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Review

Amphiatlantic Dolphins' Prey: Indicators of Speciation, Trophic Competition and Global Warming? A Review

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Abstract: A review of the prey of three amphiatlantic dolphin species, *Tursiops truncatus*, *Stenella coeruleoalba* and *Delphinus delphis*, is carried out. The main objective of this work is to review the feeding of these species in the Atlantic in order to assess the degrees of trophic competition and speciation pressure. A total of 103 fish families, 22 cephalopod families and 19 crustacean families have been counted, from which the species identified to the genus level only included seventy-one fish, twenty cephalopods and five crustaceans, and the total species identified included three-hundred-one fish, fifty cephalopods and twenty-six crustaceans. The most consumed prey were fish, followed by cephalopods and crustaceans. The exclusive prey consumed by each of the three dolphin species, as well as those shared by all or at least two of them, have also been counted. *T. truncatus* is the most general; however, the western Atlantic populations exhibit high dietary specialization compared to the eastern Atlantic populations, reflecting strong speciation pressure on both sides of the Atlantic. *D. delphis* and *S. coeruleoalba*, despite their amphiatlantism, have hardly been studied in the western Atlantic, except for a few references in the southern hemisphere, so the fundamental differences between the two species and their comparison with *T. truncatus* have been established with records from the eastern Atlantic. All three dolphin species have been observed to be expanding, especially *D. delphis*. This northward expansion and that of their prey is discussed.

Keywords: *Tursiops*; *Delphinus*; *Stenella*; food; feeding; Delphinidae; depth; climate change; Atlantic

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1. Introduction

The main objective of this paper is to review the prey species of three species of dolphinids in the western Atlantic (including the Caribbean Sea) (hereafter **WA**) and in the eastern Atlantic (including the Mediterranean Sea and adjacent seas) (hereafter **EA**) given the hydrological isolation that both geographical areas, which are very distant, suffer from regarding the giant central mass of central Atlantic water, which generates selective pressures and degrees of specialization. The species are the bottlenose dolphin *Tursiops truncatus* (Montagu, 1821) (hereafter ***Tt***), the common dolphin *Delphinus delphis* Linnaeus, 1758 (hereafter ***Dd***) and the striped dolphin *Stenella coeruleoalba* (Meyen, 1833) (hereafter ***Sc***).

The exclusivity or prey sharing of three species of amphiatlantic dolphinids is reviewed and discussed, and differences in diet and the degree of trophic niche overlap on both sides of the Atlantic are tested. In turn, dietary speciation pulses could be inferred that could support studies of morphological, physiological, biochemical and genetic differences that show signs of speciation and isolation between their populations on the same or opposite side of the Atlantic. Likewise, this review will contribute to detecting future dietary changes, either by shifts in diet with global warming or at depth (searching for colder waters locally) or on a geographic scale, expanding or reducing their distribution.

1.1. Geographical Distribution, Global Warming and Speciation Pressure

The three species studied have populations in the Pacific, Indian and both sides of the Atlantic, being absent in the polar areas. They are expanding in relation to global warming [1], two of them—***Dd*** and ***Tt***—towards the north [2]. It is obvious that species with a wide geographic distribution suffer significant selective pressure, especially in their more distant areas, such as the western and eastern Atlantic coasts and associated seas, even if they are offshore or near-shore populations. This is particularly noticeable in ***Tt*** [3]. However, it is generally noted that the different populations of the three species under study are referred to by their scientific name without even considering the possible identification of subspecies. This has posed a delicate problem in this review (especially for ***Tt***) since under the same name of ***Tt*** there is veiled information pertaining to other species of the genus already described or to populations in a strong process of speciation. In this respect, the near-shore and offshore populations eat very different prey, catch them at different depths and have genetic and physiological (including morphological) differences, as will be considered below. This work may contribute in the future to the definition of trophic niche vectors, whether or not they overlap and, ultimately, to better characterize the taxonomic identity of the target species based on the information extracted from the revised populations from very different areas of the Atlantic (including the Caribbean and the Mediterranean).

1.2. Preliminary Taxonomic Considerations

The three species concerned, although their scientific names are accepted (e.g., see World Register of Marine Species, WORMS and List of Marine Mammal Species and Subspecies of the Society for Marine Mammalogy), are frequently discussed and compared in the literature in terms of their morphological differences and taxonomic status (see [4–8]) and their genetic and physiological differences, including offshore and near-shore populations [3,9–11], which sometimes complicates reviews such as the one carried out here given the difficulty of assigning prey species to specific predator taxa or adaptive variants thereof undergoing speciation. The specific status of these distinct forms remains unresolved to satisfaction. As an example, ***Tt*** has long been recognized by most authors as the only species of the genus ([12,13] but was subsequently recognized as a valid species *T. aduncus* (Ehrenberg, 1832 (1833)) (see [3,14,15]) and also *T. gephyreus* Lahille, 1908 [16]. In addition, *T. erebennus* (Cope, 1865) has recently been described [17] *. This is a consequence of the great geographical distance of the populations, which leads to unstoppable processes of genetic isolation and, therefore, speciation. On the other hand, *D. capensis* is currently considered synonymous with ***Dd*** [18], not even as a subspecies, although it was admitted as a valid species for many years, and some of the studies consulted refer to this species, so we have transferred the information to ***Dd***. According to the Society for Marine Mammalogy's List of Marine Mammal Species and Subspecies, ***Dd*** currently has four subspecies: *D. d. delphis* Linnaeus, 1758; *D. d. ponticus* Barabash, 1935; *D. d. bairdii* Dall, 1873 and *D. d. tropicalis* van Bree, 1971, the latter two from Pacific Ocean waters.

* *T. australis* has been reported from parts of Victoria, Australia [19], although it is not listed as a species in the Marine Mammal Species and Subspecies List of the Marine Mammal Society but is considered accepted in WoRMS.

1.3. Background from Genetic, Biochemical and Physiological Studies

A recent review of the genus *Tursiops* and closely related Delphininae reflects important genetic differences between the ***Tt*** populations in the **WA**, offshore **WA**, Mediterranean and Black Seas [3]. There are two distinct ecotypes of bottlenose dolphins in the northwestern Atlantic Ocean: a shallow warm-water ecotype near the coast and a deep cold-water ecotype offshore [7,20–22]. On the other hand, analyses of the mitochondrial DNA and nuclear DNA sequences confirm the differences between the near-shore and offshore forms in the western North Atlantic [9–11]. The different near-shore and offshore forms of ***Tt*** also show differences in other physiological properties, with the offshore forms showing

different electrophoretic profiles for coastal dolphin hemoglobin and higher hemoglobin concentrations, higher hematocrits and higher red blood cell counts than the near-shore forms [4,5,23]. Additionally, the authors of [7] were also able to differentiate the ecotypes based on the prey preferences and differences in the parasite load. Both the near-shore and offshore ecotypes of ***Tt*** [5] are present in the Gulf of Mexico (western Atlantic) [10], but the distribution of each is unknown.

In the northwestern Atlantic Ocean, ref. [24] found a statistically significant break in the ecotype distribution 34 km offshore. In waters further than 34 km offshore and deeper than 34 m, all the ***Tt*** individuals were of the offshore ecotype. Genetic differences and phylogenomic relationships between ***Dd***, ***Sc*** and ***Tt*** have been reported by [3].

1.4. Background to Feeding Studies

Dolphinids are one of the great predators of the sea, feeding mainly on fish and cephalopods, and to a lesser extent on other invertebrates. These prey are located in a wide variety of habitats within the water column and can be epipelagic, mesopelagic or demersal, and, depending on the species of dolphinid involved, it will have a preference for some prey or others [25,26].

There are numerous studies that analyze the stomach contents of ***Tt*** [27–29], ***Dd*** [30–33] and ***Sc*** [34–37]. Some studies only analyze fish as prey species [27], others only cephalopods [34,38] and others also account for crustaceans [39,40]. Some authors even add the polychaetes found in dolphin stomachs [41]. We understand that, when only fish or cephalopods are counted, dolphins do not feed only on these types of prey. In general, all these contributions focus on local or regional studies without addressing the general diversity of the prey that form part of the diet of the species concerned in a wide geographical area such as the one that has been the subject of this review, centered on the **WA** and the **EA** and the associated seas (Caribbean and Mediterranean).

1.5. Maximum Depth Potential for Prey Capture

Dd is a pelagic species found mainly over the continental shelf approximately around the 100–200 m depth contour, or over areas with prominent topographic bottom features [42]. This species can travel to depths of 260 m, but most dives do not exceed 100 m depth [43,44]. ***Sc***, to reach potential prey, may dive between 200 and 700 m [45], although the study in [46] indicates that they prefer waters between 900 and 1900 m deep. The depth ranges reported in the literature should only be used as a reference for the maximum depth at which prey can be found or to which predators could descend, but reliable data on the latter are scant. In this manuscript, it is of particular interest to explore the efficient possibility of catching some deep-sea fish and cephalopod species found in their stomachs.

In shallow habitats, ***Tt*** tends to make relatively short dives, surfacing on average twice every minute. In deep-water habitats, such as the Bermuda Pedestal, dives to over 500 m and for more than 5 min have been documented, correlating with the reported nocturnal vertical migrations of mesopelagic prey [47]. ***Tt*** feeds both solitarily and cooperatively, and the presence of deep-water fish in the stomachs of deep-sea individuals suggests that they dive to depths of more than 500 m [48]. In this study, the review of the percentages and frequencies of the prey species consumed, as well as their depths and the minimum and maximum depths of the three dolphinid species compared, will serve to better understand the availability of prey based on their functional capacity to capture them at depth and the expense required to capture them (adult specimens) based on their size.

