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Variation in the stable isotope trophic position of the bluefish *Pomatomus saltatrix* (Linnaeus, 1766) from two Mediterranean sites: insights from a global meta-analysis

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Abstract

A direct consequence of sea warming is the shift in the distribution range of thermo-tolerant species that have the potential to determine novel inter-specific interactions, ultimately altering food web structures and ecosystem processes. In this study, we investigated the trophic position of the bluefish *Pomatomus saltatrix* (Linnaeus, 1766), a pelagic predator that has recently expanded its distribution in the Mediterranean basin and for which scant information is available on its functional role in recently-colonised areas. Nitrogen and carbon stable isotopes were determined in muscle tissues of bluefish specimens collected in south-east Italy in the Gulf of Taranto (NW Ionian Sea) and in the Strait of Otranto (SW Adriatic Sea) at two coastal sites showing contrasting oceanographic conditions. The bluefish trophic position (TP) was estimated using locally abundant forage fish species as isotopic baselines. The results indicated for bluefish from the Strait of Otranto a TP value of 5.1, significantly higher than that determined in the Gulf of Taranto (4.2), and exceeding stomach content-based estimations reported by the online database FishBase and by literature sources. A synthesis of 30 publications reporting isotopic data for the bluefish and its potential prey at a global scale indicated that the species' trophic position varied considerably between 2.7 and 5.2. The observed variability depended on location and on the baseline species used in the estimations. Yet, a significant difference in trophic position was observed for bluefish from transitional and inshore environments as compared with offshore areas, mirroring the results obtained from the Gulf of Taranto and the Strait of Otranto. The findings of the study highlight the high trophic plasticity characterizing the bluefish in recently colonized areas, suggesting that it may play a key role in facilitating the expansion of its distribution range. However, additional investigations are essential to provide an advanced resolution of the bluefish functional role in Mediterranean coastal food webs.

Keywords: tailor; trophic level; $\delta^{13}C$; $\delta^{15}N$; Mediterranean Sea; native invaders.

Introduction

In the last three decades the Mediterranean Sea has experienced a more than 1°C rise in summer sea surface temperatures and a remarkable increase in the frequency and intensity of heat wave events, thus resulting among the oceanic regions characterized by the highest warming rates (Marbà *et al.*, 2015). Moreover, climatic models have predicted in the next century a further increase in mean winter and summer temperatures along with the frequency of extreme events (Darmaraki *et al.*, 2019).

Warming is acknowledged to significantly influence the physiology, phenology, as well as the abundance and distribution of both pelagic and benthic biota at any level of marine food webs (Lejeusne *et al.*, 2010; Marbà *et al.*, 2015; Pita *et al.*, 2021). Range-shifting species can determine novel species interactions in the form of competition, mutualism or predation (Woodward *et al.*, 2010).

Specifically, the strength of novel predatory interactions may vary from negligible to relevant, ultimately altering the structure and dynamics of food webs and affecting ecosystem processes (Bartley *et al.*, 2019; Wallingford *et al.*, 2020; Henry & Sorte, 2022) analogously to what is observed for non-indigenous invasive species ("native invaders", sensu Simberloff, 2011; Carey *et al.*, 2012). For ichthyofauna, in particular, a number of thermophilic pelagic species have increased their distribution range and relative abundance in the Mediterranean (Givan *et al.*, 2018; Azzurro *et al.*, 2019). The ecological consequences of these shifts have only started to be unravelled, yet they are predicted to have a disproportionate influence on the structure and dynamics of fish assemblages (Ojea *et al.*, 2020; Pita *et al.*, 2021); in view of this, an advanced resolution of the trophic ecology of range-shifting species may provide key pivotal information for assessing their impact on recipient communities (Sunday *et al.*, 2015; Albo-Puigserver *et al.*, 2019).

Among other examples, the bluefish *Pomatomus saltatrix* (Linnaeus 1766), which belongs to the Pomatomidae family, is a pelagic predator distributed in temperate and subtropical coastal waters worldwide (Wilk, 1977) that provides an illustrative example of a range-shifting native species in the Mediterranean Sea. The species, originally distributed only in the south-eastern areas of the basin (Tortonese, 1986), in the past decades has greatly extended its distribution in north-western Mediterranean (Fig. S1 in supplementary materials), reaching considerable abundances e.g., in the Balearic and Adriatic Sea (Sabatés *et al.*, 2012; Iveša *et al.*, 2021).

The feeding ecology of the bluefish has been widely investigated outside the Mediterranean Sea. Immature juveniles prey mainly on crustaceans, cephalopods, and small fish, while sexually mature adults become opportunistic generalists preying on pelagic and demersal fish depending on local conditions and prey availability (Juanes & Conover, 1994; Buckel *et al.*, 1999a; Lucena *et al.*, 2000; Potts *et al.*, 2016; Schilling *et al.*, 2017). Noticeably, for the Mediterranean Sea dietary studies have been carried out mainly in the south-eastern sectors (Dhieb *et al.*, 2001; Karachle & Stergiou, 2008; Bal *et al.*, 2020; see also Georgieva & Daskalov, 2019 for the Black Sea); in contrast, beside the pan-Mediterranean preliminary assessment by Sanchez-Jerez *et al.* (2008), only Iveša *et al.* (2021) have focused on bluefish populations in recently colonized areas.

Here we investigated the trophic position of the bluefish in the Gulf of Taranto and in the Strait of Otranto (SE Italy) using nitrogen and carbon stable isotope analysis (SIA hereafter). When comparing among ecosystems, the δ^{15}N and δ^{13}C isotopic values of the target consumer alone provide little information about its absolute trophic level or ultimate source of carbon. This is because the isotopic value of the base of the food web may vary among ecosystems (Post, 2002). To this end, in order to assess the trophic position of bluefish from the two sites, their δ^{15}N isotopic values were normalized by those of local fish prey used as baselines. Estimations were compared with published information based on stomach content analysis reported in the online database FishBase and in other literature references. SIA has gained in the last decades a huge popularity for the study of aquatic food webs, allowing for robust comparisons of species' dietary habits at a local as well as regional- and global scale (Mancinelli, 2012; Mancinelli *et al.*, 2017; Annabi *et al.*, 2018; Pethybridge *et al.*, 2018; Mancini *et al.*, 2021). Accordingly, a recently published database collating isotopic data on bluefish and baseline fish prey from literature sources was used to verify the generality of the results obtained for the two study areas and assess the variability of the species' trophic position on a global scale.

