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Feeding Habits of Both Deep-Water Red Shrimps, *Aristaeomorpha foliacea* and *Aristeus antennatus* (Decapoda, Aristeidae) in the Ionian Sea (E. Mediterranean)

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1. Introduction

1.1 The deep-water fishes' diet habits: Some notes on the present and the future knowledge

The study of dietary composition and feeding habits of fish has been considered as one of the most important topics in the ecology of animal marine communities. Both the biology of species (as a population level) and their interaction with biological and environmental factors are influenced by the food resources exploited by fish.

At bathyal depths, most of our knowledge on deep-sea demersal communities, mainly for both fishes and large invertebrates - e.g. decapods crustaceans, comes principally from areas where deep-water fisheries are commercially developed. Most deep-sea (>1000 m) fish are active predators, regarded as generalist (i.e. highly diversified diets) and depend mainly on benthopelagic and mesopelagic prey (Mauchline & Gordon, 1986). The distribution of these preys is closely associated with the bottom; however, many demersal fishes feed principally on vertically migrating mesopelagic organisms such as myctophids and cephalopods. Crustacean zooplanktivores constitute the majority of deep-sea pelagic fish species and families examined. Less common are predators that primarily ingest soft-bodied or gelatinous zooplankton, gastropod molluscs and polychaete worms. These categories of predators are generally represented by a few individual species within different families (Randall & Farrell, 1997)

Many deep-sea fish show diel and seasonal feeding patterns (e.g. Macpherson, 1980; Mauchline & Gordon, 1984; Atkinson, 1995), which have been often related to the temporal vertical migrations of their mesopelagic prey (Gartner et al., 1997). To understand temporal (e.g. daily, seasonal) and spatial changes in the diet and trophic habits of bathyal fish it is crucial simultaneous sampling of their trophic resources (Madurell, 2003). However despite the accepted role of this fauna in the bathyal food webs, little is known about their interactions and their dynamics.

To date, studies on the feeding habits of deep-sea fish have focused mainly on depth related changes and only few studies have addressed aspects of seasonal or diel feeding cycles. Studies on food resource partitioning are scarce in non-littoral marine environments, with some studies performed in deep-sea communities at a community level and within a single feeding guild (e.g. Carrassón & Cartes, 2002). In general, food is considered as the major limiting factor in the functioning of deep-water ecosystems and trophic aspects have been considered as the most important factor on deep-sea faunal community organization (Jumars & Gallagher, 1982).

The knowledge concerning the deep-sea organisms' biology remains almost in its infancy. Many aspects about their diet are still speculative. Many gaps exist concerning the type of the bottom, the spatial and temporal distribution of many fishes and the taxonomic composition of the fauna. The result of further detailed studies could offer important elements to our learning about the taxonomic composition, life history and physiology studies, such as feeding habits (Randall & Farrell, 1997).

1.2 Feeding habits in Decapod crustaceans of shallow and deep-sea waters – General aspects

The much diversified diet of penaeids (shrimps or prawns) was first described by Williams (1955) who studied the stomach content of prawns from the eastern United States. Generally speaking, the condition of the gut contents prevents the use of the most methods of quantifying diet. Techniques such as weighting the food, measuring the size of prey or reconstituting prey cannot be used (Dall et al., 1990). Decapods can catch mobile free-swimming prey; the remains of fish and squid form a major part of the diet of several species and their preferable animal food is other small crustaceans, polychaets, mollusks (Dall et al., 1990), plant remains (Kuttyamma, 1974) and a very small portion of bacteria (Moriarty & Barclay, 1981).

Most shrimps spend the day buried in the substratum and emerge and feed at night. Because of their small stomach, they feed several times each night in order to obtain sufficient food. Under natural conditions, where food items are small and dispersed, searching and ingestion probably continue through the night and rates of ingestion and ejection are probably similar (Dall, 1968). This allows the foregut to be filled repeatedly and enables the shrimps to take in considerably more food if they fed only once per night (Dall et al., 1990).

