ORIGINAL ARTICLE

Feeding habits of the Atlantic bluefin tuna, *Thunnus thynnus* (L. 1758), in the central Mediterranean Sea (Strait of Messina)

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Abstract The study of feeding habits of the Atlantic bluefin tuna was carried out in 123 specimens, ranging from 115 to 222 cm fork length (FL) and collected during spring seasons of 2010 and 2011 in the central Mediterranean Sea (Strait of Messina). The analysis of stomach contents allowed us to identify 91 taxa of prey items, mainly belonging to Teleostea (54), Cephalopoda (20) and Crustacea (13). The percentage of index of relative abundance (*IRI*) shows the highest values for the myctophid *Hygophum benoiti* (%IRI = 22.854) and the stomiid *Chauliodus sloani* (%IRI = 15.124), followed by the oegopsid squid *Illex coindetii* (%IRI = 14.316). The broad spectrum of prey items could suggest a generalist behavior of this predator, with several species that occasionally occurs in its diet. However, if prey are grouped into food categories, the importance of mesopelagic and benthopelagic fishes can be appreciated (54.41 % of %IRI). The assessment of the hypothetical foraging rhythm of the Atlantic bluefin tuna highlighted that its feeding activity is concentrated on diel migrating fauna during night and on larger preys upon daylight. The predation on the high-energetic food as mesopelagic and bathypelagic fishes during the pre-spawning and the spawning period may bring an energetic advantage in tuna metabolism and gonadal maturation

Introduction

Thunnus thynnus L. 1758 (Scombridae) is a large migratory predator living in the pelagic ecosystems of the Atlantic Ocean and the Mediterranean Sea, including the Black Sea (Whitehead et al. 1984–1986). This species is worldwide considered a valuable fishery resource, and its management is a main issue for the international communities, social parts and scientists. The importance of the Atlantic bluefin tuna has been emphasized at international level since the 1966, during the Conference of Plenipotentiaries (Rio de Janeiro, Brazil), which established the International Commission for the Conservation of Atlantic Tunas (ICCAT) and adopted the Convention for the Conservation of Atlantic Tunas. From that moment on, several international institutions, commissions and conventions have focused their efforts on the conservation status of *T. thynnus* (i.e., GFCM of the FAO, Convention on Migratory Species of Wild Animals of Bonn in 1983, IUCN, CITES). In fact, from an ecological point of view, *T. thynnus* plays the significant role of top predator in the pelagic trophic web, regulating and controlling the ecosystem balance and prey biomass by a constant predation, assuring a positive control on biodiversity by contributing to maintain its natural level. As reported by several authors (Sinopoli et al. 2004; Sarà and Sarà 2007; Karakulak et al. 2009; Romeo et al. 2011), *T. thynnus* feeds on a broad spectrum of prey and has been described as an opportunistic feeder. Moreover, the Atlantic bluefin tuna is a long-lived

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fish (Santamaria et al. 2009), and its feeding habits are influenced by ontogenetic changes (Sarà and Sarà 2007), with a wide range of prey including zooplankton, fishes, cephalopods and crustaceans. So a significant number of links with other marine species was reported in the Atlantic bluefin tuna's feeding ecology, and the multiplicity of these connections and interactions adds complexity to the hard issue of tuna stock management. Therefore, to better manage this resource, as suggested by the principles of the Ecosystem Approach to Fisheries (EAF) (Garcia et al. 2003), is strongly recommended an improvement of the understanding of ecosystem structure and functioning (i.e., trophic web and predator–prey relationships), including increased knowledge of the component species and their role in the ecosystem. In the last decade, several efforts have been made by the scientific community to investigate the biology and ecology of *T. thynnus*, and new studies employing innovative techniques (i.e., archival tags, natural markers as genetics or otolith chemistry) shed light on tuna migration, trans-oceanic movements and the utilization of main spawning grounds and foraging areas (Rooker et al. 2003, 2006, 2007; Karakulak et al. 2004; Block et al. 2005; De Metrio et al. 2005). In the Mediterranean Sea, young-of-the-year tuna diet was investigated using stomach content analysis (Sinopoli et al. 2004), while feeding behavior of adult fishes was studied both by carbon- and nitrogen-stable isotopes and stomach analyses (Sarà and Sarà 2007; Karakulak et al. 2009). However, a significant lack on the Atlantic bluefin tuna feeding habits is still palpable, and it is mainly due to the difficult in monitoring the diet of this species during the whole year because of their migratory behavior. For this reason, the aim of this paper is to contribute to extend the knowledge on the trophic behavior of the Atlantic bluefin tuna in the Strait of Messina (central Mediterranean Sea). This location is closely joined to the primary spawning and recruitment areas of the Atlantic bluefin tuna in the southern Italy around Sicily (Sella 1924, 1929; Sanzo 1932; Piccinetti and Piccinetti Manfrin 1970; Tsuji et al. 1997; Nishida et al. 1998; La Mesa et al. 2005), and it is well known to be an important upwelling area of the central Mediterranean (Mazzarelli 1909; Vercelli 1925; Bignami and Salusti 1990). In particular, the study on the diet composition was carried out by stomach content analyses, and information was given on the feeding strategy of *T. thynnus*. An assessment of the daily foraging rhythm of the Atlantic bluefin tuna in the Strait of Messina was also given.