2. Materials and Methods

2.1. Search Platforms

The information search for subsequent analysis was centered on the feeding behaviors of the three species under investigation, particularly focusing on the WA and EA regions. Additionally, attention was afforded to understanding the depths at which the prey identified in the stomach contents are typically found. We essentially used the aca-

demic search engines Google Scholar "https://scholar.google.es/ (accessed 21 May 2024)", Scopus "https://www.scopus.com/home.uri (accessed 21 May 2024)", Mendeley "https://www.mendeley.com/search/ (accessed 21 May 2024)", Science Direct "https://www.sciencedirect.com/ (accessed 21 May 2024)", Academia.edu "https://www.academia.edu/ (accessed 21 May 2024)" as well as the Fama Catalogue of the library of the University of Seville "https://fama.us.es/discovery/search?vid=34CBUA_US:VU1 (accessed 21 May 2024)" and the interlibrary loan service of this university to access sources not available on other platforms. The search for information inherent to prey species distribution and depth was also supported by WoRMS [49], FishBase [50], SeaLifeBase [51] databases.

2.2. Design of Tables, Summary Graphs and Structuring of the Information

The data tables (see Supplementary Materials) have been established in strict alphabetical order of families, "genus sp." and species. The + symbol in Tables S1–S3 from the Supplementary Materials indicates whether the prey is distributed in the **WA** or in the **EA**. When it appears with a superscript (e.g., $+^3$), this indicates that the author(s) represented by that number have cited it as prey. To count the species, unidentified species have been discarded, although these have been considered when they were the only representatives of some families that were identified by the authors who cited them.

The prey species quantification reviewed in the literature (see, among others, [33,52,53]) has focused on numerical abundance or percentage of prey (%N), calculating the mean of the values for each prey class (fish, cephalopods and crustaceans), with all values appearing as <1 being considered 0.5. When intervals of data appear, the mean of these has been calculated for their representation in the table of the graph. Only the values described in the EA have been taken into account as the %N of prey obtained from work carried out in WA have been unrepresentative. Nematodes, polychaetes and tunicates have not been taken into account as there is little information—even taxonomic—about them in the stomach contents analyzed. Some scientific papers (e.g., [54]) have omitted prey species that were listed by common or uncommon name, but it was not clear to which species the authors were referring.

In the quantification of prey (see Tables S1 and S2 and/or S3 from the Supplementary Materials), when a species appears as exclusive and only mentioned with the generic name (e.g., *Elops* sp. of ***Tt*** in Table S1 from the Supplementary Materials) and of that same genus, there are some prey species identified as exclusive, with their full name (e.g., *Elops saurus*), and this has been taken into consideration. When some "genus sp." listed as prey of one of the dolphin species (e.g., *Conger* sp. of ***Tt*** or *Sardinella* spp. of ***Sc*** in Table S1 from the Supplementary Materials) and some identified prey species of the same genus (e.g., *Conger conger* and *Sardinella aurita*, respectively) appear in one or more dolphin species, we have counted them according to those species.

The genus *Lampanyctus* spp. (Fam. Myctophidae) is mentioned as prey of ***Tt*** **[55]**, of ***Dd*** [56] and of ***Sc*** ([57,58], but the latter two dolphin species exclusively share or consume 15 Myctophid species, while the mentioned "genus sp." is the only one recorded (without specific identification), exceptionally, as prey of *Tt* in the **EA** [55]. Furthermore, in the stomach contents of 18 ***Tt*** specimens in the WA, Myctophidae were found as main prey [7]. Since we have doubts about whether *Tt* individuals really feed on myctophids, we have not considered them in the quantification of the prey shared by the three dolphins studied.

2.3. Univariate and Multivariate Statistical Analysis

For the three dolphin species in two geographical areas, bibliographic feeding data including fish, cephalopods and crustaceans were collected. A presence (1)/absence (0) matrix was constructed for all taxa with the taxonomic group (bony fish, elasmobranchs, cephalopods or crustaceans) in the first column. Columns two and three were family and species. The remaining variables were dolphin species (n = 3) and population (n = 2), totaling six columns. Data of the dolphin diets of the different papers consulted were put as rows. This matrix of 414 × 6 binary data (the other columns are categorical vari-

ables) was subjected to different non-metric multidimensional scaling (NMDS) analyses using the mathematical measures of altGower–Canberra, Binomial, BrayCurtisHorn, Chao, Dice–Sorensen, Euclidean, Gower, Hamman, Hamming–Manhattan, Jaccard, Kulczynski, Mountford, Ochiai, Raup, Rogers–Tanimoto, Simple_Matching and Sokal-1. Some of these measures are true mathematical distances, others measures of similarity of dissimilarity. A detailed description of these measures (for different data contexts) and an explanation of the NMDS analysis and interpretation methodology can be found in [59,60]. The combination of the mathematical measure with the lowest number of axes that minimized the Kruskal stress was selected. The test used to define this combination is graphical and consists of observing the Kruskal stress linear trend decay. The number of multivariate axes that is the first to be under this linear decreasing trend is selected as the appropriate multivariate number of axes. The reason is to follow the principle of parsimony, adopting a compromise solution that avoids introducing statistical noise by unnecessary axes [61]. The following methodological step was to compare the best NMDS model with the equivalent metric multidimensional scaling (MDS) using the same mathematical measure and axis number. If the difference between both multivariate methods was less than 5%, the metric version was used as it allows us to explain the axes in terms of variance and also, in a metric model, the axes are orthogonal and independent of each other. This combination of using the NMDS form to determine the ideal combination (of mathematical measure and number of axes) and then applying the MDS form is recommended by leading experts in Numerical Ecology [62]. In this way, we take advantage of the flexibility in the model fitting of the NMDS and the possibility to improve the explanation of the functionality of each axis using an MDS. Once the multivariate axes were obtained, the dispersion of cetacean populations and species was plotted to look for the functional significance of these axes and their fit with the groups and families of prey consumed. An analysis of the significance of the convex polygons of species dispersal for significant prey families was also performed. Subsequently, the correlations of the multivariate axes with the minimum depth (DMIN), maximum depth (DMAX), mean depth (DAVG), depth range (DRAN) and a rank interval classification (DINT) obtained for each prey species were determined. DINT is defined as follows:

0. Depth between 0 and 50 m included.
1. Depth between 50 and 100 m included.
2. Depth between 101 and 150 m included.
3. Depth between 151 and 200 m included.
4. Depth greater than 200 m.

Finally, using the niche overlap index of [63,64], a comparison of diets was conducted for the eastern and western Atlantic populations of each cetacean species. Niche breadth was calculated using Levin's formula [65].

3. Results

In the review, we counted the total number of prey found with a total of one-hundred-forty-four families (one-hundred-three fish, twenty-two cephalopods and nineteen crustaceans); ninety-six "genus sp." (seventy-one fish, twenty cephalopods and five crustaceans) and three-hundred-seventy-seven species (three-hundred-one fish, fifty cephalopods and twenty-six crustaceans). Figure 1 shows that dolphins consume the greatest variety of fish prey, followed by cephalopods and crustaceans.

Figure 2a–c illustrate, comparatively in **WA**, **EA** and on both sides of the Atlantic (**WA/EA**), the number of prey (families, "genus sp." and species) of fish, cephalopods and crustaceans recorded.

Fish, one-hundred-three families, seventy-one "genus sp." and three-hundred-one species have been identified: twenty-eight families, twenty-six "genus sp." and one-hundred-twenty-eight species in **WA**; fifty-two families, thirty-six "genus sp." and one-hundred-twenty-nine species in **EA** and on both sides of the Atlantic (**WA/EA**), twenty-one families, two "genus sp." and seven species. Cephalopods, twenty-two families, twenty

"genus sp." and fifty species have been recorded: one family, zero "genus sp." and nine species in **WA**; seventeen families, nineteen "genus sp." and thirty-nine species in **EA** and on both sides of the Atlantic (**WA/EA**), four families, zero "genus sp." and two species. Finally, crustaceans nineteen families, five "genus sp." and twenty-six species were counted: one family, one "genus sp." and four species in **WA**; fourteen families, three "genus sp." and twenty-two species in **EA** and on both sides of the Atlantic (**WA/EA**), four families, one "genus sp." and zero species.