Materials and Methods

Study sites and sample collection

Pomatomus saltatrix was sampled at two Italian coastal sites (Fig. 1) located in the Gulf of Taranto (NW

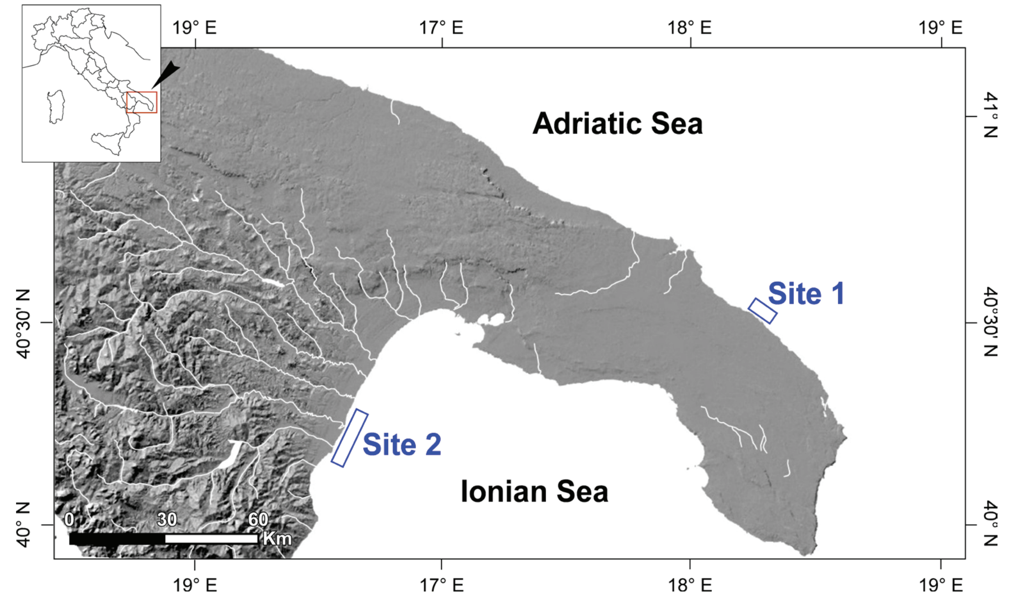

Fig. 1: Map of the sampling areas in the Gulf of Taranto (NW Ionian Sea) and in the Strait of Otranto (SW Adriatic Sea).

Ionian Sea) and in the Strait of Otranto (SW Adriatic Sea). The Gulf of Taranto extends from Santa Maria di Leuca to Punta Alice covering an area of approximately 16,000 km^2 including the coasts of the Apulia, Basilicata, and Calabria regions (Ciancia *et al.*, 2018). The north-western coasts of the gulf generally consist of low sandy beaches characterized by the mouths of five main rivers (i.e., Bradano, Basento, Agri, Sinni, and Crati) and a wide continental shelf gradually slanting toward the continental slope (Aiello *et al.*, 2013; Verri *et al.*, 2018; Pellicani *et al.*, 2020). The basin-scale circulation is characterized by cyclonic and anticyclonic gyres with a rim current which undergoes instabilities and forms sub-mesoscale structures (Federico *et al.*, 2020). In contrast, the Italian coasts of the Strait of Otranto are characterized by narrow beaches, a negligible hydrographic network and a steep shelf slope, reaching depths of 200 m at less than 8 nautical miles from the coast (Cataudella & Spagnolo, 2011; Pantusa *et al.*, 2018). The area is influenced by the West Adriatic Current interacting with the South Adriatic Gyre and conveying nutrient-rich water masses from the northern Adriatic southward along the eastern coasts of the Puglia Region (Malavolti *et al.*, 2018 and literature cited).

Bluefish from the Gulf of Taranto were obtained in early October 2018 from local anglers fishing from the beach in a nearshore shallow area (depths between 2 and 5 m; Lillo, personal observation) extending for approximately 20 km between the towns of Policoro (40.200955°N, 16.733212°E) in the Basilicata Region, and Montegiordano Marina (40.037579°N, 16.601141°E) in the Calabria Region. In addition, samples from the Strait of Otranto were collected in late October 2018 by professional fishermen operating gillnets at a depth of approximately 20 m along a 10 km-long coastal stretch in the Salento Peninsula between the localities of Frigole (40.419644°N, 18.269055°E) and Torre Chianca (40.468163°N, 18.203026°E).

After capture, *P. saltatrix* were transferred to the laboratory in refrigerated containers and frozen at -20°C. Together with bluefish specimens, several individuals (*n* = 10 per site) of the fish species *Lithognathus mormyrus* (Linnaeus, 1758) (Ionian Sea) and *Engraulis encrasicolus* (Linnaeus, 1758) (Adriatic Sea) were obtained from local anglers and fishermen and transferred to the laboratory according with the aforementioned procedures. The two species were used as baseline references for trophic positions estimation (see further in this section). *L. mormyrus* was selected for the Gulf of Taranto as reports from anglers have highlighted how in the study area bluefish gather on shallow bottoms close to river mouths to forage on schools of demersal fish species, including *L. mormyrus* (Lillo, personal observation; see also Fig. S2). For the Strait of Otranto, *E. encrasicolus* was chosen as it is a highly preferred prey for pelagic *P. saltatrix* populations (e.g., Georgieva & Daskalov, 2019; Bal *et al.*, 2020); indeed, large schools of bluefish are frequently observed in the fall chasing forage fish shoals moving along the Adriatic coast of the Salento Peninsula (Mancini, personal observation).

Laboratory procedures

In the laboratory, all the fish specimens were thawed and had their standard length (i.e., from the tip of the snout to the posterior end of the last vertebra; SL hereafter) measured to the nearest mm using a ruler. In addition, bluefish were individually wet weighed to the nearest gram. For stable isotope analysis, the dorsal muscle tissue was removed from each bluefish using a ceramic scalpel, stored in falcon tubes, frozen (-20°C, 48h), freeze-dried for 48h, and powdered using a mortar and pestle. Subsequently, subsamples (0.80 ± 0.02 mg, mean ± 1SE) were pressed into Ultra-Pure tin capsules (Costech Analytical Technologies) and analysed using an Elemental Analyser connected with an Isotope Ratio Mass Spectrometer (Thermo Scientific Flash EA 1112 and Delta Plus XP, respectively). Isotopic signatures were expressed in conventional ‰ δ notation in relation to international standards (atmospheric N_2 for nitrogen and PeeDee Belemnite for carbon). Analytical precision based on the standard deviation of replicates of internal standards (International Atomic Energy Agency IAEA-NO-3 for $\delta^{15}N$ and IAEA-CH-6 for $\delta^{13}C$) was 0.2‰ for both $\delta^{15}N$ and $\delta^{13}C$. Similarly, dorsal muscle tissues of the baseline fish species (i.e., *L. mormyrus* and *E. encrasicolus*) were frozen, freeze-dried and powdered. Ten subsamples (0.39 ± 0.13 mg, mean ± 1SE) per species were analysed for nitrogen and carbon total content and stable isotopes according to the aforementioned procedures.