Materials and methods

Overall, 123 stomachs of *T. thynnus* were collected during spring seasons of 2010 and 2011 in the Strait of Messina (central Mediterranean Sea) (Fig. 1). Samples were
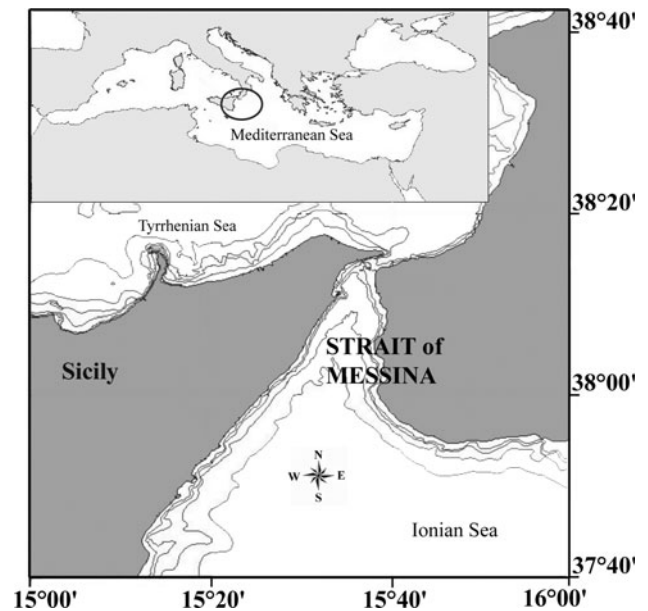

Fig. 1 Location of the study area in the Strait of Messina

obtained from hand line fishery, carried out during daylight by small crafts in the study area already described by several Authors (Berdar et al. 1995; Potoschi and Sturiale 1996; Di Natale et al. 2005). At landings, the fork length (FL in cm), the gilled and gutted weight (GWT) of each individual and the hour of the catch were recorded, while the stomach was removed and frozen at −18 °C. Fishermen were asked about the bait used during fishing operation, in order to recognize this one from real prey and exclude it from analysis.

Stomachs were dissected in laboratory, and their content was observed using stereomicroscope. Qualitative analysis allowed us to identify entire or partially digested prey to the lowest possible taxa, following taxonomic features reported by Whitehead et al. (Whitehead et al. 1984–1986) for fishes, Roper et al. (1984), Jereb and Roper (2005, 2010), Young et al. (2010) for cephalopods, Falciai and Minervini (1992), Riedl (1991) for crustaceans and invertebrates. When prey were found in an advanced status of digestion, the identification of otoliths and cephalopod lower beaks was a powerful mean in their classification, which was performed using taxonomic keys (Clarke 1986; Tuset et al. 2008), as well as a reference to ISPRA collections (Pedà et al. 2009; Battaglia et al. 2010).

The identified preys were counted and weighed; entire specimens were preserved in 70 % ethanol, while beaks were immersed in a mixture of ethanol, glycerine and water.

Quantitative analysis was performed only on fresh prey found in the stomach content, while accumulated prey items were excluded. In fact, hard parts are resistant to digestion (i.e. cephalopod beaks and otoliths) and may

cumulate in the stomachs over more meals, leading to an overestimation of the importance of prey they belong to. Then, as hypothesized by Santos et al. (2001), only prey bearing fleshy remains were supposed to have been recently eaten by the predator.

The importance of the different prey items to the diet of *T. thynnus* was assessed by calculating the following dietary indexes: abundance percentage (%N = number of individuals of prey *i*/total number of prey × 100) and weight percentage (%W = weight of prey *i*/total weight of all prey × 100), frequency of occurrence (%F = number of stomachs containing prey *i*/total number of stomachs containing prey × 100). These values were combined to calculate the *IRI* for each prey and the *%IRI* was also estimated (Pinkas et al. 1971; Hyslop 1980; Hacunda 1981): $IRI = (\%N + \%W)(\%F)$ and $\%IRI_i = (IRI_i/\sum IRI) \times 100$.

The feeding behavior of *T. thynnus* was assessed by a Costello graphical method (Costello 1990) modified by Amundsen et al. (1996), plotting the prey-specific abundance against the frequency of occurrence in a two-dimensional graph. The prey-specific abundance is summarized as follows:

$$P_i = \left(\sum S_i / \sum S_{ti} \right) \times 100$$

where P_i is the prey-specific abundance of prey *i*, S_i is the total abundance (as weight or number) of prey *i*, and S_{ti} is the total stomach content in only those specimens with prey *i* in their stomachs. According to Amundsen et al. (1996), information on prey importance, feeding strategy and niche width contribution can be inferred through the position of prey types in the two-dimensional plot.

In order to assess the hypothetical daily foraging rhythm of the Atlantic bluefin tuna, preyed items (and, specifically, the predominant species detected in the stomach content) were separated into four subgroups according to the digestion stage: (1) Entire prey; (2) Intermediate 1 (low degree of digestion); (3) Intermediate 2 (high degree of digestion, but fleshy remains are present); (4) Accumulated prey (hard remains, that is, cephalopod beaks, fish otoliths). Following Pusineri et al. (2005), the digestion stage was then compared with the hour of catch and was estimated the hour of feeding, taking into account that tunas are able to totally digest a fish of medium size in about 24 h (transit time assessed from the examination of stomach contents), as stated by Aloncle and Delaporte (1973). Moreover, as cephalopod beaks are resistant to digestion (Santos et al. 2001), beaks without fresh remains were considered belonging to cephalopods caught prior to the day of sampling, whereas beaks still in the buccal mass were related to specimens eaten during early evening, in a time less than 24 h of tuna catch (Pusineri et al. 2005).

Results

Tuna ranged from 115 to 222 cm FL (mean FL = 154.0 ± 27.4 cm) and from 26 to 172 kg of gilled and gutted weight (mean GWT = 56.7 ± 33.2 kg). The size distribution of all specimens is given in Fig. 2. Over 123 stomachs analyzed, only 11 resulted empty (8.9 %), while in the remaining 112 (91.1 %) one prey at least was found.