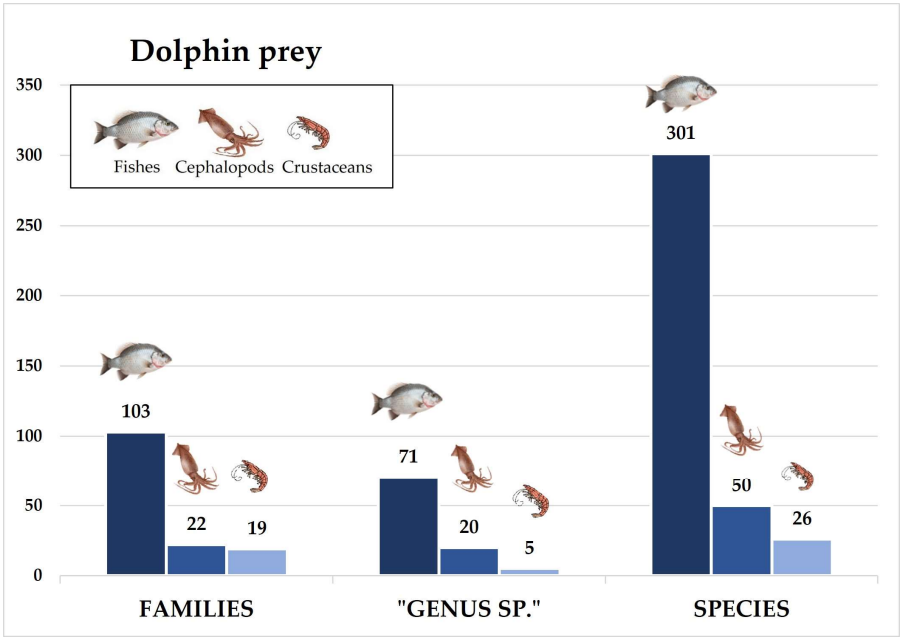


Figure 1. Quantification of prey (families, "genus sp." and species) of fish, cephalopods and crustaceans recorded in the stomachs of ***Tt***, ***Dd*** and ***Sc*** in this review.

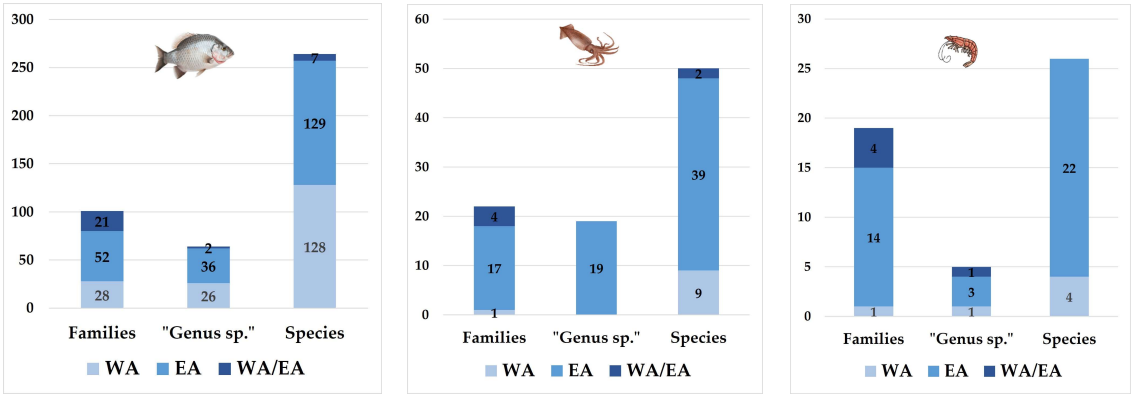


Figure 2. (**a**–**c**) illustrate, comparatively in **WA**, **EA** and **WA/EA**, the number of prey (families, "genus sp." and species) of fish, cephalopods and crustaceans recorded.

Table S1 (see Supplementary Materials) compiles the fish prey (families, "genus sp." and species) identified at ***Tt***, ***Dd*** and ***Sc*** in both the **WA** and **EA**. Table S2 (see Supplementary Materials) compiles the prey of cephalopods (families, "genus sp." and species) identified at ***Tt***, ***Dd*** and ***Sc*** in both the **WA** and **EA**. Table S3 (see Supplementary Materials) compiles the crustacean prey (families, "genus sp." and species) identified at ***Tt***, ***Dd*** and ***Sc*** in both **WA** and **EA**. It residually includes nematodes, polychaetes and/or tunicates through unidentified species whose families have not been identified either.

3.1. Exclusive Prey

Families, "genus sp." and exclusive species to each dolphin species have been counted. The exclusive prey of ***Tt*** are forty-six families, thirty-four "genus sp." (from twenty-seven different families) and one-hundred-seventy-nine species (from sixty-eight different families) of fish; zero families, zero "genus sp." and two species of cephalopods (from two different families) and five families, one "genus sp." and nine species of crustaceans (from six different families). From ***Dd***, ten families, zero "genus sp." and forty fish species (from thirty different families); two families, one "genus sp." and five cephalopod species (from five different families) and zero families, zero "genus sp." and zero crustacean species. From ***Sc***, four families, one "genus sp.", ten fish species (from seven different families); four families, two "genus sp.", fourteen cephalopod species (from twelve different families) and seven families, one "genus sp.", fourteen crustacean species (from ten different families). Figure 3 shows the percentages (%) of exclusive prey over the total number of fish, cephalopods and crustaceans consumed by each of the three dolphin species studied (***Tt***, ***Dd*** and ***Sc***) (a) families; (b) "genus sp." and (c) species.

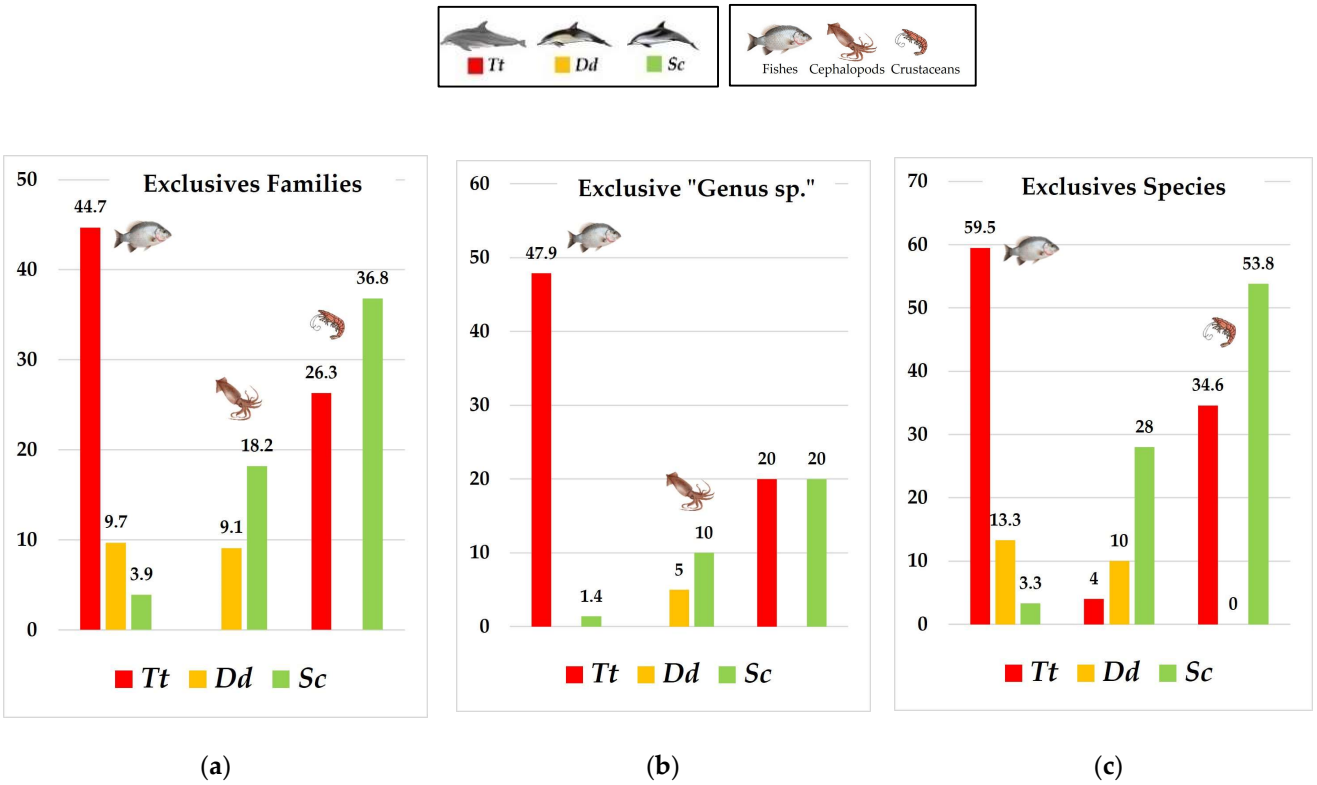
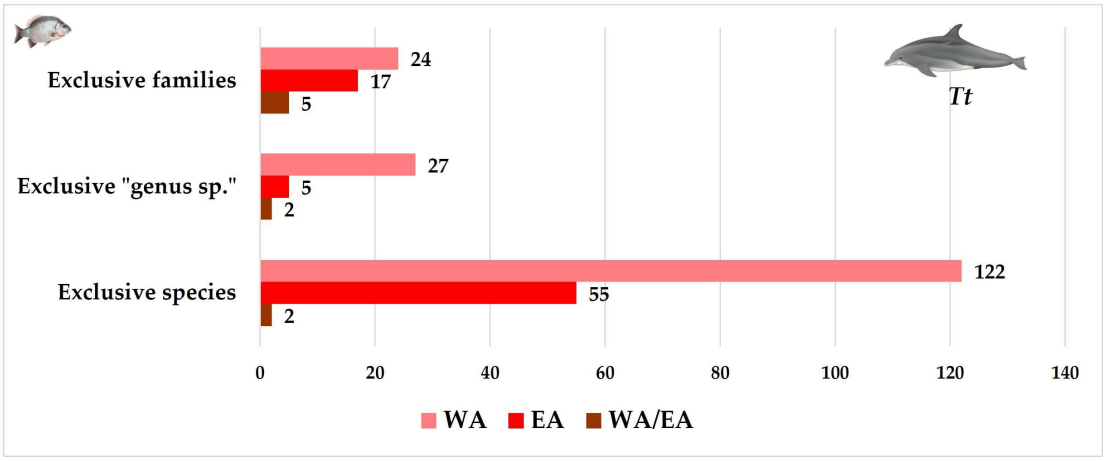


Figure 3. Percentages (%) of exclusive prey over the total number of fish, cephalopods and crustaceans consumed by each of the three dolphin species studied (***Tt***, ***Dd*** and ***Sc***) (**a**) families; (**b**) "genus sp." and (**c**) species.