Decapods can even be dominant in some deep-water regions, including the deep Mediterranean, where subtropical species dominate in terms of biomass (Cartes & Sardà, 1992). It has been suggested that this dominance is due to the low metabolic rates of this taxon, which has low feeding rates and hence is better adapted to live under oligotrophic conditions than, for instance, fishes (Cartes & Sardà, 1992). In bathyal ecosystems, decapods occupy a variety of ecological niches and exhibit a similar range of trophic levels to fish (Polunin et al., 2001). They also have a wide variety of feeding habits or guilds (Cartes et al., 2002), ranging from deposit feeders to carnivores, the latter including specialized species preying on benthos (e.g. Crangonidae: Lagardère, 1977) or macrozooplankton (e.g. Pandalidae: Cartes, 1993a). As a consequence, decapods are an ideal group in which to analyze changes in the structure and dynamics of ecosystems exposed to temporal (e.g. Seasonal) or spatial (e.g. depth) gradients (Cartes et al., 2007).

2. Mediterranean deep sea waters

The Mediterranean Sea – *Mare Nostrum*, *Mare Internum* or *Mediterraneum* is a relatively small, deep basin that is surrounded by continents. It is 4000 km in length and is located between 30° and 46° N and 5.50° W and 36° E (excluding the Black Sea). The Mediterranean Basin is subdivided by a series of tranverse ridges with a north-south trend. These ridges exist in the western (Alboran, Balearic, Tyrrhenian basins) and the eastern part (Ionian, Aegean, Levantine) (Sardà et al., 2004 and references herein).

Deep-sea ecosystems include the waters and sediments beneath approximately 200 m depth (Emig & Geistdoerfer, 2004) and represent the world’s largest biome, covering more than 65% of the earth’s surface and including more than 95% of the global biosphere. The deep-sea domain of the Mediterranean is divided in three zones: bathyal, abyssal and hadal (Table 1). The edge of the continental shelf is the boundary between the neritic (inshore) domain and the deep-sea oceanic (offshore) domain. Its depth varies with the ocean or Sea.

The deepest point in the Mediterranean, 5,121 m, is found at the North Matapan-Vavilov Trench, Ionian Sea. The deep-sea floor includes regions characterized by complex sedimentological and structural features: (a) continental slopes, (b) submarine canyons, (c) base-of-slope deposits, and (d) bathyal or basin plains with abundant deposits of hemipelagic and turbidity mud’s (Danovaro et al., 2010).

	Neritic Domain	Deep-Sea Oceanic Domain		
	Continental Shelf	Bathyal Zone	Abyssal Zone	Hadal Zone
Limits in m				
World Ocean	0 m to Shelf-break	Shelf-break to 3,000 m	3,000 to 6,000 m	More than 6,000 m
Mediterranean Sea	0 to 100-110 m	100-110 to 3,000 m	3,000 to 5,093 m	-
Extension in % of the entire area				
World Ocean	7 %	15 %	77 %	1 %
Mediterranean Sea	15 %	72 %	13 %	-

Table 1. Comparison of the ranges in depth of the deep-sea zones of the World Ocean and the Mediterranean Sea (Emig & Geistdoerfer, 2004).

A further unique feature of the Mediterranean is that it is one of the few warm deep-sea basins in the world, where temperatures remain largely uniform at around 12,5-14,5°C at all depths, with high salinity (38,4-39,0 PSU) and high oxygen levels (4,5-5,0 ml, Hopkins, 1985). The constant temperature and salinity regime of the Mediterranean contrasts with the Atlantic at comparable latitudes, where temperature decreases and salinity increases with depth.

The Eastern and Western Mediterranean display important geological and biological differences. First, the Eastern Mediterranean is geologically more active, because it is a contact zone between 3 major tectonic plates: African, Eurasian and Arabian. The Western Mediterranean is relatively featureless in comparison, although still not devoid of unique environments. Biologically, the Western Mediterranean, whilst still oligotrophic by North Atlantic standards, has relatively high primary production, especially in the Gulf of Lions, due to the river Rhone runoff and wind mixing. The Eastern Mediterranean has very low primary production. The existing deep Mediterranean appears to be much younger than any other of the world's deep ocean and only a small fraction of specialized taxa exists in its deep-sea fauna. Traditionally the Mediterranean Sea is one of the most intensively investigated areas of the world in both terrestrial and coastal marine biodiversity, but it lags other regions of the world in studies of its deep-sea fauna.