Overall 91 taxa of prey items were identified in the stomach content of the Atlantic bluefin tuna, mainly belonging to Teleostea (54), Cephalopoda (20) and Crustacea (13). However, some of them were excluded from the quantitative analysis since only hard remains were found in the stomachs: the cephalopod *Tremoctopus violaceus* Delle Chiaje 1830 and the teleosts *Gymnammodytes cicerelus* (Rafinesque, 1810), *Mora moro* (Risso 1810), *Coelorinchus coelorhinchus* (Risso 1810), *Hymenocephalus italicus* Giglioli 1884.

Diet composition of *T. thynnus* and dietary indexes (abundance percentage, weight percentage, frequency of occurrence, *IRI* and *%IRI*) calculated for each prey item are reported in Table 1. The percentage of IRI shows the highest values for the myctophid teleost *Hygophum benoiti* (Cocco 1838) (*%IRI* = 22.854) and the stomiid *Chauliodus sloani* Bloch & Schneider, 1810 (*%IRI* = 15.124), followed by the oegopsid squid *Illex coindetii* (Vérany 1839) (*%IRI* = 14.316) and the lanternfish *Ceratoscopelus maderensis* (Lowe 1839) (*%IRI* = 11.680). However, an elevated contribute in terms of number of prey (%N) was given by the sergestid shrimps *Sergestes corniculum* (Kroyer 1855) (%N = 19.439) and *Sergestes robustus* (Smith 1882) (%N = 16.552), while the carangid *Trachurus picturatus* (Bowdich 1825) (%W = 11.167) and *Anguilla anguilla* (Linnaeus 1758) (%W = 9.558) together with *C. sloani* (%W = 13.711) and *I. coindetii* (%W = 11.200) represented 45 % of prey biomass. Furthermore, the most frequently consumed prey were myctophids, *H.*
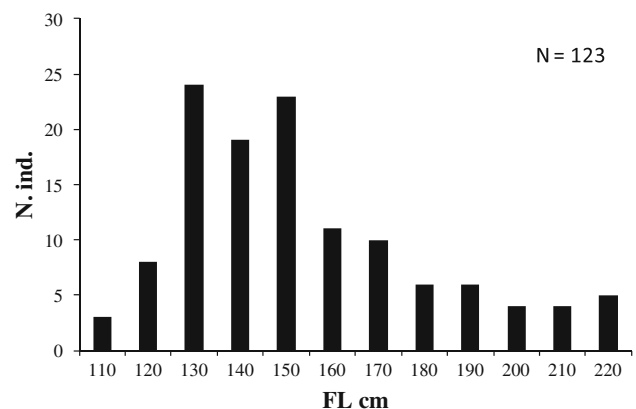

Fig. 2 Fork length frequency distribution of Atlantic bluefin tuna specimens sampled in the Strait of Messina

Table 1 Diet composition of *T. thynnus* and dietary indexes calculated for each prey item: abundance percentage (%N), weight percentage (%W), frequency of occurrence (%F), index of relative abundance (IRI), IRI percentage (%IRI)