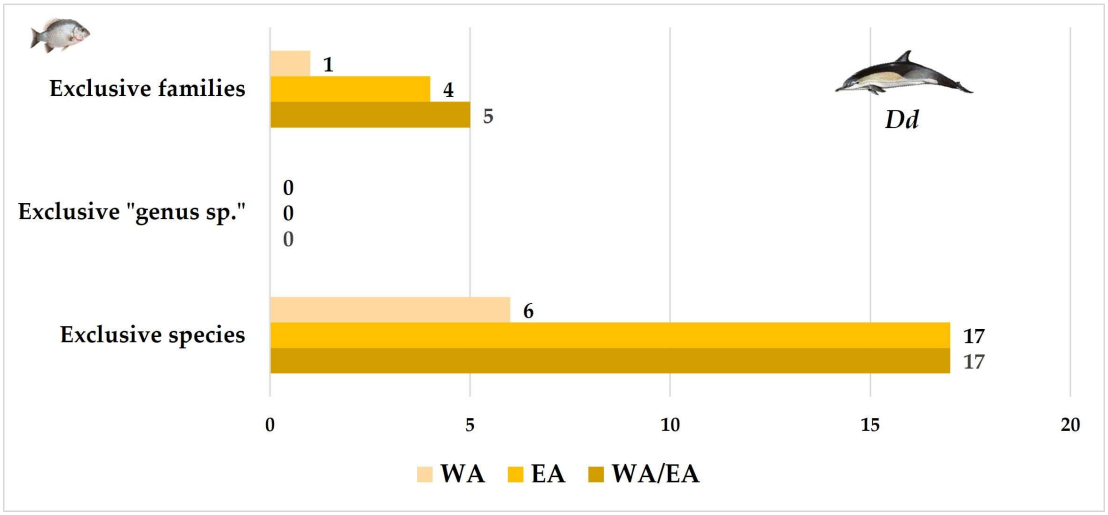
Of exclusive prey, ***Tt*** is the dolphin that preys on the greatest number of fish species at the family, genus and species levels. ***Dd*** feeds on a greater diversity of fish (at family and species levels) than ***Sc***. However, ***Sc*** is the dolphin species that, exclusively, consumes the greatest number of families and species of cephalopods and crustaceans.

When analyzing the exclusive prey of ***Tt***, prey fish from forty-six families were counted (twenty-four in **WA**, seventeen in **EA** and five in **WA/EA**). Of the thirty-four "genus sp." counted, twenty-seven were in **WA**, five in **EA** and two in **WA/EA**. Finally, of the one-hundred-seventy-nine fish prey species counted, one-hundred-twenty-two are from the **WA**, fifty-five from the **EA** and two from **WA/EA**. In this dolphin species, it can be seen that it is in **WA** where there is the greatest diversity of species that are fish prey exclusive to

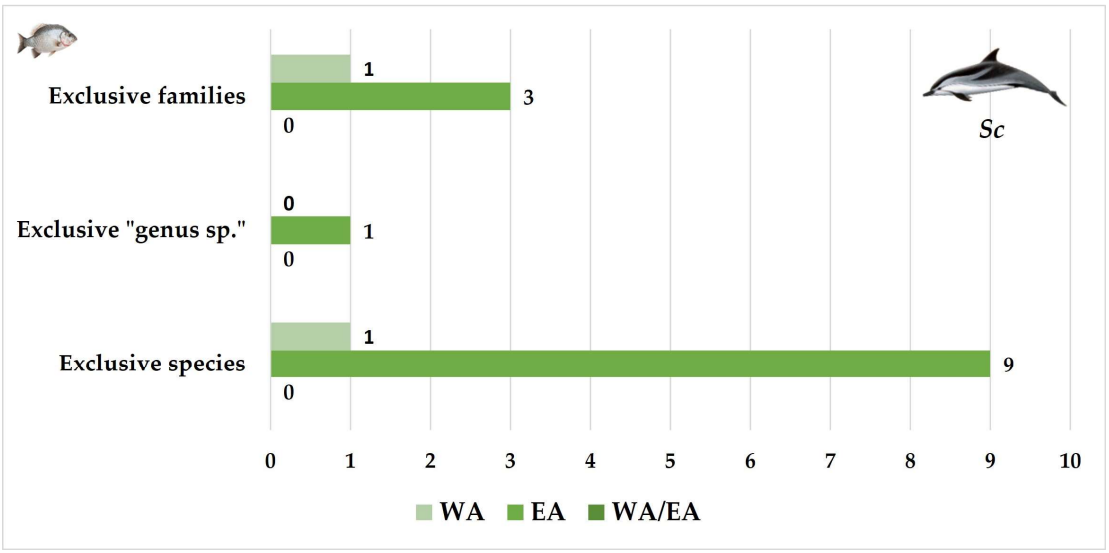
Tt. However, in ***Dd*** and ***Sc***, more exclusive fish prey were found in the **EA** than in the **WA** (Figure 4).



(**a**)



(**b**)



(**c**)

Figure 4. Exclusive fish prey cited in the **WA**, **EA** and on both sides of the Atlantic (**WA/EA**) (**a**) of ***Tt***; (**b**) of ***Dd*** and (**c**) of ***Sc***.

Regarding the cephalopod prey exclusive to dolphins in the **WA**, **EA** and **WA/EA**, it is noted that ***Sc*** is the dolphin species that consumes the most exclusive cephalopod prey, mostly recorded in the **EA**. None of the three dolphin species consumes exclusive cephalopod prey at the family, "genus sp." or species levels that have been found on both sides of the Atlantic (Figure 5).

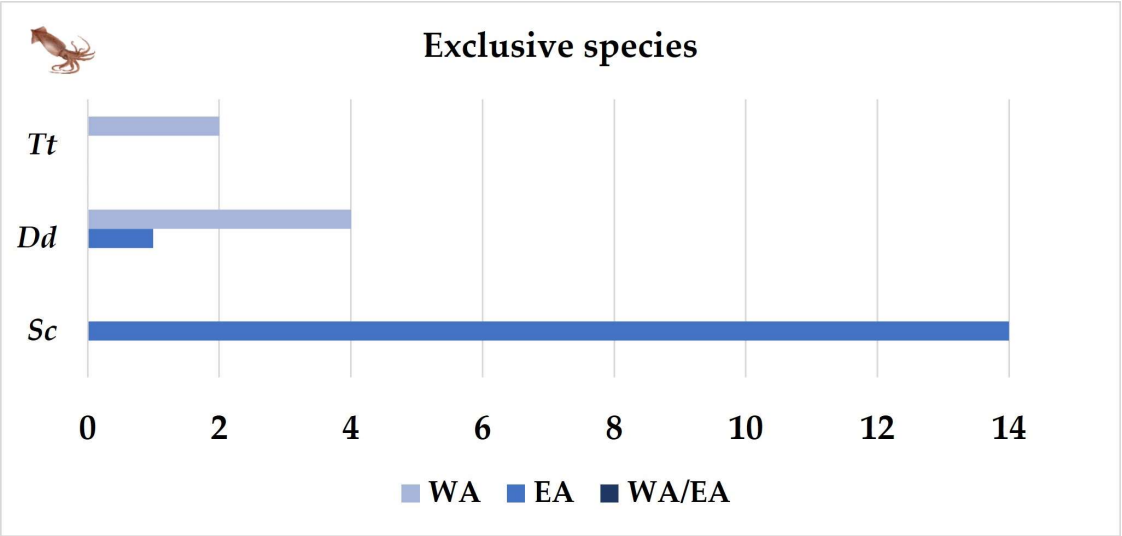


Figure 5. Exclusive cephalopod prey species to each dolphin species recorded in the **WA**, **EA** and **WA/EA**.

3.2. Shared Prey

The numbers of families, genera and prey species shared by the three (or two of them) dolphin species are shown, comparatively, in Figure 6. ***Tt–Dd–Sc*** share twenty-two families, eleven "genus sp." and twenty-six fish species; regarding cephalopods, ten families, twelve "genus sp." and ten species; and, regarding crustaceans, two families, zero "genus sp." and one species.