2.1 Mediterranean deep sea fauna

The Mediterranean appears to be a remarkable natural laboratory for the study of the processes of recent colonization as related to the unique history of each of the two great Mediterranean basins (western and eastern) (Emig & Geistdoerfer, 2004) and, due to the presence of few endemic species, is an important centre of evolution. Its fauna is composed mainly of primitive taxonomic groups among the phyla represented, whereas a small fraction of specialized taxa exists in the deep-sea fauna. Despite its small dimensions (0,82% of the ocean surface), the basin hosts more than 7,5% of global biodiversity (Bianchi & Morri, 2000). However, this information is almost completely confined to coastal ecosystems, and data on deep-sea assemblages are still limited (e.g. Ramirez-Llodra et al., 2009).

The stable environment of the deep Mediterranean Sea permits that the biotic (e.g. trophic) factors may have a comparatively strong influence on the ecology and biology (e.g. food intake and reproduction) of deep-Mediterranean species (Madurell & Cartes, 2006). Also, the depth overlap between and the depth range inhabited by megafaunal fish and decapod crustaceans (Cartes and Carrasson, 2004) are mainly explained by trophic variables (e.g. trophic level).

The deep Mediterranean fauna displays a number of characteristics that differentiate it from other deep-sea faunas of the world's oceans (Bouchet & Taviani, 1992): *i*) the high degree of eurybathic species; *ii*) absence (or low representation) of typical deep-water groups, such as macroscopic foraminifera (Xenophyophora), glass sponges (Hexactinellida), Sea-cucumbers of the order Elasipodida, primitive stalked Sea-lilies (Crinoidea) and tunicates (Sea-squirts) of the class Sorberacea (Monniot & Monniot, 1990); and *iii*) the number of endemic species (26.6% of the Mediterranean fauna: Ruffo, 1998) declines with increasing depth, with comparatively low endemisms below 500 m (see also Fredj & Laubier, 1985).

The existing quantitative data from this basin are scarce. Several investigations have described low-abundance and low-diversity conditions of marine invertebrates in the Eastern Mediterranean (Tselepides & Eleftheriou, 1992). Scientific knowledge of deep megafaunal communities (mainly fish, crustaceans and cephalopods) was limited to the bathymetric range exploited by fishing (down to 800-1000-m) until the early 1980's, when scientific expeditions began quantitatively sampling the bathyal grounds in the Mediterranean. Such studies in the Western and Central Mediterranean have focused on the

two most abundant groups below 600 m depth: fishes (D'Onghia et al., 2004) and decapod crustaceans (e.g. Company et al., 2004). At depths below the 1500 m, there is an increase in the relative abundance of crustaceans in comparison to fish (Company et al., 2004). This change in the relative abundance of these two groups has been explained by the low food availability at greater depths and the higher adaptation of crustaceans to low energy levels (e.g. Company et al., 2004).

2.2 Mediterranean deep sea crustacean fauna

Decapod crustaceans are one of the dominant megafaunal groups in the deep-sea communities of the Mediterranean Sea (Sardà et al., 1994a). The relatively oligotrophic nature of Mediterranean waters has been presented as one of the environmental factors contributing to the high abundance of decapod crustaceans in comparison with other oceans, in which other megafaunal invertebrates, chiefly echinoderms, predominate (Tyler & Zibrowius, 1992). However, though the Mediterranean is a relatively small Sea compared with other oceans, existing data and our understanding of the continental margins at depths below 2000 m lags behind. Decapods are much more abundant than other invertebrate groups in the Mediterranean, in contrast to more productive oceans like the Atlantic, where echinoderms are the dominant invertebrate group (e.g. Sardà et al., 1994a), because these crustaceans be more competitive than other invertebrate or vertebrate megafauna in oligotrophic environments (Maynou & Cartes, 2000).