Class and order	Family	Species	%N	%W	%F	IRI	%IRI
Hydrozoa							
Siphonophora	Diphyidae	Diphyidae unid.	0.503	0.002	8.929	4.514	0.135
Crustacea							
Amphipoda	Phronimidae	*Phronima sedentaria* (Forskal, 1775)	0.344	0.009	3.571	1.263	0.038
	Phrosinidae	*Phrosina semilunata* (Risso, 1882)	0.212	0.009	4.464	0.984	0.030
	Platyscelidae	*Platyscelus ovoides* (Risso, 1816)	0.053	0.002	1.786	0.098	0.003
	Lycaeidae	Lycaeidae unid.	0.424	0.000	0.893	0.379	0.011
Copepoda		Copepoda unid.	0.026	0.000	0.893	0.024	0.001
Decapoda	Aristeidae	*Aristaeomorpha foliacea* (Risso, 1827)	0.026	0.144	0.893	0.152	0.005
	Benthesicymidae	*Gennadas elegans* (Smith, 1882)	0.026	0.002	0.893	0.025	0.001
	Sergestidae	*Sergestes corniculum* (Kroyer, 1855)	19.439	1.270	15.179	314.331	9.433
		Sergestes robustus (Smith, 1882)	16.552	1.671	16.964	309.138	9.277
	Oplophoridae	*Acanthephyra purpurea* (Milne-Edwards, 1881)	0.026	0.003	0.893	0.027	0.001
	Pasiphaeidae	*Pasiphaea multidentata* (Esmark, 1866)	0.662	0.071	5.357	3.927	0.118
		Pasiphaea sivado (Risso, 1816)	0.079	0.012	1.786	0.164	0.005
		Pasiphaea sp.	0.132	0.005	1.786	0.246	0.007
		Crustacea unid.	0.026	0.000	0.893	0.024	0.001
Cephalopoda							
Sepiolida	Sepiolidae	*Heteroteuthis dispar* (Rüppell, 1844)	0.477	0.161	7.143	4.555	0.137
Teuthida	Brachioteuthidae	*Brachioteuthis riisei* (Steenstrup, 1882)	0.026	0.013	0.893	0.036	0.001
	Cranchiidae	*Galiteuthis armata* (Joubin, 1898)	0.026	0.006	0.893	0.029	0.001
	Thysanoteuthidae	*Thysanoteuthis rhombus* (Troschel, 1857)	0.026	5.651	0.893	5.069	0.152
	Enoploteuthidae	*Abralia veranyi* (Férussac, 1835)	0.238	0.149	3.571	1.384	0.042
		Abraliopsis morisii (Vérany, 1839).	0.106	0.011	1.786	0.210	0.006
	Pyroteuthidae	*Pyroteuthis margaritifera* (Ruppell, 1844)	0.053	0.006	0.893	0.053	0.002
	Onycoteuthidae	*Onychoteuthis banksii* (Leach, 1817)	0.556	0.298	7.143	6.102	0.183
		Ancistroteuthis lichtensteinii (Férussac, 1835)	0.053	0.030	1.786	0.148	0.004
	Ommastrephidae	*Ommastrephes bartramii* (Lesueur, 1821)	1.033	1.723	7.143	19.686	0.591
		Illex coindetii (Vérany, 1839)	2.860	11.200	33.929	477.055	14.316
		Todarodes sagittatus (Lamarck, 1798)	0.477	2.305	7.143	19.867	0.596
	Histioteuthidae	*Histioteuthis bonnellii* (Férussac, 1835)	0.821	2.166	8.929	26.669	0.800
		Histioteuthis reversa (Verrill, 1880)	0.053	0.606	1.786	1.177	0.035
	Octopoteuthidae	*Octopoteuthis sicula* Rüppell, 1844	0.026	0.015	0.893	0.037	0.001
	Chiroteuthidae	*Chiroteuthis veranyi* (Férussac, 1835)	0.079	0.458	2.679	1.439	0.043
		Teuthida unid.	0.026	0.002	0.893	0.026	0.001
Myopsida	Loliginidae	*Loligo vulgaris* Lamarck, 1798	0.026	0.007	0.893	0.030	0.001
Octopoda	Argonautidae	*Argonauta argo* Linnaeus, 1758	0.212	0.272	5.357	2.590	0.078
		Cephalopoda unid.	0.159	0.024	5.357	0.979	0.029
Tunicata							
Salpida		Salpida ind	0.583	0.043	1.786	1.117	0.034
	Pyrosomatidae	*Pyrosoma atlanticum* Péron, 1804	0.132	0.033	0.893	0.147	0.004
Doliolida	Doliolidae	*Doliolum* sp.	1.033	0.067	5.357	5.890	0.177
Teleostea							
Aulopiformes	Paralepididae	*Paralepis coregonoides* Risso, 1820	0.053	0.005	1.786	0.104	0.003
		Paralepis speciosa Bellotti, 1878	0.026	0.010	0.893	0.032	0.001
		Sudis hyalina Rafinesque, 1810	0.079	0.029	2.679	0.290	0.009
		Arctozenus risso (Bonaparte, 1840)	0.079	0.022	2.679	0.272	0.008
		Paralepididae unid.	0.026	0.015	0.893	0.037	0.001