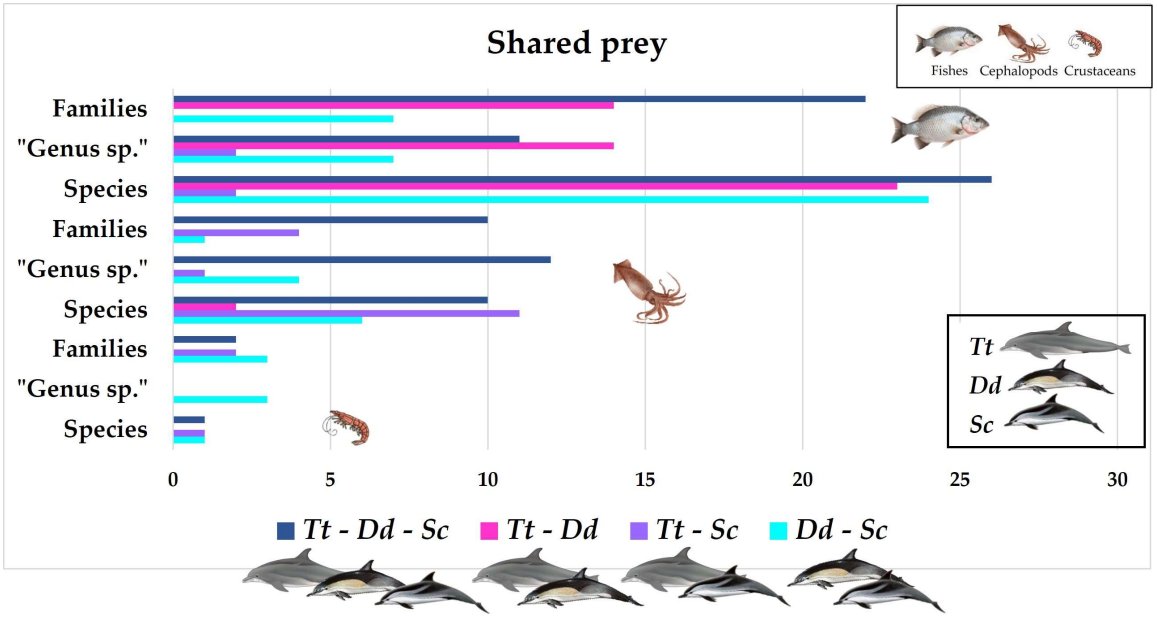


Figure 6. Families, "genus sp". and prey species shared by the three (or two of them) dolphin species ***Tt***, ***Dd*** and ***Sc***.

Prey shared by ***Tt–Dd*** alone, not consumed by ***Sc***, are fourteen families, fourteen "genus sp.", twenty-three fish species and two cephalopod species. Those shared by ***Tt–Sc*** not consumed by ***Dd*** are two "genus sp.", two species of fish; four families and eleven species of cephalopods and two families and one species of crustaceans. Finally, those shared by ***Dd–Sc*** not consumed by ***Tt*** are eight families, seven "genus sp." and twenty-four fish species; one family, four "genus sp.", six cephalopod species and three families, three "genus sp." and one crustacean species.

At the species level (Figure 5), ***Dd–Sc***, in addition to the prey shared with ***Tt***, share more fish, and ***Tt–Sc*** more cephalopods. The prey type most shared by ***Tt–Dd*** and ***Dd–Sc*** is fish, followed by cephalopods and crustaceans. ***Tt–Sc*** primarily share cephalopods, followed by fish and crustaceans.

The fish species shared by ***Tt–Dd–Sc***, indicating partial trophic niche overlap, are *Xenodermichthys copei*, *Argentina sphyraena*, *Atherina presbyter*, *Belone belone*, *Trachurus trachurus*, *Cepola macrophthalma*, *Citharus linguatula*, *Sardinella aurita*, *Sardina pilchardus*, *Sprattus sprattus*, *Engraulis encrasicolus*, 7 species of Gadidae, *Merluccius merluccius*, *Platichthys flesus*, *Scomber colias*, *Scomber scombrus*, *Boops boops*, *Chauliodus sloani* and *Aphanopus carbo*.

3.3. Numerical Percentage of Prey in Stomach Contents

A review of the numerical percentage (%N) values of prey in the stomach contents of the dolphinids discussed here is provided in Table S4.

The quantitative analysis of each species group (Table S4) is shown in Figure 7. The average of the %N of all the reviewed papers is represented. It can be seen that all three dolphin species consume mostly fish species, followed by cephalopods and crustaceans. ***Sc*** consumes more cephalopods but less fish and crustaceans than ***Tt*** and ***Dd***.

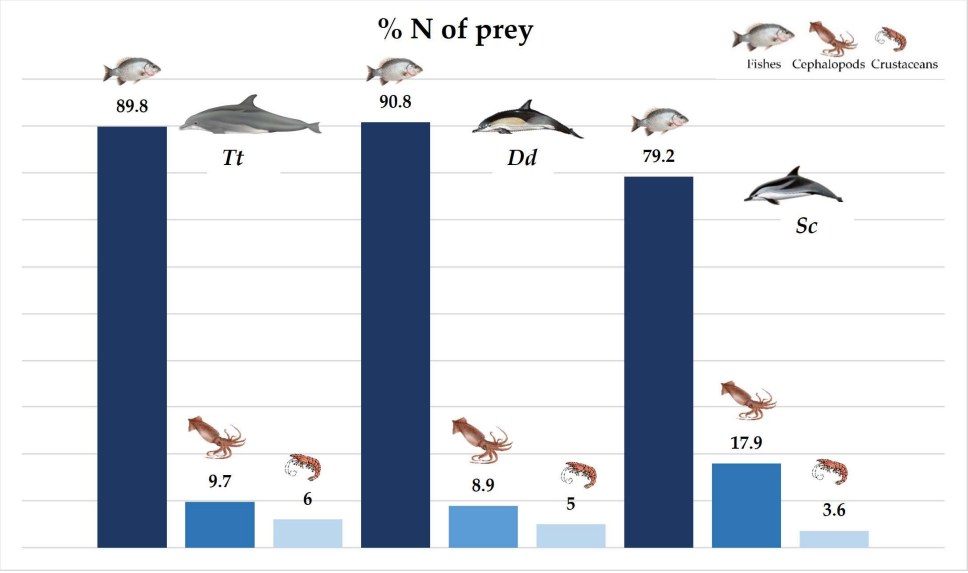


Figure 7. Percentages of prey (% N) of stomach according to the reviewed literature.

3.4. Statistical Analysis

The stress decaying from one to twenty multivariate axes for 17 mathematical measures is plotted in Figure 8. It can be seen that the best combination is the Ochiai metric with three axes as more axes do not substantially decrease stress. In fact, the Kruskal stress drop is 53% with the first axis, with two we decrease by 77% and with three by 84.8%. Adding a fourth axis would decrease the stress by only 1.5% more. In other words, the increase in complexity of the multivariate representation is not justified in terms of stress reduction. This graphical test is similar to the one used in Principal Component Analysis, where the number of axes that capture 85% of the cumulative variance is selected. In NMDS, there is no independent variance on each axis as the axes are not orthogonal [61].

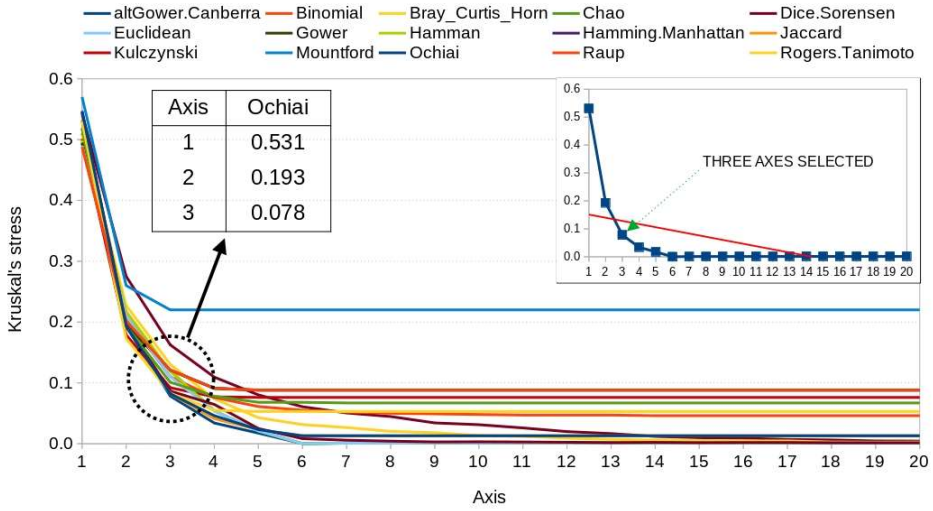


Figure 8. Stress measures on the 17 mathematical measures (distances, similarities and dissimilarities) from 1 to 20 multivariate axes calculated using the binary feeding data matrix in fish, cephalopods and crustaceans prey.

With the chosen combination (Ochiai with three axes), 30 trials with 30 iterations were performed. The different trials differed between them by less than 3.4% from the Kruskal stress, but in no case was there convergence to a stable solution. The differences in fit between NMDS (R2 = 1.00) and MDS (R2 = 0.99) were less than 1%, so we opted for a metric model (MDS) based on the Ochiai measure with three axes. Figure 9 shows the dispersion of dolphin populations and prey families with significant differences between them. Axis one separates the western bottlenose dolphins from the rest of the populations. Axis two separates the eastern bottlenose dolphins from the rest of the populations. Therefore, axes one and two combined separate three groups of populations: western bottlenose, eastern bottlenose and the rest. Axis three separates striped dolphins from the rest (Figure 9). The three axes were chosen in terms of the Kruskal stress in the NMDS, the overall variance explained by the MDS and above all for allowing us to clearly separate the population groups of western bottlenose, eastern bottlenose, striped and common dolphins.

