).



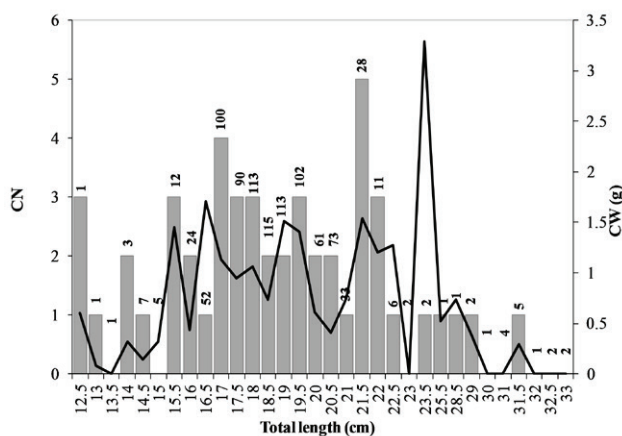
**Fig. 5.** Time-series of SST versus %GaSI (a) and SST versus % VI (b). Pearson correlation between SST and %GaSI is 0.795 and between SST and % VI is -0.863, both significant at  $p < 0.01$ . Spearman correlation between SST and %GaSI is 0.679 ( $p < 0.1$ ) and between SST and % VI is -0.893 ( $p < 0.01$ ).



**Fig. 6.** Vacuity index (%VI) (a) and Gastro-somatic index (% Ga.SI) (b) of bluefish by length classes, September-November 2013-2015, Bulgarian landings. The total number of bluefish specimens in each length group for the sampling period is shown above each bar.

**Table 3.** Crude body protein and total lipid contents (g per g fish body wet weight) for bluefish and its main prey items

Species	Protein content	Data source	Lipid content	Data source
<i>S. sprattus</i>	0.146	WWW.FISHBASE.ORG	0.054	MERDJANOVA (2014)
<i>E. encrasicolus</i>	0.153	WWW.FISHBASE.ORG	0.122	WWW.FAO.ORG; MERDJANOVA (2014)
<i>T. mediterraneus</i>	0.169	WWW.FISHBASE.ORG	0.08	WWW.FAO.ORG; MERDJANOVA (2014)
<i>S. scombrus</i>	0.173	WWW.FISHBASE.ORG	0.125	NDB.NAL.USDA.GOV
<i>S. sarda</i>	0.179	WWW.FISHBASE.ORG	0.151	WWW.FAO.ORG
<i>P. saltatrix</i>	0.182	WWW.FISHBASE.ORG	0.158	WWW.FAO.ORG; MERDJANOVA (2014)



**Fig. 7.** Individual bluefish food intake, expressed as average prey number CN (grey bars) and average prey biomass CW (black line) consumed per fish in each length group, Bulgarian landings, 2013-2015. The total number of bluefish specimens in each length group for the sampling period is shown above each bar.

Bluefish spawning occurs in late spring and summer. Our sampling period covered mainly the autumn months because no fishing was carried out in Bulgarian waters in spring and summer in the last years. Our research on literature did not find recent information on bluefish maturity-at-age/length in the Black Sea. Previous studies have reported that bluefish reaches sexual maturity during the second year (STOYANOV 1963, TARANENKO 1973, POTTERN et al. 1989, CEYHAN et al. 2007). During the 1950s-1970s, the oldest recorded specimens in the Black Sea were 7 years old, while in the recent period the oldest registered fish was 3 years old. Immature individuals dominate the landings in the Black, Marmara and Aegean Seas (CEYHAN et al. 2007), which is consistent with the global tendency that 35% of the landed bluefish individuals are juvenile (IUCN 2011). In 1959-1971, the main share of the Bulgarian landings (90%) consisted of mature fish caught in May-July (reproductive season, KOLAROV 1970). In recent years, the Bulgarian landings are concentrated in September-December (96% of the annual landing, NAFA 2016), when small and im-

mature fish are dominant in the catches. The dramatic decrease in bluefish body size over the last few decades in the Black Sea landings (IUCN 2011) and the predominance of young individuals may be a result of growth overfishing of this highly valued fish (5 euro the kg, GOULDING et al. 2014).