Table 1 continued

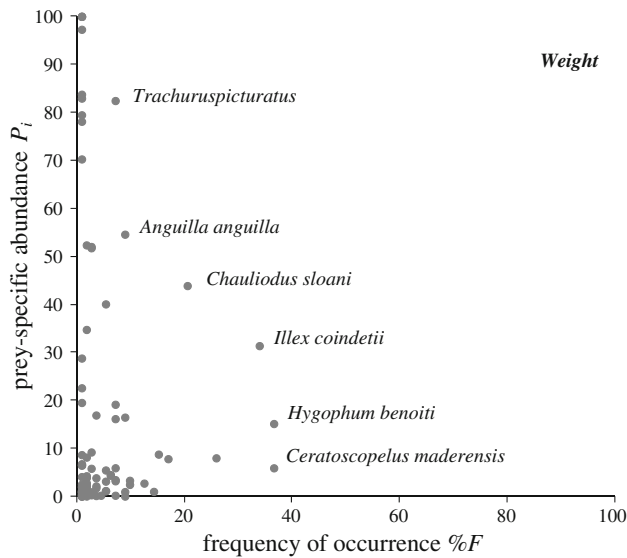| Class and order	Family	Species	%N	%W	%F	IRI	%IRI
Clupeiformes	Clupeidae	*Sardinella aurita* (Valenciennes, 1847)	0.106	2.476	2.679	6.917	0.208
Perciformes	Carangidae	*Caranx crysos* (Geoffroy Saint Hilaire, 1809)	0.026	3.113	0.893	2.803	0.084
		Trachurus picturatus (Bowdich, 1825)	0.318	11.167	7.143	82.033	2.462
		Trachurus mediterraneus (Steindachner, 1868)	0.053	0.028	1.786	0.145	0.004
		Trachurus sp.	0.079	0.131	0.893	0.188	0.006
		Carangidae unid.	0.026	1.161	0.893	1.061	0.032
	Centracanthidae	*Spicara maena* (Linnaeus, 1758)	0.053	0.261	1.786	0.560	0.017
	Centrolophidae	*Centrolophus niger* (Gmelin, 1788)	0.026	0.020	0.893	0.041	0.001
		Schedophilus medusophagus (Cocco, 1839)	0.026	0.027	0.893	0.048	0.001
	Nomeidae	*Cubiceps gracilis* (Lowe, 1843)	0.026	0.024	0.893	0.045	0.001
	Scombridae	*Auxis rochei* (Risso, 1810)	0.026	4.320	0.893	3.881	0.116
		Sarda sarda (Bloch, 1793)	0.026	4.213	0.893	3.786	0.114
		Scomber japonicus (Gmelin, 1789)	0.026	0.662	0.893	0.614	0.018
	Sparidae	*Boops boops* (Linnaeus, 1758)	0.344	3.934	5.357	22.918	0.688
		Dentex gibbosus (Rafinesque, 1810)	0.026	0.629	0.893	0.585	0.018
		Sarpa Salpa (Linnaeus, 1758)	0.026	1.393	0.893	1.268	0.038
		Sparidae unid.	0.132	0.074	3.571	0.736	0.022
	Trichiuridae	*Lepidopus caudatus* (Euphrasen, 1788)	0.106	1.154	2.679	3.376	0.101
Beloniformes	Belonidae	*Belone belone gracilis* (Linnaeus, 1761)	0.026	0.005	0.893	0.028	0.001
	Scomberesocidae	*Scomberesox saurus* (Walbaum, 1792)	0.265	0.134	3.571	1.426	0.043
Stomiiformes	Gonostomatidae	*Gonostoma denudatum* Rafinesque, 1810	0.053	0.068	1.786	0.216	0.006
	Phosichthyidae	*Ichthyococcus ovatus* (Cocco, 1838)	0.106	0.011	0.893	0.105	0.003
		Vinciguerria attenuata (Cocco, 1838)	0.715	0.022	7.143	5.263	0.158
		Vinciguerria poweriae (Cocco, 1838)	0.079	0.027	1.786	0.190	0.006
	Sternoptychidae	*Argyropelecus hemygimnus* Cocco, 1829	0.079	0.023	1.786	0.182	0.005
		Maurolicus muelleri Gmelin, 1789	0.715	0.224	14.286	13.411	0.402
	Stomiidae	*Chauliodus sloani* Bloch & Schneider, 1810	10.832	13.711	20.536	504.003	15.124
		Stomias boa boa (Risso, 1810)	0.079	0.032	2.679	0.298	0.009
Myctophiformes	Myctophidae	*Benthosema glaciale* (Reinhardt, 1837)	1.377	0.344	7.143	12.296	0.369
		Ceratoscopelus maderensis (Lowe, 1839)	8.316	2.317	36.607	389.215	11.680
		Diaphus holti Tåning, 1918	1.457	0.265	12.500	21.525	0.646
		Electrona risso Cocco, 1829	1.192	0.292	6.250	9.276	0.278
		Hygophum benoiti (Cocco, 1838)	15.810	4.994	36.607	761.597	22.854
		Hygophum hygomii (Lütken, 1892)	0.980	0.073	8.929	9.398	0.282
		Lampanyctus crocodilus Risso, 1810	0.900	0.531	6.250	8.950	0.269
		Lampanyctus pusillus (Johnson, 1890)	0.265	0.026	3.571	1.039	0.031
		Myctophum punctatum Rafinesque, 1810	3.708	1.272	25.893	128.946	3.869
		Notoscopelus elongatus (Costa, 1844)	1.536	0.237	9.821	17.415	0.523
		Symbolophorus veranyi (Moreau, 1888)	0.026	0.031	0.893	0.051	0.002
Zeiformes	Caproidae	*Capros aper* (Linnaeus, 1758)	0.344	1.870	1.786	3.955	0.119
Gadiformes	Gadidae	*Micromesistius poutassou* (Risso, 1827)	0.053	0.253	0.893	0.273	0.008
	Merlucciidae	*Merluccius merluccius* (Linnaeus, 1758)	0.026	0.122	0.893	0.132	0.004
Anguilliformes	Anguillidae	*Anguilla anguilla* (Linnaeus, 1758)	0.662	9.558	8.929	91.247	2.738
Osmeiformes	Microstomatidae	*Microstoma microstoma* (Risso, 1810)	0.106	0.126	2.679	0.620	0.019
		Nansenia oblita (Facciolà, 1887)	0.053	0.011	1.786	0.114	0.003
		Teleostea unid.	0.900	0.106	9.821	9.880	0.296

Unid. unidentified

Fig. 3 Relationship between prey-specific abundance (P_i), expressed as weight, and frequency of occurrence (%F) of prey items in the diet of *T. thynnus*, collected in the Strait of Messina
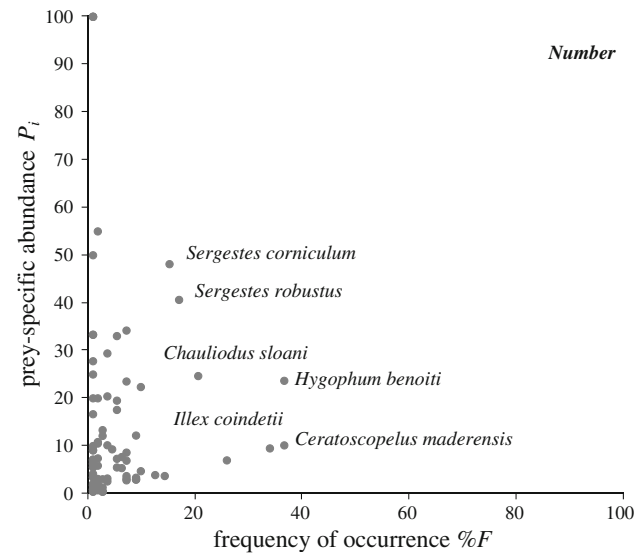

Fig. 4 Relationship between prey-specific abundance (P_i), expressed as number of prey, and frequency of occurrence (%F) of prey items in the diet of *T. thynnus*, collected in the Strait of Messina

benoiti and *C. maderensis*, that recorded the same value of %F = 36.607.