Literature search

On September 16th, 2021 the online databases ISI Web of Science and Scopus were searched for publications by a multiple search criterion using the term "*Pomatomus saltatrix*" in conjunction with "stable isotopes". The results were complemented with those obtained from queries on Google Scholar (https://scholar.google.com/) using identical keywords and subsequently saved using the freeware Harzings's Publish or Perish ver. 7.27.284953. The literature search resulted in a total of 522 entries; subsequently, their titles and abstracts were screened in order to remove laboratory studies and field investigations not performed in marine environments. The full text of the remaining 247 studies was examined in detail to select those where the occurrence of the bluefish was reported explicitly, together with information on the country, latitude and longitude, the year of the record, and at least the mean $\delta^{15}N$ value of sampled specimens. Publications where the sampling location had no exact coordinates but was reported in maps were also included in the selection. In addition, in order for the literature sources to be eligible, they had to include isotopic information on potential fish prey of the bluefish. To this end, the prey genera listed for *P. saltatrix* by the online database FishBase (www.fishbase.org; Froese & Pauly, 2022) were used as a reference, together with information from the published literature on the diet of the species in the Mediterranean and Black Sea (Sanchez-Jerez *et al.*, 2008; Georgieva &

Daskalov, 2019; Habib *et al.*, 2020). Similarly, FishBase provided the trophic position of prey species; estimations from individual prey items were generally considered, but if they were not available estimations from diet composition of original samples were used.

Thirty (30) eligible publications meeting the aforementioned criteria were eventually selected. Mean δ^{15}N values were extracted from tables and figures together with mean δ^{13}C values and, when available, δ^{15}N and δ^{13}C standard deviations and sample numerosity. Figures were digitized after a fivefold enlargement and converted to numerical form using the graph capture freeware WebPlotDigitizer (ver. 4.5; https://automeris.io/WebPlotDigitizer/). Information on the country, location, season of the study, size of bluefish specimens and of prey species were also extracted when available. For those studies where sampling locations had no coordinates but were reported in maps, all contextual information was used to locate the geographic area of the study in Google Earth. Maps were extracted using the freeware GIMP (ver. 2.10.20; https://www.gimp.org/), overlaid to the study area in Google Earth, and adjusted to match the background (see Mancinelli *et al.*, 2021 for further details). Subsequently, the sampling area was georeferenced using place marks; the coordinates of the area were used to estimate the latitude and longitude in decimal degrees of its centroid using the centroid function in the R package *geosphere* (Hijmans *et al.*, 2019). The final version of the dataset is freely available on Figshare at https://doi.org/10.6084/m9.figshare.16764382.v2, complemented with information regarding the description of the fields included in the dataset and of the literature sources used to extract the data.

Data analysis

All statistical analyses were performed in the R development statistical environment (R Development Core Team, 2022). Two-tailed Student's *t*-tests with separate variance estimates ($\alpha = 0.05$) were used to check for inter-specific and inter-site differences in δ^{15}N and δ^{13}C values in *P. saltatrix* and in prey species. One-way ANOVA was used to assess differences in TP values among countries or habitat typologies from the global dataset. Data were preliminarily checked for normality (Shapiro-Wilks test) and homoscedasticity (Levene's test). Given the relatively low sample sizes (Table 1), the R software *pwr* (Champely *et al.*, 2020) was used to perform a power analysis for each test showing a significant outcome (see Results). Without exception, the analyses indicated that the power to detect the observed effects at the 0.05 level was always > 95%.

The muscle tissues of *E. encrasicolus*, *L. mormyrus*, and *P. saltatrix* from the Gulf of Taranto were characterized by C:N ratios < 3.5 (see Table 1 in Results), indicating a negligible contribution of lipids to tissue carbon pool (Post *et al.*, 2007). In contrast, bluefish from the Strait of Otranto had a C:N ratio > 3.5 (Table 1). Since lipids are depleted in ^{13}C compared to proteins and carbohydrates and can significantly bias δ^{13}C estimations (Logan *et al.*, 2008), samples with a C:N ratio > 3.5 had their δ^{13}C values mathematically corrected for lipid content (Post *et al.*, 2007).

The trophic position (TP hereafter) of *P. saltatrix* was calculated according to the equation (Vander Zanden *et al.*, 1997; Jepsen & Winemiller, 2002):

$$TP = (\delta^{15}N_{Consumer} - \delta^{15}N_{Baseline})/\Delta^{15}+\lambda$$

where $\delta^{15}N_{Consumer}$ is the nitrogen isotopic signature of *P. saltatrix*, Δ^{15}N is the one-trophic level fractionation of

Table 1. Sample size, average (±1SE) total standard length (TSL, in mm; min - max range in round brackets) and muscle tissues C:N ratio of individuals of *Pomatomus saltatrix* and baseline prey species (*Lithognathus mormyrus* for the Gulf of Taranto; *Engraulis encrasicolus* for the Strait of Otranto) analysed in the present study. For *P. saltatrix*, the average (±1SE) total wet weight (WW, in g; min - max range in round brackets) are also reported.