The most important prey items for bluefish in the Black Sea have historically been the mackerel, horse mackerel and anchovy (STOYANOV, 1963, KOLAROV 1970). The importance of mackerel in bluefish diet has been reported by various authors (BIGELOW & SCHROEDER 1953, WILK 1977). Bluefish has extremely strong and sharp teeth which are present in fishes of all sizes, allowing prey larger than the predator's mouth to be bitten and swallowed (BEMIS et al. 2005). It is also possible that young bonito has been consumed by bluefish (PRODANOV et al. 1991).

KOLAROV (1970) has reported slower growth of bluefish due to insufficient amounts of horse mackerel and mackerel. Currently, larger fish such as mackerel and bonito are not found in bluefish stomachs. Therefore, the slower growth rate and low feeding intensity in our study might be due to low food supply.

Juvenile fish has higher feeding intensity but a smaller individual consumption in weight (LAWSON et al. 2018). The high consumption rate of juveniles is a result of consuming prey items containing less energy (BARTELL et al. 1986, BEAUCHAMP et al. 1989, LAWSON et al. 2018). The larger individuals have greater total metabolic costs due to the reproduction processes (ENBERG et al. 2012). Their food requirements are generally higher and their feeding is also stimulated by larger prey size (OLLA et al. 1970, WILK 1977, ENBERG et al. 2012). Therefore, larger fish tend to choose fewer large preys, rather than abundant but less energetically valuable smaller preys (OLLA et al. 1970, WILK 1977).

The quantity and the nutritive quality of the food also affect the growth parameters (KOLAROV 1970, VALIELA 1995, SANTIC et al. 2002, ENBERG et al. 2012). Different food items are assimilated to a different degree that affects the amounts of energy provided by them (MACHOVSKY-CAPUSKA et al.

2016). For example, yellowfin tuna *Thunnus albacares* needs to consume 66% more prey to maintain growth rates if feeding solely on cephalopods rather than fish (WEXLER et al. 2003). In fact, growth is not sustained below a certain nitrogen content of the food and it is optimal when relatively large prey is available, even if it is rare (VALIELA 1995). Thus, for instance, the northern silverside populations may increase their growth rate by voluntarily ingesting larger meals (LANKFORD et al. 2001). This theory may explain the tendency of decrease of the ingested prey numbers (CN) observed in this study and the absence of such a modifying trend in the consumed biomass (CW) with the predator's body length increments. Although the bluefish is reported to be an opportunistic generalist predator in other areas (POTTERN et al. 1989, SCHILLING et al. 2017, LAWSON et al. 2018), in the Black Sea we found their diet to be restricted to fish with sprat and horse mackerel as dominant preys (Appendix 2, Fig. 4). The only species registered in the stomachs of large size groups was horse mackerel, which is the largest and most nutritive of all food items in the present day bluefish diet (see Table 3). The decrease of size and growth in 2013-2015 relative to 1959-1971 may be due to reduction of large prey in the bluefish diet, as nutritional value of larger fish is clearly higher. In the present-day ecosystem, where mackerel has disappeared and stocks of bonito and horse mackerel are low, the balance of energy might have shifted toward costly metabolic expenditures (in terms of hunting time) to gather the necessary food intake from smaller preys. The nutritional value of the juvenile sprat, which nowadays constitutes a significant part of the bluefish diet, may be insufficient to provide energy for growth rate comparable with the one in the previous period.