Of the four prey groups (teleosts, elasmobranchs, cephalopods and crustaceans) grouped into one-hundred bony fish families, three elasmobranchs, twenty-two cephalopods and nineteen crustaceans only a few families are significant for separating population groups with three multivariate axes (Figure 9). Table 1 indicates that there are nine significant teleost families and only one significant cephalopod family according to the convex polyhedron area analysis. That is, neither crustaceans nor elasmobranchs can be recognized as significant in determining trophic differences between the populations and species of the studied dolphinids on the three multivariate axes. Teleosts are by far the most important group for explaining the trophic behavior in dolphinids. The most important families are Sparidae, Gadidae and Scianidae. The rest of the families (Haemulidae, Lutjanidae, Myctophidae, Paralepididae, Paralichthyidae and Scaridae), although significant, do not have such a relevant contribution in terms of the trophic niche space.

In Figure 9, the ***Sc*** population of the **EA** is especially associated with a diet that includes the cephalopods of the family Sepiolidae and lanternfish (Myctophidae), and to a lesser extent the ***Sc*** population of the **WA**. Fish of the family Paralepididae are associated with the ***Dd*** of the **EA** and to a lesser extent with those of the **WA**.

Finally, the fish of the Gadidae family are particularly associated with the ***Tt*** of the **EA**, and the rest of the families are linked to the ***Tt*** of the **WA**.

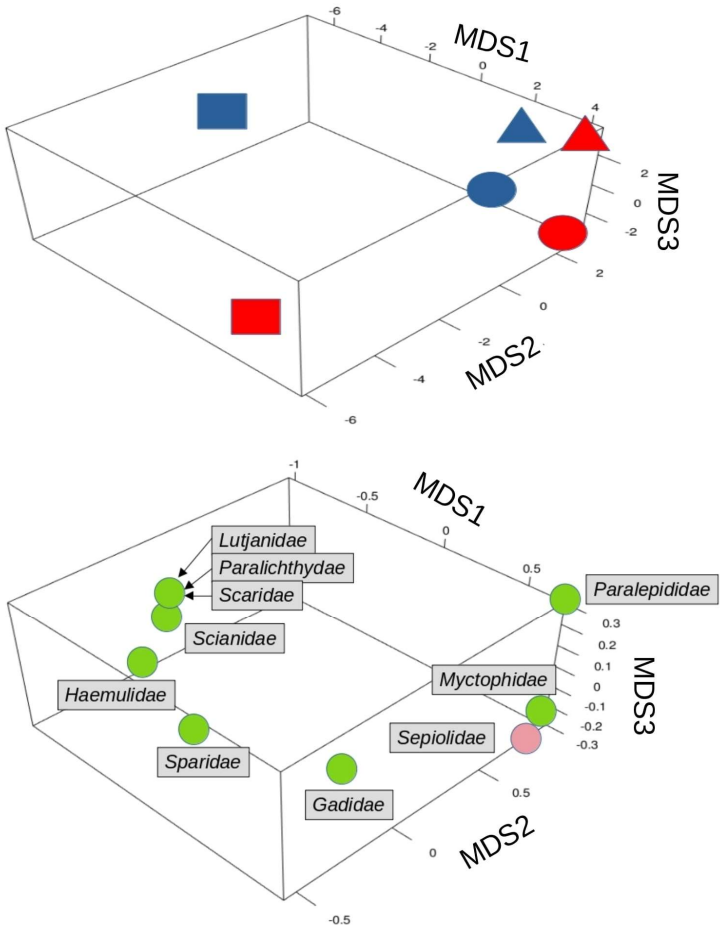


Figure 9. Top image: representation of dolphin populations and species in the three-axis multivariate space of the metric multidimensional scaling (MDS). In blue **WA** populations. In red **EA** populations. Squares: ***Tt***; triangles: ***Dd***; circles: ***Sc***. Below: distribution of fish families (green) and cephalopods (pink) showing significance in the analysis of polyhedron area test.

Table 1. Area of the convex polyhedron for each taxonomic unit in the three-axis multivariate space and its probability of fit are shown. *: $p < 0.05$; **: $p < 0.01$; ***: $p < 0.001$.

	Family	Area	*p*-Value
Bone fish			
	Gadidae	0.985	0.010 **
	Haemulidae	0.001	0.001 ***
	Lutjanidae	0.001	0.004 **
	Myctophidae	0.002	0.001 ***
	Paralepididae	0.014	0.024 *
	Paralichthyidae	0.001	0.010 ***
	Scaridae	0.001	0.021 *
	Sciaenidae	0.629	0.001 ***
	Sparidae	2.261	0.050 *
Cephalopods			
	Sepiolidae	0.011	0.020 **

These results indicate that ***Tt*** individuals, especially from the **WA**, have more varied diets based on larger and epipelagic prey. ***Dd*** feeds on small pelagic fish and probably deep-water pelagic fish when these species migrate to shallower waters at night. ***Sc*** preferentially consumes mollusks and lanternfish.

These results of the multivariate analysis are complemented by the Pianka niche overlap index between the **EA** and **WA** populations, which was 0.314 for ***Tt***, 0.656 for ***Dd*** and 0.738 for ***Sc.*** Fewer fish species families are available for slow-swimming, deep-water stripers, so their diets tend to overlap more between populations. ***Tt*** feed in shallower waters and on larger species, so their diets are more variable. The Morisita index indicated 0.311, 0.627 and 0.693 for ***Tt***, ***Dd*** and ***Sc***. The Levin index is plotted for each population and species in Figure 10. According to these results, the ***Tt*** from the **WA** is the least specialized in its diet, followed by the ***Tt*** from the **EA**. It would be followed by ***Dd*** and ***Sc*** from the **EA** and, finally, ***Dd*** and ***Sc*** from the **WA**. ***Tt*** shows a great deal of variability in its trophic behavior between populations (little overlap). ***Dd*** would be in an intermediate situation and ***Sc*** would be the species showing the least variability in its fish diet, i.e., the greatest overlap between populations. The high specialization of striped dolphins seems to contradict the fact that no significant fish family is exclusively associated with them, but this may be precisely due to their specialization: feeding on the fish that other dolphins leave behind. In turn, ***Tt*** of **EA** and **WA** show such a different feeding spectrum that justifies that they are distinct populations, of high or total isolation, justified by the genetic differences already known (see [3]). The calculation of these indices has not been carried out on cephalopods because their association is exclusive to ***Sc*** and only one family is significant in the polyhedron test.

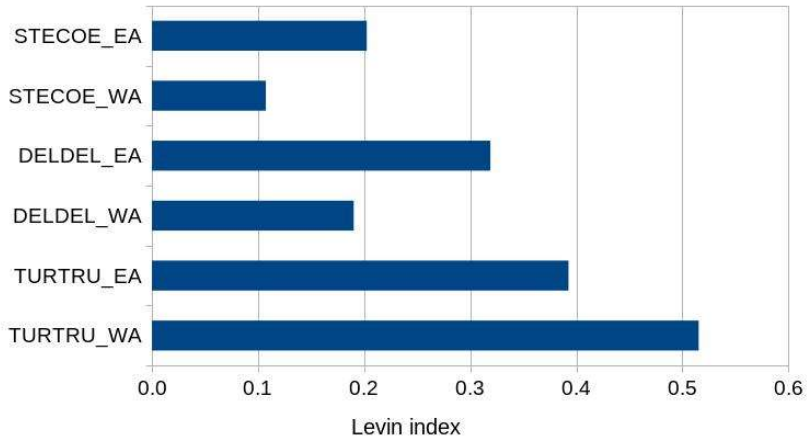


Figure 10. Levin index of niche breadth for fish consumption at ***Tt*** (TURTRU), ***Dd*** (DELDEL) and ***Sc*** (STECOE) for **WA** and **EA** populations.

Finally, the correlations with the depth of the prey using the three multivariate axes for the significant fish families as well as with the single significant cephalopod family are shown in Table 2.

It can be seen that all the depth values show significant correlations with the MDS-1 axis. On axis two, there is no correlation with the minimum depth. If we observe the bony fish families of Figure 2 associated with the dolphin population groups and we compare them with the depths of Table S2 (see Supplementary Materials), we conclude that axes 1 and 2 separate the superficial fish species associated with bottlenose dolphins from the west and east populations, respectively. Axis three separates the pelagic species from benthic species of similar depths. The sum of the three axes allows us to discriminate that the diet obeys a zonation between the species according to their depth and movement habits. This is evident because the depth variable in the 50 m range and from 200 m onwards is the one that correlates best with axis 1. We believe that, in further work, it is necessary to better break down the prey habitat to understand the ecological niche of the dolphin species in greater depth.

Table 2. Top: Pearson correlations of the minimum (DMIN), maximum (DMAX), mean (DAVG), depth range (DRAN) and depth interval (DINT) depth measures (in meters) with three axes of the metric multidimensional scaling analysis (MDS). Bottom: means and standard deviations of the above depth measurements for the significant bony fish and cephalopod families in the multivariate analysis. ***: $p < 0.001$.