In the W. Mediterranean 28 decapod species were identified, including 6 Dendrobranchiata, 1 Stenopodidean, 7 Caridea, 2 Thalassinidea, 2 Palinura, 3 Anomura, and 7 Brachyura. The most pronounced qualitative changes in the fauna were recorded between 1000 and 1200 m and at around 2000 m. The bathyal decapod fauna mainly composed by species belonging to the families Crangonidae, Galatheidae and Geryonidae, and the genera *Nematocarcinus* and *Stereomastis*. In addition to this the tropical species *A. antennatus*, *AcanthePHYRA eximia*, and *Plesionika acanthonotus* are widely distributed and frequent in the deep western Mediterranean (Cartes, 1993b). Thirty nine decapod species have been reported in the Eastern Ionian Sea (E. Mediterranean), of which eight were Dendrobranchiata and 31 Pleocyemata (17 Caridea, 9 Brachyura, 3 Anomura, 1 Astacidea and 1 Palinura) (Politou et al., 2005). Concerning their depth distribution, 30 species were found in the depth zone 300-500 m, with *Parapenaeus longirostris* being the most abundant species. Of the 27 species caught in the zone 500-700 m, *A. foliacea* and *Plesionika martia* were the most abundant. In the zone 700-900 m, 19 species were found and *A. foliacea* with *A. antennatus* were the most numerous. Finally, the 18 decapod species encountered in the zone 900-1200 m showed low abundance, and *Sergia robusta* with *Polycheles typhlops* predominated in numbers. From the identified decapods, *AcanthePHYRA eximia*, *Philoceras echinulatus* and *Pontophilus norvegicus* were mentioned for the first time in the E. Ionian Sea. Some other species, such as *AcanthePHYRA pelagica*, *Geryon longipes*, *Munida tenuimana*, *Paromola cuvieri*, *Parthenope macrochelos*, *Pasiphaea multidentata*, *Plesionika narval*, *Polycheles typhlops*, *Sergestes arachnipodus* and *Sergestes arcticus* have been reported for the area only in the gray literature.

3. Aristeidae: Distribution and particular hydrological conditions

In updated systematic approaches (Pérez-Farfante & Kensley, 1997) both deep-sea red shrimps - *A. antennatus* and *A. foliacea* - are the only Mediterranean representatives of the Aristeidae

family (superfamily Penaeoidea, Order: Decapoda, Sub-order: Dendrobranchiata). The species of the family (*Aristaeomorpha*, *Aristeus* and *Plesiopenaeus*), all large-size commercial shrimps, occur in deep water off the continental shelf. Important morphological characteristics of both species are i) light exoskeletons and long pleopods suggesting good swimming ability; ii) secondary sexual dimorphism concerning body size and the rostrum; and iii) an open thelicum. The spermatophores are larger in *A. antennatus*, in relation to a greater fecundity: in fact the females of *A. antennatus* produce about four times more eggs than *A. foliacea* females of the same size (Orsi Relini & Semeria, 1983). The life history of the two species therefore begins with a very different energy budget and probably body development.

3.1 *Aristaeomorpha foliacea*: Distribution and importance

The giant red shrimp or deep-sea red shrimp *A. foliacea* (Risso, 1827) is a species of a very wide geographical distribution in the world. It occurs in the Mediterranean Sea and the eastern Atlantic, the western Atlantic, the Indian Ocean and the western Pacific from Japan to Australia, New Zealand and the Fiji Islands (Pérez Farfante & Kensley, 1997) Gracia et al. (2010) recently explored deep waters off the Yucatan Peninsula in Mexico and showed that *A. foliacea* represents a potential fishing resource. Nowadays, *A. foliacea* constitute a valuable deep shrimp fishery off the south-eastern and southern sectors of the Brazilian coast (Dallagnolo et al., 2009). The giant red shrimp has been recently found in large quantities in the Colombian Caribbean Sea (Paramo & Ulrich, in press) (Figure 3).