OLLA & STUDHOLME (1975) reported that the bluefish feeding was relatively stable until the temperature dropped to 13.7°C, while at 12°C the fish showed little interest in food. In 2013-2015 autumn seasons, the average sea water temperatures in Bourgas Bay were higher than these critical levels. However, the low feeding intensity observed in the current study cannot be fully explained by the reduction of the sea water temperature but is likely caused by the low prey abundance of *T. mediterraneus* and *E. encrasicolus*. These stocks have dropped considerably after 1990 (DASKALOV et al. 2007) and although anchovy has partially recovered, its northward migrations in the Bulgarian shelf area are much less pronounced than before 1990 (STECF 2015).

Intensive fishing may induce changes in fish life history traits, in both ecological and on evolutionary

time-scales (ENBERG et al. 2012). Such changes in response to fishing are the slower growth rate and the small body size of top predators (BIANCHI et al. 2000, ENBERG et al. 2012). As a consequence of the declined body size, a weakened predation impact may lead to strong trophic cascades (SHACKELL et al. 2010). SHACKELL et al. (2010) noted that a higher fraction of the production of the smaller-sized top predators will be lost to respiration rather than accumulated as biomass that may result in less energetically efficient populations. It is likely that the slow growth rate and feeding activity of bluefish in 2013-2015 are a consequence of a combination of factors, such as disappearance of mackerel, reduction of horse mackerel and anchovy and heavy fishing.

In the Black Sea, the commercial fish stocks are shared between the riparian countries and an implementation of a cooperative fishery management system is needed to achieve sustainable exploitation of the fish resources (CADDY 2008). According to the Bulgarian legislation, there is no minimum landing size (MLS) for bluefish (*Fisheries and Aquaculture Act 2017*). Conservation measures to reduce the fishing mortality of the juvenile bluefish are applied in terms of MLS of at least 20 cm (TL) as was initiated by the Turkish Ministry of Food, Agriculture and Livestock (2011) for the Turkish Black Sea. A science-based monitoring of landings, discards, size/age structure and regular international stock assessments of the bluefish in the Black Sea are needed in order to create conditions for science-based management of this important fish resource.

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**APPENDIX 1.** Average body length at age (TL, cm) input data used for the VBGM. The shown TLs are calculated based on FLs from TURGAN (1959), STOYANOV (1963), KOLAROV (1964) and TARANENKO (1973).

Age group/Year	1959	1959	1960	1961	1962	1962	1963	1967	1968	1969	1970	1971
1	21.4	19.9	25.2	26.7	-	16.0	21.3	18.3	26.1	-	23.5	20.3
2	37.1	30.9	34.5	39.4	31.9	33.9	32.4	38.4	37.4	40.8	38.0	34.1
3	51.8	47.6	43.4	46.7	49.2	47.4	41.1	48.2	49.9	47.4	47.4	46.4
4	62.1	53.7	-	52.9	53.6	58.0	56.5	56.3	52.6	54.7	57.4	-
5	64.7	59.4	66.1	62.2	58.2	62.4	61.8	-	62.0	65.1	62.4	63.4
6	70.1	65.4	69.4	-	-	66.2	66.6	-	67.9	72.5		66.2

**Appendix 2.** Average values of the indices Numerical abundance (%Cn), Gravimetric composition (%Cw) and Index of Relative Importance (%IRI) for prey items found in the bluefish stomachs in the Bulgarian Black Sea in September-November, 2013-2015.

Food item	Cn (%)	Cw (%)	IRI (%)
<i>M. barbatus</i>	2.9	4.0	0.5
<i>T. mediterraneus</i>	28.0	54.7	58.2
<i>E. encrasicolus</i>	9.4	15.8	4.5
<i>S. sprattus</i>	52.8	19.6	36.2
<i>M. batrachocephalus</i>	0.4	1.8	+
<i>Z. ophiocephalus</i>	0.2	0.5	+
<i>M. merlangus</i>	0.4	0.1	+
Gobiidae	0.2	0.2	+
Pisces	3.1	1.5	0.4
Caridea	2.0	1.5	0.2
Polychaeta	0.2	+	+
Scyphozoa	0.2	0.1	+

Values less than 0.1 are marked with “+”