Factor	DMIN	DMAX	DAVG	DRAN	DINT
MDS-1	0.331 ***	0.473 ***	0.476 ***	0.466 ***	0.685 ***
MDS-2	0.173 ns	0.431 ***	0.447 ***	0.430 ***	0.408 ***
MDS-3	0.131 ns	−0.083 ns	−0.999 ns	−0.091 ns	0.038 ns
Bone fish					
Gadidae	45 ± 47	640 ± 807	272 ± 277	594 ± 278	3 ± 1
Haemulidae	3 ± 5	76 ± 55	40 ± 29	73 ± 52	0 ± 1
Lutjanidae	7 ± 9	173 ± 112	73 ± 31	165 ± 112	1 ± 1
Myctophidae	32 ± 32	1132 ± 384	569 ± 209	1100 ± 375	4 ± 0
Paralepididae	42 ± 80	2330 ± 1256	1186 ± 619	2289 ± 1279	4 ± 0
Paralichthyidae	7 ± 8	131 ± 64	59 ± 32	124 ± 61	1 ± 1
Scaridae	2 ± 1	26 ± 14	14 ± 7	24 ± 14	0 ± 0
Sciaenidae	8 ± 8	112 ± 93	58 ± 45	104 ± 93	1 ± 1
Sparidae	15 ± 35	248 ± 188	108 ± 93	233 ± 163	1 ± 2
Cephalopods					
Sepiolidae	26 ± 17	1181 ± 945	566 ± 495	1155 ± 945	3 ± 1

4. Discussion

4.1. Exclusivity vs. Prey Species Sharing

Regarding fish prey species, ***Tt***, ***Dd*** and ***Sc*** share twenty-six species (three in the **WA** and twenty-three in the **EA**), while ***Tt*** and ***Dd*** share twenty-three (one in the **WA**, fifteen in the **EA** and seven on both sides (**WA** + **EA**), ***Tt*** and ***Sc*** share two (one in the **EA** and one in the **WA** + **EA**) and ***Dd*** and ***Sc*** share twenty-four (three in the **EA** and twenty in the **WA** + **EA**). Of the exclusive fish species, ***Tt*** consumes 179, ***Dd*** consumes 40 and ***Sc*** 10 (Table 3).

Table 3. Prey fish species distributed in **WA**, **EA** and both sides of the Atlantic (**WA/EA**) consumed exclusively by each dolphin species and shared by all three dolphin species and two of them.

Exclusive Prey Fish Species	WA	EA	WA + EA	TOTAL
Tt	122	55	2	179
Dd	6	17	17	40
Sc	1	9	0	10
Shared fish prey species	**WA**	**EA**	**WA + EA**	**TOTAL**
Tt–Dd–Sc	0	23	3	26
Tt–Dd	1	15	7	23
Tt–Sc	0	1	1	2
Dd–Sc	0	3	20	24

The Myctophidae family, with numerous prey species, is the one with the greatest dissimilarity between ***Tt*** (it does not feed on any of the species identified in Table S1 from the Supplementary Materials) and the ***Dd–Sc*** duo, species that share a good number of prey species and also feed exclusively on other species of the aforementioned family. Given the small size of Myctophidae adults and the maximum depth at which they are found, we suggest that ***Tt*** ad hoc avoids this type of prey given their small size and the energy expenditure resulting from descending very deep for them.

In addition, ***Tt***, ***Dd*** and ***Sc*** share three amphiatlantic fish species. ***Tt*** and ***Dd*** share twenty-three (from sixteen different families), one in the **WA**, fifteen in the **EA** and seven amphiatlantic; ***Tt*** and ***Sc*** share two (from two different families), one in the **EA** and

one amphiatlantic and ***Dd*** and ***Sc*** share twenty-four (from fourteen different families), three in the **EA** and twenty amphiatlantic (Table 3).

4.2. Eastern vs. Western Atlantic and Selective Prey Exclusivity Pressure

It is worth noting that the fish prey species shared by the three dolphinid species in the global Atlantic are twenty-six (from seventeen different families) and only three (*S. aurita*, *M. potaussou* and *S. scombrus*) have been identified in dolphin stomachs on both sides of the Atlantic. Of these twenty-six species, twenty-three have been recorded only in the **EA** (*X. copei*, *A. sphyraena*, *A. presbyter*, *B. belone*, *T. trachurus*, *C. macrophtalma*, *C. linguatula*, *S. pilchardus*, *S. sprattus*, *E. encrasicolus*, *C. heterurus*, *G. argenteus*, *M. aeglefinus*, *M. merlangus*, *P. polachius*, *T. luscus*, *T. minutus*, *M. merluccius*, *P. flesus*, *S. colias*, *B. boops*, *C. sloani* and *A. carbo*), together with eleven "genus sp." (*Ammodytes*, *Argentina*, *Arnoglossus*, *Atherina*, *Trachurus*, *Clupea*, *Sardinella*, *Gadiculus*, *Pollachius*, *Trisopterus* and *Ophidion*), which contrasts with the **WA**, where only prey from one "genus sp." (*Scomber*) has been recognized and no prey identified has been recorded exclusively in the stomachs of the three dolphin species despite the greater diversity of species identified in the stomachs of the latter.

This may be due to a higher level of specialization and also to the high diversity of the specie in the **WA** that live at shallow depths (especially the tropical Caribbean ichthyofauna), where ***Tt*** (coastal variant) seems more efficient than ***Dd*** and ***Sc***, which live, as in the **EA**, further from the coast where there are pelagic or deep resources not exploited by ***Tt***, such as the prey species of Myctophidae, seven of which are shared by ***Dd*** and ***Sc***. Their remoteness from the coast, the depth of capture and their small size may explain the lack of trophic niche overlap between ***Tt*** and ***Dd–Sc***. It can be deduced from the above that trophic competition (fish) between the three taxa compared occurs in the **EA** for the species mentioned above and is non-existent or residual in the **WA**.

Because the species discussed coexist over wide geographic areas of the Atlantic [66], this suggests that a slight difference in diet may indicate a separation of the ecological niches, which reduces the direct competition for food resources when dolphins are sympatric. Large differences in diet, such as those compiled here, imply the consideration of well-established or minimally overlapping ecological niches. On the other hand, [67] justified the coexistence of species either by an overabundance of food or by a slightly different diet that may eliminate the competitive pressure between species. Some authors have observed different prey preferences for sympatric dolphins [14,68].

Although traditionally ***Dd*** has been considered an opportunistic predator feeding mainly on small pelagic fish [69,70] depending on the availability and abundance of its prey [43,71,72], other studies have revealed a certain degree of specialization with a strong preference for fish with a high caloric content [31,73,74], being able to adopt two types of feeding strategies depending on the type and availability of prey: an opportunistic and a selective one [75]. We agree with these observations as this species has been found in submarine canyons [76] where there may be fertilization (upwellings) and mesopelagic prey, more specialized for predation, such as Myctophidae, although the adults of this family are small in size and have a lower caloric content than other migratory epipelagic species, such as sardines, horse mackerel or mackerel.

4.3. The Depth of the Prey Species and the Demersal, Benthic, Epi and Mesopelagic Compartments

The taxonomic families unique to ***Tt*** forty six provide a clue that the more general character of this species is mainly due to its predatory versatility mainly of nectobenthic or demersal ichthyofauna: Acanthuridae, Achiridae, Acropomatidae, Anoplograstidae, Ariidae, Batrachoididae, Blennidae, Centropomidae, Chaetodontidae, Cottidae, Cynoglossidae, Cyprinidae, Dasyatidae, Diretmidae, Elopidae, Ephippidae, Gerreidae, Giganturidae, Haemulidae, Hemiramphidae, Labridae, Lotidae, Lutjanidae, Melamphaidae, Monacanthidae, Mugilidae, Mullidae, Ophictidae, Osmeridae, Ostraciidae, Paralichthyidae, Percidae, Phycidae, Pomatomidae, Rajidae, Salmonidae, Scaridae, Scophtalmidae, Scorpaenidae, Scyliorhinidae, Setarchidae, Sillaginidae, Spratelloididae, Tetraodontidae, Uranoscopidae

and Zeidae. The last three families are elasmobranch fish, a group that does not include any prey that is part of the diet of ***Dd*** and ***Sc***, even accidentally.

The species consumed by ***Tt*** from these families are generally found in shallow waters or down to a depth of between 50–200 m, with some of them also being cited (see Table S1 from the Supplementary Materials) at greater depths that ***Tt*** individuals probably do not access for feeding (due to a lack of energy yield due to their size—the largest of the three dolphin species—and that of their prey and prey density) or only do so exceptionally. The families exclusive to ***Dd*** ten are Bramidae, Caproidae, Centrolopidae, Chiasmodontidae, Gonostomatidae, Macrouridae, Nettastomatidae, Platytroctidae, Pomacentridae and Tracchichthyidae, while ***Sc*** has only four: Chauliodontidae, Moridae, Phosichthydae and Racinipitidae (the first three with only one recorded, unidentified species). ***Sc*** is therefore the species with the least taxonomic specificity at the family level. However, both species (***Dd*** and ***Sc***) exclusively share the Myctophidae (only *Lampanyctus* spp. as prey of ***Tt***; hence, we discard it for the possibility of an erroneous family identification) family, constituted by exclusively bathypelagic species, while, for example, Sciaenidae has nectobenthic/benthopelagic species, larger than those of Myctophidae, which provides an idea of the trophic segregation of ***Tt*** with respect to ***Dd*** and ***Sc*** and of the adaptive versatility and preference of ***Tt*** with respect to the benthic environment, as well as of ***Dd*** and ***Sc*** with respect to the pelagic environment (epi or mesopelagic prey, essentially), which can also be observed by carefully analyzing the taxa compiled in Table S1 from the Supplementary Materials, for the three dolphinid species concerned.