		Gulf of Taranto	Strait of Otranto
Pomatomus saltatrix	N. ind.	8	14
	TSL	403 ± 37 (291 - 600)	402 ± 28 (333 - 578)
	WW	1163 ± 323 (340 - 2940)	973 ± 244 (520 - 2520)
	C:N	3.1 ± 0.03	4.6 ± 0.17
Prey	N. ind.	10	10
	TSL	153.8 ± 20.6 (118 - 181)	124 ± 9.1 (107 - 137)
	C:N	3.3 ± 0.15	3.1 ± 0.12

$\delta^{15}N$, while $\delta^{15}N_{Baseline}$ and λ are the mean nitrogen isotopic value and the trophic level of the baseline species; respectively. A $\Delta^{15}N = 3.4‰$ was used (Post, 2002), while trophic levels for baseline forage species in the Mediterranean Sea were taken from Karachle & Stergiou (2008; 2017), with $\lambda = 3.38$ for *E. encrasicolus* (Adriatic Sea) and $\lambda = 3.42$ for *L. mormyrus* (Ionian Sea), assuming basal resources = trophic level 1, primary consumers = trophic level 2, etc. These values were chosen following the recommendations by Mancinelli *et al.* (2013) and Kjeldgaard *et al.* (2021) as they were consistent with previously published isotopic estimations for both *E. encrasicolus* (e.g., 3.3: Rumolo *et al.*, 2016) and *L. mormyrus* (3 - 3.8: Mancinelli *et al.*, 2016; Signa *et al.*, 2017). Bluefish TP values were calculated for each specimen to consider inter-individual variations in trophic habits; for the global dataset, estimations were made at each location using the mean $\delta^{15}N$ values reported for bluefish and baseline species. The overall distribution of TP values was visually explored using a kernel density estimation approach; the 'density()' function implementing the 'bw.nrd0' method available in the base distribution of the R package was used to select the appropriate bandwidth for the kernel.

Results

Biometry

In total, 22 *Pomatomus saltatrix* specimens were analysed, 8 from the Gulf of Taranto and 14 from the Strait of Otranto. The average size of bluefish specimens from the two populations was similar (Table 1), and *t*-tests confirmed that the two groups were characterized by negligible biometric differences either in terms of WW ($t = 0.01$, $P = 0.99$, 10.9 d.f.) or SL values ($t = 0.54$, $P = 0.59$, 10.4 d.f.).

CN isotopic values and trophic position

Bluefish from the Gulf of Taranto and the Strait of Otranto differed significantly in both $\delta^{15}N$ and $\delta^{13}C$ values (Fig. 2; $\delta^{15}N$: $t = 2.9$, $P = 0.01$, 9.5 d.f.; $\delta^{13}C$: $t = -4.7$, $P = 0.0002$, 18.8 d.f.). Additionally, independently from the location, they differed significantly from baseline species in $\delta^{15}N$ (Gulf of Taranto: $t = 8.4$, $P < 0.0001$, d.f. = 7.1; Strait of Otranto: $t = 34.3$, $P < 0.0001$, d.f. = 21.1) but not in $\delta^{13}C$ (Gulf of Taranto: $t = 1.8$, $P = 0.08$, d.f. = 14.9; Strait of Otranto: $t = -0.6$, $P = 0.56$, d.f. = 15.1).

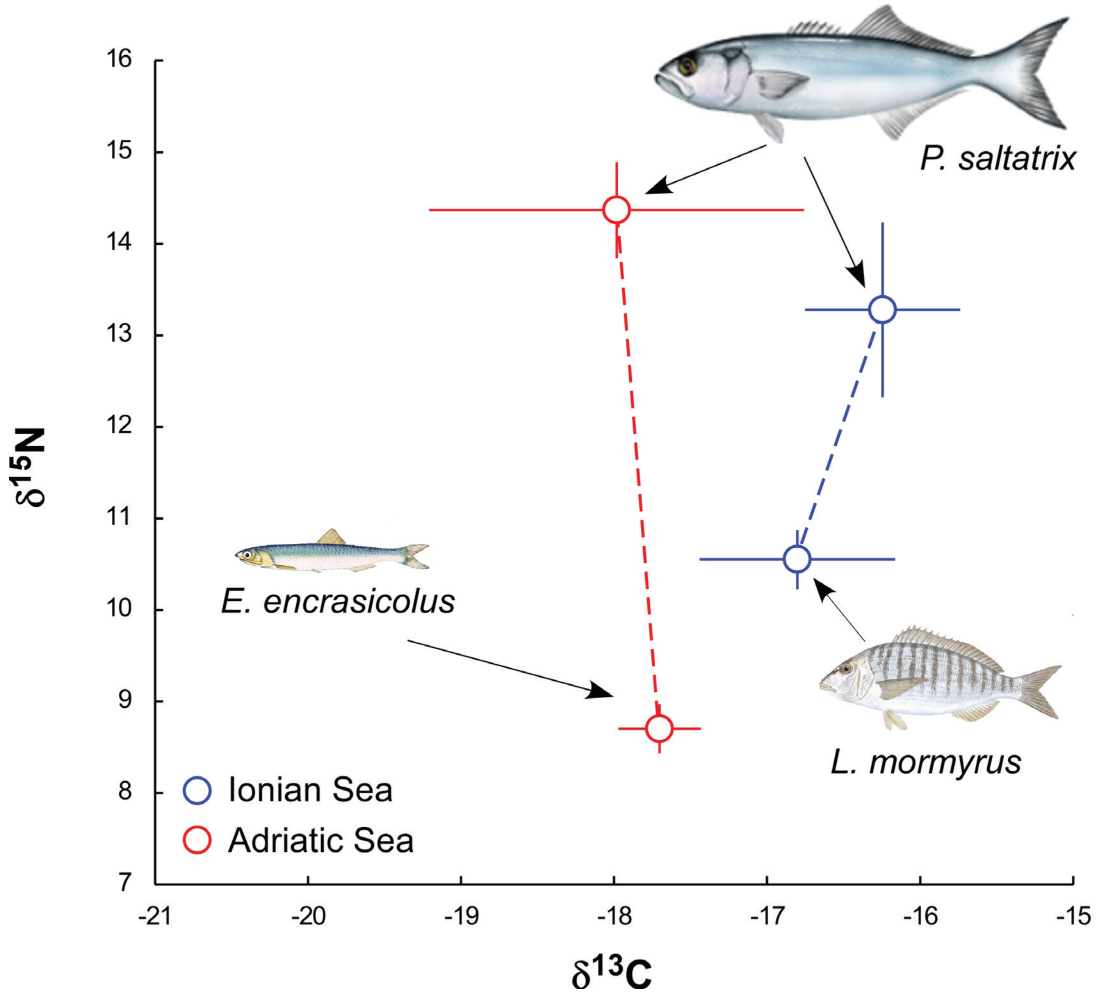

Fig. 2: CN isotopic bi-plot of *Pomatomus saltatrix* and baseline prey species (*Engraulis encrasicolus* and *Lithognathus mormyrus*) from the Gulf of Taranto and the Strait of Otranto. Data reported as means, whiskers are ± 1SD. $\delta^{13}C$ values for *P. saltatrix* from the Adriatic Sea have been mathematically lipid-corrected (see text for details); the original $\delta^{13}C$ value is -19.22 ± 1.41 (mean ± 1SD).