The feeding pattern of the Atlantic bluefin tuna is graphically represented in Figs. 3 and 4, where the frequency of occurrence (%F) is plotted against prey-specific abundance (P_i), expressed, respectively, as weight and number. In Fig. 5, the explanatory Costello diagram (modified from Amundsen et al. 1996) for the interpretation on feeding strategy is reported. Most of the food categories are located in the lower left corner of the diagrams or close to the vertical axis, in a region of low prey importance. Then, all these species are rare or unimportant prey, being consumed by a low percentage of predators, as indicated by the low values of frequency of occurrence. However, some prey items resulted most frequently eaten by *T. thynnus* (*H. benoiti*, *C. maderensis*, *I. coindetii*, *C. sloani*).

Looking at the Costello diagram (modified from Amundsen et al. 1996), no single species can be defined as dominant in the diet of the Atlantic bluefin tuna in the study area; in spite of this, grouping prey into food categories (Fig. 6), the importance of migrating mesopelagic and benthopelagic fishes are well evident by the value of %IRI (54.41 %), followed by oegopsid squids (%IRI = 18.95 %). The pelagic shrimps (mainly Sergestidae) were largely preyed by the Atlantic bluefin tuna, but their contribution in terms of biomass (%W) resulted low. As regards eels and epipelagic fishes, they were both represented in most cases by few medium–large prey.

The digestion status of prey and the hypothetical foraging rhythm of the Atlantic bluefin tuna in the Strait of Messina are shown in Fig. 7. The Atlantic bluefin tuna
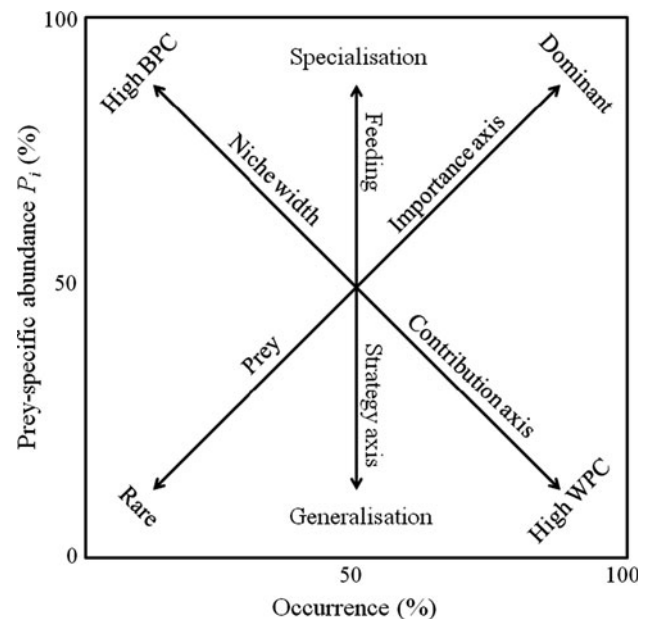

Fig. 5 The explanatory Costello diagram (modified from Amundsen et al. 1996) and its interpretation on feeding strategy. (*BPC* = between-phenotype component, *WPC* = within-phenotype component)

feeding activity during night was concentrated on diel migrating fauna (Myctophidae, Stomiidae, Paralepididae, crustaceans and cephalopods). By the analysis of digestion status of prey, the predation on crustaceans and cephalopods was carried out also during daylight, while carangids and eels were usually eaten during day. However, an occasional feeding on eels during night was also recorded.
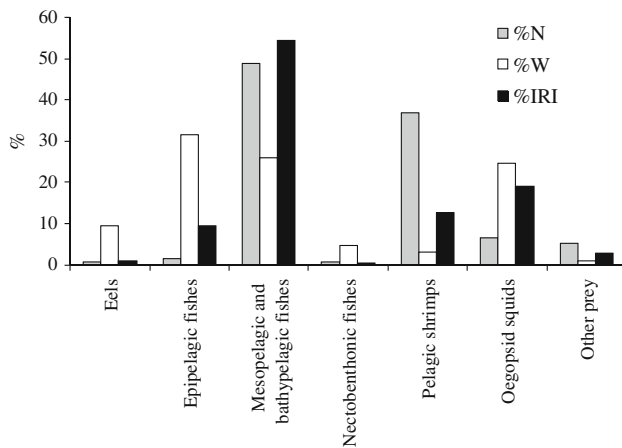
Fig. 6 Abundance (%N), weight (%W) and IRI (%IRI) percentage for Atlantic bluefin tuna food items grouped into 7 categories: eels, epipelagic fishes, mesopelagic and bathypelagic fishes, nectobenthonic fishes, pelagic shrimps, oegopsid squids, other prey