4.4. Statistical Considerations

The parameters observed with univariate and multivariate techniques clearly show a strong divergence between cetacean species in terms of diet selection. Basing the analysis on binary presence/absence data does not make it difficult to draw clear conclusions. Univariate indices such as Pianka's, Morisita's and Levin's must be handled with care because, although we assume that the original data are continuous and normally distributed, our variables are binary. This theoretical requirement forces us to qualify the Pianka index with the Morisita index, although both provide similar results, but the Pianka index shows more overlap in the listings of both populations, which is to be expected. Multivariate techniques, to be clear and easy to interpret, must be based on the right metrics. In this sense, NMDS is usually provided an exploratory profile since it presents more flexibility in defining the gradients by defining the most parsimonious solution possible [77]. However, the non-metric form can pose, precisely because it does not have restrictions in the direction of the axes, convergence problems, and it is then necessary to adopt a metric form to confirm the results. This metric also has the advantage of defining the axes in terms of independent variance as they are orthogonal [78]. It should be understood that, although multivariate data are self-contained, i.e., they allow comparison between the items in the same dataset, there are techniques to compare with similar studies with other species or in other areas. In this sense, this work is open to extension with further studies. The results obtained also serve in an evolutionary context, indicating the high specialization of ***Dd*** towards predation on shallow and small pelagic fish species. In contrast, ***Sc*** shows specialization towards deep-water species. Finally, ***Tt*** is versatile and not very selective, and perhaps this explains the evolution towards a larger size that displaces the more specialized and competitive small dolphin species from the coexistence zones, although the NMDS analysis highlights with special attention the different trophic specialization of ***Tt*** in the **WA** and **EA**, reflecting the strong selective pressure on both sides of the Atlantic, which is not observed in ***Dd*** and ***Sc***. The low diet selection by families established with cephalopods is striking, so we can conclude that, although some dolphins use these resources, they are not really specialists in them and they would be associated with opportunistic patterns.

4.5. Global Warming and Predator–Prey Migration

Ectotherm species potentially have different sensitivities to global warming depending on whether they are stenotherms (essentially tropical, subtropical and polar) or eurytherms (mid-latitude zones). The former, as noted by [79], are more likely to change their distribution in response to global warming, unlike deep-sea species. Most of the prey diversity of ***Tt***, ***Dd*** and ***Sc*** involves fish.

For this zoological group, changes in distribution are being observed worldwide, and, therefore, these changes may result in a mismatch between the quotas and regional abundances within the management areas, with possible repercussions regarding their status and with respect to the species worldwide. In the case of the species of commercial interest, changes are being observed in their distribution throughout the world, which may lead to a mismatch between the quotas and regional abundances of this group within the management areas, with possible repercussions on the state of their stocks and the fisheries that depend on them [80]. This could in turn drive changes in the distribution of their predators, including the three dolphin species compared here.

The numerous prey species compiled in Table S1 (see Supplementary Materials), with a particular focus on fish and cephalopods, are potentially vulnerable to global warming, which may cause them to move to higher-latitude waters or, locally, to deeper waters. Northward latitudinal migration may facilitate the co-migration of their specific predators ***Tt***, ***Dd*** and ***Sc***, which may then expand their range. Some of the exclusive or shared prey of ***Tt***, ***Dd*** and ***Sc*** have already expanded their distribution northwards (see below), which will allow future tracking of the possible expansion of the respective ranges of their predatory dolphins and adaptation of protection and conservation rules for them.

As dolphins are endothermic (hence having a higher potential range of temperature tolerability), their northward expansion may be essentially explained by the prior migration of their usual ectothermic prey from lower latitudes. In the future, this migration may be further facilitated as the summer sea ice extent in the Arctic has decreased by approximately 50% during the first decade of the 21st century [81], resulting in polar and sub-polar waters becoming more fertile as a consequence of the progressive melting of the ice-pack. This contributes to an increase in the water temperature (by decreasing the high albedo of the missing sea ice) and light penetration near the poles, leading to an increase in the net primary productivity (NPP) and thus in the fertilization of their waters, which has been estimated to be up to 20% higher [82].

This may stimulate the migration of pelagic species from lower latitudes, facilitating the subsidiary migration of their predators. This situation has meant that, already in the subarctic zone, the species that inhabit it only have the option of expanding horizontally (towards higher latitudes) or vertically (depth). The exchange of numerous fish species in the trans-Arctic zone between the Atlantic and Pacific oceans has already been mentioned [83,84].

In the North Sea, the rise in the winter bottom temperatures led to a deepening of the entire demersal fish community, although the latitudinal response to warming was heterogeneous: northward movement in the mid-latitude of abundant and widespread thermal specialists, and southward movement of relatively small and abundant southern species with limited occupancy and distribution on the northern North Sea boundary [85]. The species listed in Table S1 (see Supplementary Materials), such as sardine (*Sardina pilchardus*), anchovy (*Engraulis encrasicholus*), mackerel (*Scomber scombrus*) and horse mackerel (*Trachurus trachurus*), are becoming increasingly abundant in the North Sea [86,87], hence the subtropicalization of the North Sea [87]. In addition, ***Dd*** and ***Tt*** have increased their range northwards [2], which may also be directly related to the increased availability of migrant prey, as discussed above.

Ref. [87] indicates that sardines and other fish—which have fast life cycles, planktonic larval stages and low habitat dependence—are highly vulnerable to changes in ocean temperature, making them "an exceptional bioindicator for measuring the direction and speed of climate change expected in the recent future". This suggests that pelagic, gen-

eralist prey species can significantly condition the modifications in the distribution area of the dolphinids that preferentially consume them. In this respect, in relation to climate change, the authors of [1] consider the distribution of the three species discussed here to be "expanding", which may be related to what has been argued above.

Therefore, the broad collection of prey species, their depth ranges, their epipelagic, meso-bathypelagic or demersal typology, as well as their presence or absence in the **WA** and/or the **EA**, can be very useful to monitor their distribution changes at depth or towards the poles in the future, and thus to study their possible relationship with synchronized or uncoupled changes in time, expansiveness, increasing the geographical distribution of ***Tt***, ***Dd*** and ***Sc*** or their bathymetric range in order to access prey that have descended to greater depths.

5. Conclusions

1. The first integrated review of the diet (stomach contents) of the amphiatlantic dolphins *Tursiops truncatus* (***Tt***, bottlenose dolphin), *Delphinus delphis* (***Dd***, common dolphin) and *Stenella coeruleoalba* (**Sc**, striped dolphin) is carried out. In the northern hemisphere, the comparison between the **WA** and **EA** shows that ***Tt*** presents the greatest differences among those observed between the species treated; for ***Dd*** and ***Sc***, in this hemisphere, no information has been recorded in the **WA**, although it has been recorded in the **EA**, so, in the northern hemisphere, for both species, **WA**–**EA** comparisons could not be established. In the southern hemisphere, there are few prey studies in the **WA** for ***Tt***, ***Dd*** and ***Sc*** and no studies, however, in the **EA** for the same hemisphere; this makes the West African coast the most unknown (prey species) of all the continental coastal areas in the **WA**–**EA** binomial.

2. In terms of prey diversity and abundance, fish are the most consumed and best exploited zoological prey group by ***Tt***, ***Dd*** and ***Sc***, followed by cephalopods and crustaceans.

3. For the different prey consumed on both sides of the Atlantic, a strong selective pressure is detected in ***Tt*** and little trophic niche overlap between its **WA** and **EA** populations, as well as large differences with ***Dd*** and ***Sc*** prey (little trophic overlap), whose distance in multivariate space is remarkable.

4. The expansion of the ranges of the three species studied may be related, at least in part, to global warming and the global warming-related migration of some of their usual prey. Of these, some of the species "shared" by ***Tt***, ***Dd*** and ***Sc*** have already expanded their distribution northwards (e.g., *S. pilchardus*, *E. encrasicholus*, *S. scombrus* and *T. trachurus)*, which will allow us to track the possible future expansion of the respective ranges of their predatory dolphins and to adapt the existing protection and conservation regulations for these cetaceans, as well as fisheries, as these constitute one of their main threats not only because of the competition for the trophic resource but also because of incidental catches of individuals.

5. In the future, the depth ranges in which the prey species are most abundant and at what times of the year should be further investigated as their extreme values here do not allow us to approximate, beyond speculation, the diving capacity of ***Tt***, ***Dd*** and ***Sc*** to catch them. Furthermore, to refine the research on the speciation on both sides of the Atlantic, competition for food resources and trophic niche overlap, studies on relative prey abundance (with maximum effort on taxon identification, preferably at the species level) and geographic availability of prey, their selection by predators, as well as their vulnerability to global warming, should be carried out.

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/jmse12060978/s1, Table S1: Families, genera and prey species of fish consumed by ***Tt***, ***Dd*** and ***Sc*** in the in the **WA** and **EA**; Table S2: Families, genera and prey species of cephalopods consumed by ***Tt***, ***Dd*** and ***Sc*** in the in the **WA** and **EA**; Table S3: Families, genera and prey species of crustaceans, polychaetes and nematodes consumed by ***Tt***, ***Dd*** and ***Sc*** in the in the **WA** and **EA**; Table S4: Numerical percentage (%N) of prey (fish, cephalopods and crustaceans) found in the stomachs of ***Tt***, ***Dd*** and ***Sc***.

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