Bluefish collected in the Gulf of Taranto were characterized by a trophic position significantly lower than those captured in the Strait of Otranto (Fig. 3: 4.25 ± 0.09 *vs.* 5.05 ± 0.04, mean ± 1SE; t = 7.41, P < 0.0001, 9.46 d.f.). Negligible relationships were observed between the TP value characterizing each bluefish specimen and its weight or length (Gulf of Taranto: max r = 0.61, P = 0.11, 6 d.f., for TP *vs*. WW; Strait of Otranto: max r = 0.42, P = 0.13, 12 d.f., for TP *vs*. SL). Noticeably, the mean trophic position of bluefish from the Strait of Otranto was remarkably higher than the average of the values reported by Karachle & Stergiou (2017; TP = 2.48) for the north Aegean Sea (Greece; TP = 4.5, after Karachle & Stergiou, 2008) and the Gulf of Gabes (Tunisia; TP = 4.46, after Dhieb *et al.*, 2001), as well as by FishBase (i.e., TP = 4.53 and 4.33 estimated from diet composition of the original sample and on unfished populations respectively, and 4.08 estimated from individual food items; t = 7.2, P < 0.001, 6.1 d.f.; Fig. 3). In contrast, the trophic position of bluefish from the Gulf of Taranto was not significantly different from those reported by the aforementioned sources (t = -0.9, P = 0.33, 10.9 d.f.).

Trophic positions from literature data

The 30 selected studies were published from 1988 to 2021 (Table 2). The majority were from the USA (17 studies, 57% of the total), followed by Australia and Brazil (6 and 5 studies; 20 and 16.7%, respectively); only one study was from the Mediterranean Sea (Spain), one from the Black Sea (Romania), and none from Italian waters (Table 2; see also Fig. S3). 58 trophic positions were estimated in total, with an average TP value of 3.97 ± 0.07 (±1SE; Fig. 4). Values varied remarkably between 2.72 and 5.24, depending on the location and the baseline prey for those locations where trophic positions were calculated using multiple prey species (Table 2). Overall, the kernel density curve of TP estimations (bandwidth = 0.13) was characterized by two distinct peaks, the first occurring at values roughly comprised between 3.4 and 3.6 and the second between 4.5 and 4.7 (Fig. 4). After averaging TP values over locations, no significant differences were observed among countries [One-way ANOVA with four levels (USA, Australia, Brazil, and “other” including Spain and Romania): $F_{3,27}$ = 0.33, P = 0.26]. Conversely, the mean trophic position of bluefish sampled in coastal and transitional (i.e., lagoons and estuaries) waters was significantly lower than that calculated for samples collected under open sea conditions (Fig. 5; 3.79 ± 0.11 *vs.* 4.29 ± 0.12; t test, t = -3.11, P = 0.001, 26.2 d.f.).

Discussion

Our study revealed that in the Strait of Otranto (SW Adriatic Sea) the bluefish *Pomatomus saltatrix* has a trophic position higher than in the Gulf of Taranto (NW Ionian Sea), and exceeding stomach content-based estimations reported by the online database FishBase and by literature sources. A global-scale scrutiny of isotopic investigations showed for the bluefish a huge variability in TP values, consistent with the differences observed between Adriatic and Ionian bluefish, and related with the specific habitat where the species occurs.

In open-sea environments adult bluefish primarily

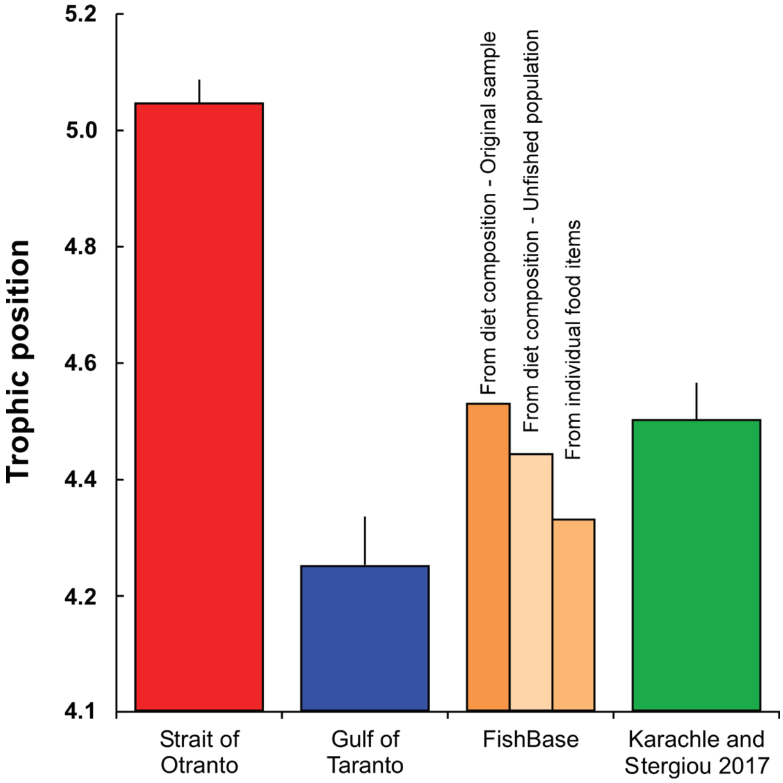

***Fig. 3**:* Mean trophic position (± 1SE) of *Pomatomus saltatrix* from the Gulf of Taranto and the Strait of Otranto, compared with data reported in FishBase and the average of the values reported by Karachle & Stergiou (2017). See text for further details.

Table 2. List of studies and corresponding publication year included in the global dataset on CN isotopic signatures of *Pomatomus saltatrix* and its potential prey available at https://doi.org/10.6084/m9.figshare.16764382.v2. Table 3, available at the same DOI, contains the complete references for the studies. Information on the country, location, typology of the environment from which the samples were collected (i.e., Open Sea, Coastal Area, Estuary, and Lagoon), baseline prey species are also reported. The trophic position of baseline species from FishBase and the estimated trophic position of the bluefish are included (Prey TP and Bluefish TP, respectively).