Further considerations on the foraging rhythm of *T. thynnus* are given in the discussion.
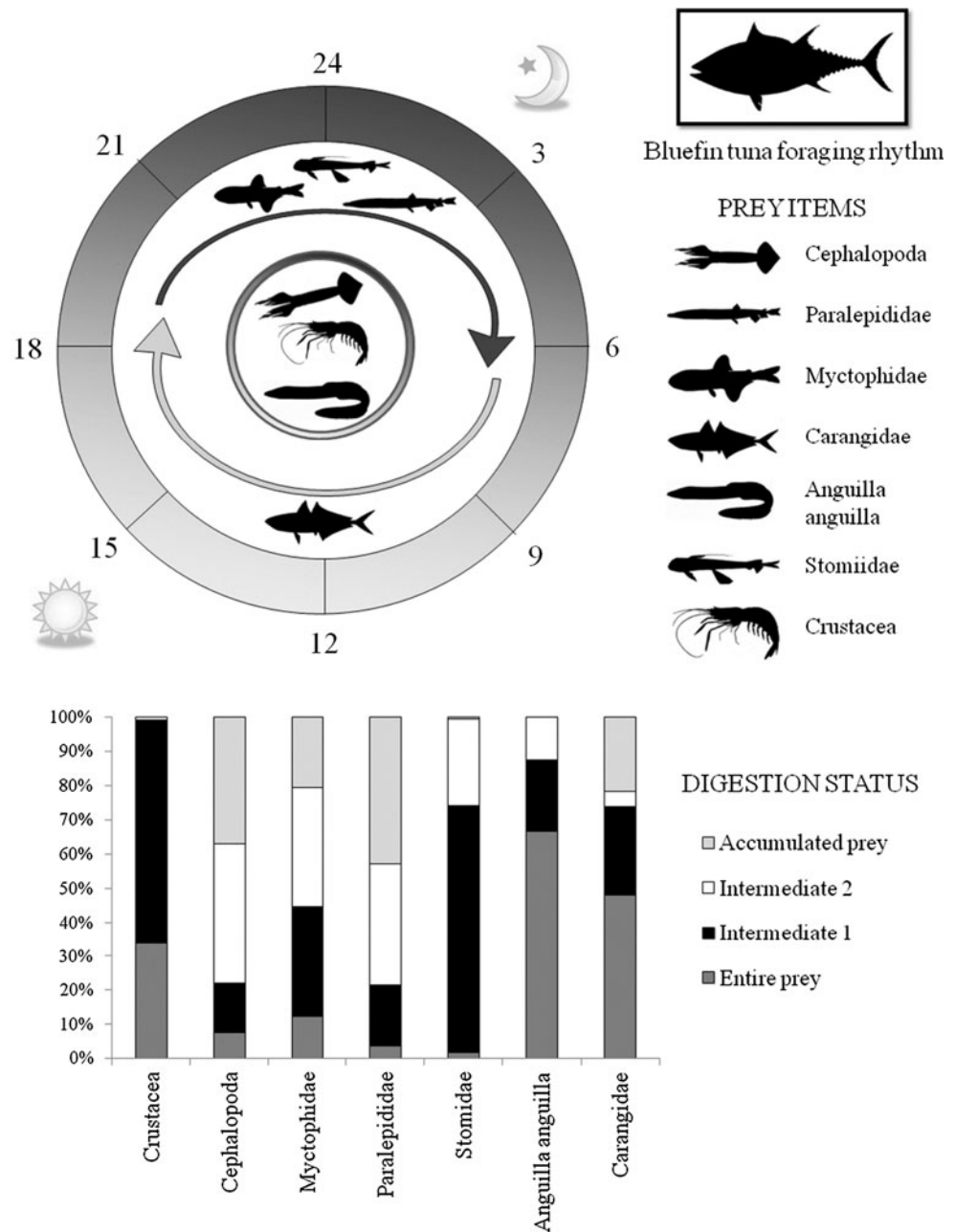
Discussion

The analysis of feeding habits of the Atlantic bluefin tuna in the central Mediterranean (Strait of Messina) showed that teleosts represent the main fraction of food during spring season, even if cephalopods and crustaceans can be considered other important source of energy, while remaining systematic taxa (Hydrozoa and Tunicata) have a negligible impact on the diet. This supports the results of other Authors in Mediterranean (Genovese 1960; Genovese and Alonzo 1961; Karakulak et al. 2009) and Atlantic Ocean (Eggleston and Bochenek 1990; Chase 2002; Logan et al. 2011), which described adult Atlantic bluefin tuna as primarily piscivorus predator. On the contrary, the diet of young-of-the-year *T. thynnus* seems to vary depending on area and available prey, relying mainly on cephalopods and fishes in the northern Tyrrhenian Sea (Piccinetti and Piccinetti Manfrin 1970), crustaceans and fishes in the Ligurian Sea (Orsi Relini et al. 1998), whereas fishes, followed by crustaceans and cephalopods, were the most abundant prey items in the southern Tyrrhenian and in the western Mediterranean (Sanz Brau 1990; Sinopoli et al. 2004).

According with similar studies (Chase 2002; Sinopoli et al. 2004; Karakulak et al. 2009), the Atlantic bluefin tuna shows a broad spectrum of prey items (91); this could underline a generalist behavior of this predator, with several species that occasionally occurs in its diet, as also indicated by the application of Costello graphical method modified by Amundsen et al. (1996). However, if prey are grouped into food categories, the importance of

mesopelagic and benthopelagic fishes can be appreciated, reaching the 54.41 % of *%IRI*. Schoolings of vertically migrating Myctophidae, Stomiidae, Paralepididae, Sternoptychidae, Gonostomatidae, Microstomatidae and Phosichthydae are in fact abundant in the area, being concentrated by currents and upwelling phenomena (Mazzarelli 1909; Genovese et al. 1971) and constituting easily available food for the Atlantic bluefin tuna and other predators (Guglielmo et al. 1995). The diel vertical migration of pelagic organisms offers also to *T. thynnus* the possibility of collecting planktonic crustaceans (mainly Sergestidae and Pasiphaeidae) and squids (in particular Ommastrephidae). On the other hand, if the predation on mesopelagic fauna is facilitated by the rising of these species toward upper water layers during their nocturnal movements, it is also true that the Atlantic bluefin tuna is also able to perform vertical excursion to hunt in deeper waters (i.e., >600 m, as reported by Block et al. 2001). The evidence of this behavior in the study area can be ascribed to the finding of deep-sea demersal species in the stomachs, such as the crustacean *Aristaeomorpha foliacea* (Risso 1827) and the teleosts *Capros aper* (Linnaeus 1758), *M. moro*, *C. coelorhinchus* and *H. italicus* as well as deep-sea squids during daytime. The ingestion of demersal preys in deep or coastal waters was also reported by other Authors (Genovese 1960; Genovese and Alonzo 1961; Chase 2002; Karakulak et al. 2009); then, it appears that the Atlantic bluefin tuna sporadically moves to the bottom to feed on benthic organisms.