Ref #	Authors	Publication year	Country	Location	Habitat	Taxon	Prey TP	Bluefish TP
1	Fry	1988	USA	Georges Bank	Open Sea	*Clupea harengus*	3.29	4.47
						Ammodites dubious	3.27	4.74
2	Little and Schoeninger	1995	USA	Nantucket	Coastal Area	*Stenotomus chrysops*	3.57	4.6
3	Deegan and Garritt	1997	USA	Plum Island Sound	Estuary	*Menidia menidia*	3.19	3.32
						Alosa aestivalis	3.42	3.44
4	Moncreiff and Sullivan	2001	USA	Horn Island	Coastal Area	*Menidia beryllina*	3.19	3.95
						Anchoa mitchilli	3.46	3.7
5	Connolly *et al.*	2003	Australia	Moreton Bay	Estuary	*Mugil cephalus*	2.48	3.83
						Hyporhamphus quoyi	2.86	3.98
6	Schlacher *et al.*	2005	Australia	Maroochy Estuary	Estuary	*Mugil cephalus*	2.48	2.77
7	Bànaru	2005	Romania	Sfantu-Gheorge	Coastal Area	*Sprattus sprattus*	3.01	3.2
8	MacNeil	2005	USA	Georges Bank	Open Sea	*Clupea harengus*	3.29	4.76
9	Svensson *et al.*	2007	Australia	Leschenault Inlet	Estuary	*Engraulis australis*	3	3.79
						Mugil cephalus	2.48	4.51
10	Wrast*	2008	USA	Lavaca Bay	Estuary	*Mugil cephalus*	2.48	4.22
						Leiostomus xanthurus	3.23	3.67
						Cynoscion arenarius	4.17	4.19
						Cynoscion nebulosus	3.98	4.44
						Peprilus paru	3.87	4.14
11	De Masi	2009	Brazil	Lagoa da Conceicao	Lagoon	*Mugil brasiliensis*	2.68	3.53
						Peprilus paru	3.87	5.24
12	Logan	2009	USA	Mid-Atlantic Bight	Open Sea	*Clupea harengus*	3.29	4.61
13	Harbeson	2010	USA	South Bay	Lagoon	*Menidia menidia*	3.19	3.25
						Anchoa mitchilli	3.46	3.28
						Cynoscion regalis	4.01	4.48
14	Szczebak and Taylor	2011	USA	Narragansett Bay	Estuary	*Menidia menidia*	3.19	3.54
						Anchoa mitchilli	3.46	3.85

Continued

Table 2 continued

Ref #	Authors	Publication year	Country	Location	Habitat	Taxon	Prey TP	Bluefish TP
15	Hoeinghaus *et al.*	2011	Brazil	Tramandai Lagoon	Estuary	*Brevoortia tyrannus*	2.61	3.68
						Mugil liza	2	3.68
						Atherinella brasiliensis	3	3.53
16	Woodland	2011	USA	Chesapeake Bay	Estuary	*Anchoa mitchilli*	3.46	3.88
				Maryland's inner continental shelf	Open Sea	*Anchoa mitchilli*	3.46	3.57
17	Cardona and Borrell	2012	Spain	South Catalan Sea	Open Sea	*Engraulis encrasicolus*	3.12	4.59
						Sardina pilchardus	2.94	4.73
18	Woodland and Secor	2013	USA	Middle Atlantic Bight	Coastal Area	*Anchoa mitchilli*	3.46	3.57
						Anchoa hepsetus	3.25	3.67
						Peprilus triacanthus	3.68	4.28
19	Heithaus	2013	Australia	Shark Bay	Coastal Area	*Rhabdosargus sarba*	3.25	4.31
20	Deehr and Luczkovich	2014	USA	Core Sound	Estuary	*Brevoortia tyrannus*	2.61	3.37
						Anchoa mitchilli	3.46	3.7
21	Oakley and Simons	2014	USA	Lavaca Bay	Estuary	*Menidia menidia*	3.19	4.7
						Mugil cephalus	2.48	4.22
						Cynoscion arenarius	4.17	4.19
						Cynoscion nebulosus	3.98	4.44
						Brevoortia patronus	2.61	3.14
22	Logan *et al.*	2015	USA	Gulf of Maine	Open Sea	*Clupea harengus*	3.29	4.61
23	Zenteno	2015	Brazil	Southern Brazil	Open Sea	*Engraulis anchoita*	2.51	3.66
						Sardinella brasiliensis	3.1	5.22
24	Condini *et al.*	2015	Brazil	Carpinteiro Bank	Open Sea	*Anchoa marinii*	3.4	4.53
25	Malek and Collie	2016	USA	Island Sounds	Open Sea	*Clupea harengus*	3.29	4.19
26	Xue *et al.*	2017	USA	Indian River Lagoon	Open Sea	*Anchoa mitchilli*	3.46	4.2
27	Schneider *et al.*	2018	Australia	Lake Macquarie	Lagoon	*Mugil cephalus*	2.48	3.42
28	Garcia *et al.*	2019	Brazil	Southern Brazil	Open Sea	*Brevoortia pectinata*	3.4	3.99
29	Peterson *et al.*	2020	USA	NW Florida coast	Open Sea	*Brevoortia patronus*	2.61	3.4
						Brevoortia smithi	2.32	3.2
30	McCluskey *et al.*	2021	Australia	Bunbury coast	Open Sea	*Sillago bassensis*	3.31	4.06
						Spratelloides robustus	3.4	4.58

* The prey *Brevoortia patronus* was not considered given the lack of a reliable TP estimate on FishBase.

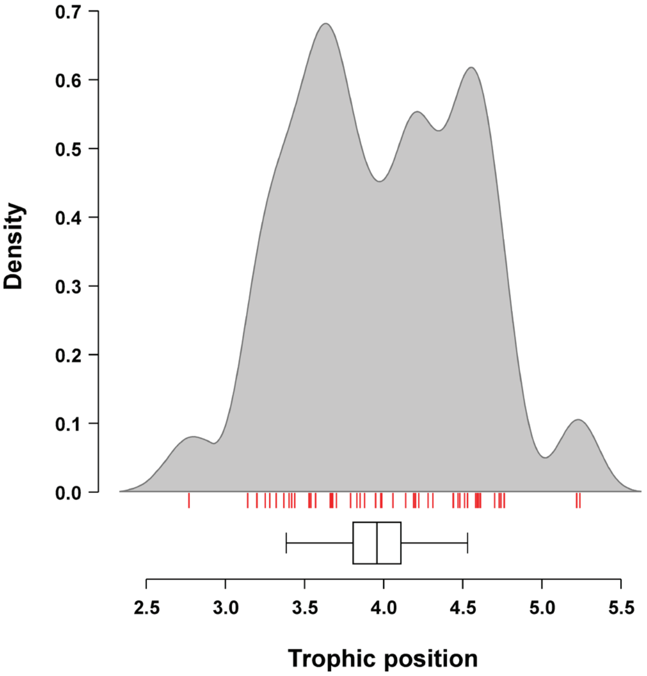

Fig. 4: Kernel density Distribution of *Pomatomus saltatrix* trophic positions calculated from the references listed in Table 2. The mean, 95% confidence intervals (box), and SD (whiskers) are showed.

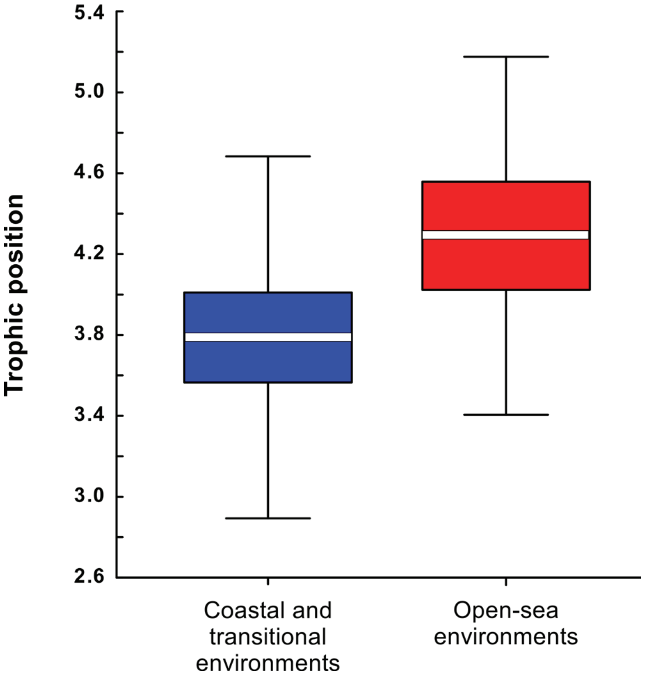

Fig. 5: Pomatomus saltatrix mean trophic positions from inshore coastal and transitional (i.e., lagoons and estuaries) waters and from open sea environments. Data are from the references listed in Table 2, averaged over locations. The mean (white bar), 95% confidence intervals (box), and SD (whiskers) are showed.

prey on forage species and pelagic predators such as cephalopods and mackerels, but in nearshore habitats they opportunistically shift to demersal invertebrate and fish prey, including decapods, mullets and gobiids (Lasiak & McLachlan, 1987; Lucena *et al.*, 2000; Harding & Mann, 2001; Artüz, 2003; Potts *et al.*, 2016; Schilling *et al.*, 2017). In this study, bluefish specimens were collected in the Gulf of Taranto from a nearshore, surf beach habitat while in the Strait of Otranto they were captured under open-sea conditions. Recent investigations have clearly indicated how differences in oceanography reflect on significant variations in the nature and structure of the food webs characterizing the two areas, with a prevalence of demersal fish species in the Gulf of Taranto and pelagic-benthopelagic species in the Strait of Otranto (Carlucci *et al.*, 2018; see also Ricci *et al.*, 2019). Accordingly, the observed shift in the level occupied by the bluefish in the food webs of the two sites can be explained by a variation in its trophic habits as determined by habitat-related changes in the composition of prey assemblages.

Does feeding in nearshore habitats necessarily imply a decrease in the trophic position of a predatory fish? Indeed, a shift to a benthic trophic pathway is commonly observed in pelagic generalist predators foraging in shallow waters (Kopp *et al.*, 2015; Giraldo *et al.*, 2017). It is an open question as to whether this reflects in a contemporaneous decrease in trophic position (but see Kopp *et al.*, 2015 for *Clupea harengus*), as a number of factors (e.g., the local composition and feeding habits of the prey assemblage, the ontogenetic stage of the predator) may interfere. Juvenile bluefish are lower in length than 250 - 300 mm (Juanes *et al.*, 1996; Able *et al.*, 2003), and forage in estuaries and inshore habitats, and have a diet constituted by benthic and pelagic prey low in the trophic hierarchy; this ultimately reflects in a trophic position generally lower than that of adults (Szczebak & Taylor, 2011; Lawson *et al.*, 2018 and literature cited). The bluefish analysed in the present study had a minimum standard length of approximately 300 mm (Table 1) and were all sexually mature (Mancini, personal observation). Furthermore, negligible inter-site differences were observed in mean standard length or wet weight; ontogenetic or size-related effects on trophic positions can thus be excluded, a conclusion further corroborated for each location by the lack of significant relationships between size and TP values at the individual scale. Given the opportunistic trophic behaviour of the bluefish, it can be hypothesised that adult specimens take advantage of the most abundant prey when foraging inshore, lowering their trophic position and "reverting" the dietary shift they experience during growth. The analysis of the global isotopic dataset actually supports this scenario. Indeed, an extremely high variability in TL values was observed, ranging from 2.8 to 5.2, ultimately indicating a remarkable trophic plasticity. It is worth noting that such variability may be attributable also to ontogenetic shifts, as only a minority of the studies included in the dataset reported explicit information on the size of the analysed specimens (see the original dataset at https://doi.org/10.6084/m9.figshare.16764382.v2). Nevertheless, a significant difference in trophic position was observed for bluefish from coastal and transitional waters as compared with open-sea habitats (Fig. 5), mirroring the inter-site pattern of variation observed here.