By comparing the digestion status of prey with the hour of predator catch by fishermen, it was possible to assess the hypothetical foraging rhythm of the Atlantic bluefin tuna in the Strait of Messina. The analysis of these data highlights a possible daily pattern in tuna diet, with a feeding activity concentrated on diel migrating fauna during night and the predation on larger preys upon daylight. Crustaceans were always found at a low stage of digestion as entire prey or fresh remains (digestion status: intermediate 1), and they were likely preyed from some hours before sunrise to daylight, although the predation on vertically migrating crustaceans also during early night cannot be excluded. In fact, the Atlantic bluefin tunas were sampled during daytime and these small-sized species are expected to be assimilated in few hours (Pusineri et al. 2005); for this reason, potential small crustacean prey eaten during early nighttime were not detected. Paralepidids were found at all digestion stages in the stomachs, but highly or fully digested individuals were mainly recorded in predators caught during the afternoon, indicating that they were preyed during night and early morning. As Paralepididae, also Myctophidae and Stomiidae were eaten during night feeding activity and sometimes at first hours of daylight. However, accumulated otoliths were detected mainly for

Fig. 7 The hypothetical foraging rhythm of the Atlantic bluefin tuna during spring season in the Strait of Messina, as derived by comparison of the digestion states of main prey in the stomachs

myctophid species, since sagittae of stomiid fishes are very small and they can be dissolved in few time. Together vertically migrating mesopelagic fishes, cephalopods were prey usually ingested during night as demonstrated by the large number of buccal masses found in the stomachs. Fully digested beaks were instead considered belonging to prey eaten at least 24 h prior to the sampling, because of their resistance to digestive processes (Santos et al. 2001). Nevertheless, entire cephalopod prey were recorded also in fishes caught during afternoon and late morning; hence, the predation on cephalopods is also stretched over all daytime. Large prey as carangids and eels were usually consumed

during day, since they were mostly found as entire prey, but there was evidence of occasional feeding on eels also during night. This tuna feeding behavior was well known by old fishermen in the study area; in fact in the past, during the night, they used to fish tunas by hand lines baited with specimens of *A. anguilla* (Berdar et al. 1995).

Analyzing the results of this research, several connections and similarities can be found with findings of Karakulak et al. (2009) on Atlantic bluefin tuna' specimens ranging from 98.5 to 294 cm FL in the eastern Mediterranean Sea. In fact, both studies highlighted the tendency of the Atlantic bluefin tuna to forage on mesopelagic fauna

(in particular Myctophidae and Stomiidae) during spring season, recording the lanternfish *H. benoiti* as the most important food item. Also, Piccinetti and Piccinetti Manfrin (1970) observed a high frequency of predation on mesopelagic fishes in the Tyrrhenian sea, but they were mainly Paralepididae. The dominance of these prey in the Atlantic bluefin tuna diet was not reported in other studies that instead underlined an high percentage of epipelagic species among fish prey, such as *Ammodytes* spp., *Clupea harengus*, *Scomber scombrus* (Eggleston and Bochenek 1990; Chase 2002; Logan et al. 2011) in the Atlantic Ocean and Engraulidae (Orsi Relini et al. 1998), Clupeidae (Sinopoli et al. 2004) and *Boops boops* and *Trachurus* sp. (Genovese 1960; Genovese and Alonzo 1961) in the Mediterranean Sea. Nevertheless, a quite important rate of mesopelagic fishes (mainly Paralepididae) among secondary prey was also recorded by Orsi Relini et al. 1998.

Mesopelagic fishes have already been reported among main prey of several like-tuna fishes. For instance, *Thunnus alalunga* is known as predator relying on Paralepididae and Sternoptychidae in Atlantic (Aloncle and Delaporte 1973; Pusineri et al. 2005) and Paralepididae in Mediterranean waters (Consoli et al. 2008). The deep-dwelling bigeye tuna *Thunnus obesus* is particularly able to exploit the migrant micronektonic species as source of regular food, feeding on significant amount of myctophids (Moteki et al. 2001; Bertrand et al. 2002), sternoptychids (Koga 1958; Moteki et al. 2001), alepisaurids (Koga 1958), paralepidids (Moteki et al. 2001; Potier et al. 2004), gempylids (Moteki et al. 2001) and scopelarchids (Potier et al. 2004). Also, yellowfin tuna *Thunnus albacares* forages on mesopelagic fishes (Sternoptychidae), as reported by Moteki et al. (2001) in eastern Pacific Ocean; however, in other areas, this species is considered a predator hunting mainly in shallower layers (Bertrand et al. 2002).

The occurrence of the mesopelagic and bathypelagic fauna in *T. thynnus* diet in the study area can be related to the presence of upwelling currents in the Strait of Messina. The abundance of these food resources may be constitute an attractive for an opportunistic feeder as the Atlantic bluefin tuna, able to forage on micronekton patches and aggregations.

However, another possible hypothesis is that the predation on this food category during the pre-spawning and the spawning period may bring an energetic advantage in tuna metabolism. In evidence, mesopelagic fishes are reported to have higher lipid content (e.g., wax esters) than several other marine fish (Benson and Lee 1972; Saito and Murata 1998; Lea et al. 2002), representing an important energy source for marine predators (e.g., Phleger et al. 1997; Moteki et al. 2001; Bertrand et al. 2002; Lea et al. 2002). Further studies should be carried out to deepen this aspect.

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