The similarity in TP values between the Gulf of Taranto and those from FishBase and literature sources provides an additional, indirect support to the hypothesis that adult bluefish in inshore environments may mirror the feeding habits of juveniles. Indeed, FishBase values (Fig. 3) represented overall estimations considering the whole biological cycle of the species, as they were based on 6 studies on the feeding habits of recruits, juveniles, and adults from a variety of in- and offshore habitats in USA, Brazil, and South Africa (see references at https://www.fishbase.se/TrophicEco/DietCompoList.php?ID=364&GenusName=Pomatomus&SpeciesName=saltatrix&fc=311&StockCode=378, accessed July 13th, 2022). Furthermore, the value (TP = 4.46) determined by Karachle & Stergiou (2017) on data by Dhieb *et al.,* (2001) was determined from juveniles and small-sized adults (length range = 109 - 445 mm) sampled in coastal areas of the Gulf of Gabès (Tunisia); finally, Karachle & Stergiou (2008) determined a trophic position virtually identical to that of Dhieb and colleagues (TP = 4.5) on 6 juveniles ranging in length between 131 and 185 mm.

Overall, our experimental results and those obtained from the global analysis emphasise the remarkable trophic plasticity of the bluefish, and its ability to occupy different trophic levels in the food webs where they occur. The recent expansion of the species in the Mediterranean Sea has been linked to concurrent, temperature-related climate changes (Sabatés *et al.*, 2012; Villegas-Hernández *et al.*, 2015). Yet, generalist trophic habits may play a crucial role in determining the establishment success of a species, independently from the fact it is an introduced alien or a native expanding its range (Mancinelli *et al.*, 2017; Albo-Puigserver *et al.*, 2019; Balzani *et al.*, 2021 and literature cited). Accordingly, future investigations focused on marine native invaders should verify whether their expansion success may be related, together with temperature-related biological characteristics of the species, also to their trophic habits.

Noticeably, some experimental and methodological biases may have potentially hampered the estimation of the bluefish trophic position in the two sampling locations and are worth addressing. Our study was performed at a single point in time on a relatively limited number of specimens (8 and 14 in the Gulf of Taranto and the Strait of Otranto, respectively). Even though power analyses corroborated the robustness of our results, they nonetheless should be taken with some caution, as Kjeldgaard *et al.* (2021) have clearly pointed out that a minimum of 5 to 10 specimens are necessary for reliable trophic position estimations. Thus, this study should be considered as preliminary and further support is needed from future isotopic investigations performed on a larger number of specimens in multiple seasons, given the non-univocal information to date available on seasonal variations in trophic habits of the species (Lucena *et al.*, 2000; Potts *et al.*, 2016; Schilling *et al.*, 2017). This will allow, beside confirming the robustness of our results, to verify potential linkages among tissue stoichiometry, diet composition, and growth in bluefish (Schindler & Eby, 1997; Pilati & Vanni, 2007; Schiettekatte *et al.*, 2020), as suggested by the trophic position-related variations in muscle tissues C:N ratio, and in growth constants observed here (Table 1, Fig. S4). In addition, the choice of an appropriate baseline represents a further key step to assess the trophic position of a species (Post, 2002; Kjeldgaard *et al.*, 2021). The global database collated here confirmed this tenet: the differences in TP values among locations was paralleled by a considerable variability observed for the same location when different baseline species were used (Table 2). Anchovies belonging to the genus *Engraulis* are a dominant item in the diet of bluefish worldwide (Juanes *et al.*, 1996; Lucena *et al.*, 2000; Schilling *et al.*, 2017; Bal *et al.*, 2020); therefore, we are confident regarding the robustness of estimations for the Strait of Otranto. For the Gulf of Taranto the demersal *Lithognathus mormyrus* was used as the baseline species. Even though demersal species are frequently included in the diet of bluefish feeding in nearshore habitats (see references in the previous section), we nonetheless confirmed the reliability of the results by re-calculating the bluefish trophic position using the δ^{13}C and δ^{15}N values of five adult individuals of the garfish *Belone belone* (TL = 233 ± 46 mm, $\delta^{13}C = -17.82 \pm 0.09$, $\delta^{15}N = 10.09 \pm 0.13$; mean ± 1SE) captured together with *L. mormyrus*. The garfish is commonly predated by the bluefish (e.g., Artüz, 2003; Ivešа *et al.*, 2021); assuming for it a trophic position $\lambda = 3.48$ (Karachle & Stergiou, 2008), consistent with other isotopic estimations (TP = 3.3 - 3.5: Kellnreitner, 2012; Vinagre *et al.*, 2019), the corresponding TP value for the bluefish was 4.4 ± 0.04 (mean ± 1SE), a value non-significantly different from that estimated using *L. mormyrus* as baseline (*t*-test, $t = -1.6$, $P = 0.15$, d.f. = 8.86).

In conclusion, *Pomatomus saltatrix* is expanding its distribution in Mediterranean habitats already impacted by other anthropogenic pressures (e.g., overfishing), with unpredictable consequences for coastal fish species of economic value that may be affected by predation or competition, like those documented for coastal fish in other geographical areas (e.g., in the USA: Buckel *et al.*, 1999b; Buckel & McKown, 2002). As highlighted by the global literature search, the present investigation is the first explicitly focusing on the trophic habits of the bluefish in Mediterranean waters using stable isotopes. It provided stimulating indications as regards with the trophic ecology of the species as affected by local environmental conditions deserving to be thoroughly investigated in future studies on Mediterranean populations.

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Supplementary Data

The following supplementary information is available online for the article:

Fig. S1: Global distribution of the bluefish. Records collated from the Global Information Biodiversity Facility – GBIF (https://www.gbif.org/). Data downloaded on September 12th, 2021 - GBIF Occurrence Download https://doi.org/10.15468/dl.26nchn. For the Mediterranean Sea, occurrences recorded after 2001 are highlighted in red.
Fig. S2: Effect of the attack of a bluefish on a *Lithognathus mormyrus* specimen caught by a beach angler on the Ionian Sea at the mouth of Sinni River (40.152830°N, 16.691038°E), close to the town of Policoro in the Basilicata Region, Italy.
Photo courtesy of Antonio Oscar Lillo.

Fig. S3: Location of the 30 investigations included in the database. Identification number (Ref#) of references reported in Table 2 are included.

Fig. S4: Allometric relationships of the type WW = a × TSL^b (Froese, 2006), linking the total standard length TSL (in cm) and total wet weight WW (in g) of *Pomatomus saltatrix* specimens from the Ionian and Adriatic Sea. The power curves are included, together with their Pearson *r* coefficient and statistical significance, and growth constant b. Noticeably, the relationship for Ionian bluefish was characterized by a growth constant significantly higher than that characterizing specimens from the Adriatic Sea (ANCOVA after log-transformation of data: $F_{2,18} = 3.9$, $P = 0.03$).

Literature cited Supplementary file

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