In the Mediterranean, the species is of great economic interest and, together with *A. antennatus* (Risso, 1816), represents the main target species of the slope trawl fisheries down to 800-1000 m (Demestre, 1994; Ragonese et al., 1994a,b; Sardà & Cartes, 1994b; Matarrese et al., 1997). This species is heavily exploited in Western Mediterranean, and is currently fished in the Central Mediterranean; its stocks are pristine in the Eastern Mediterranean (Bianchini & Ragonese, 1994; Papaconstantinou & Kapiris, 2003; Gönülal et al., 2010) and its exploitation is not yet been developed.

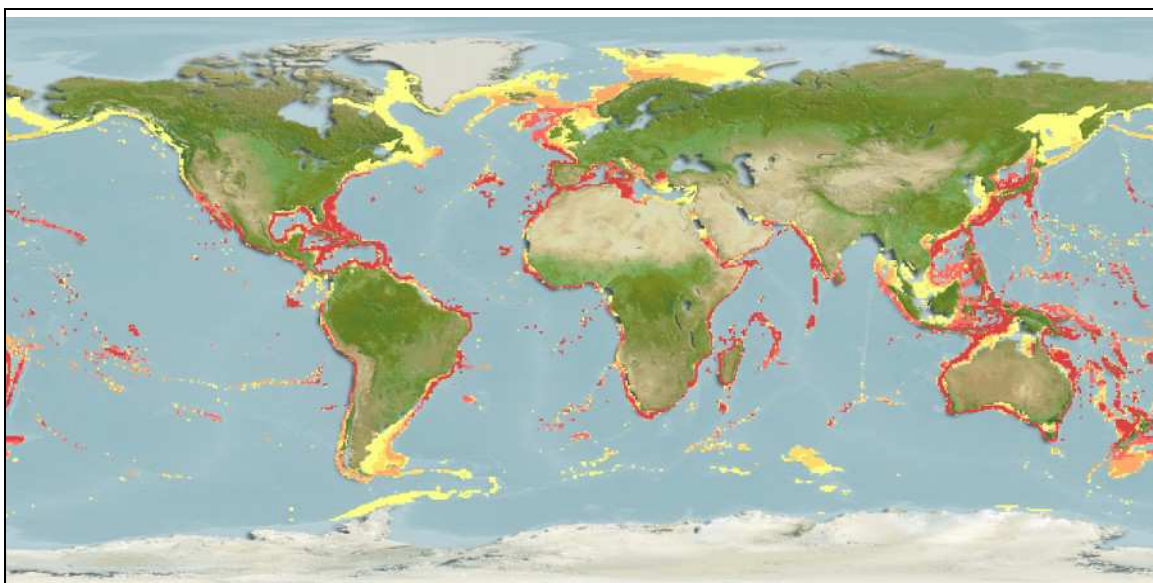


Fig. 2. Geographical distribution of *A. foliacea* (Source: <http://www.aquamaps.org/receive.php>).

The economic importance of the giant red shrimp in the Mediterranean enhanced the scientific interest of the study and evaluation of its stocks. Most scientific information on *A. foliacea* comes from the central Mediterranean, where the species is relatively abundant and exploited by the commercial fishery (e.g. D'Onghia et al., 1998). It concerns its biology (e.g. D'Onghia et al., 1994; Levi & Vacchi, 1988; Mura et al., 1997), ecology (e.g. Ragonese et al., 1994a) and fisheries (e.g. Ragonese, 1995; Matarrese et al., 1995). In the eastern Mediterranean (Greek waters), knowledge of the species was recently obtained. Some information on its distribution (Kallianiotis et al., 2000; Kapiris et al., 2001c), morphometry (Kapiris et al., 2002; Kapiris, 2005) and biology (Kapiris et al., 1999; Kapiris & Thessalou-Legaki, 2001b, 2006, 2009; Papaconstantinou & Kapiris, 2003), feeding (Kapiris et al., 2010) and fishery (Mytilineou et al., 2006) appeared in the literature. According to the present state of knowledge the species depth distribution ranges between 123 and 1047 m, with a maximum abundance from 400 to 800 m in most areas. The maximum depth of occurrence was found to be 1100 m for the whole Mediterranean basin (Politou et al., 2004).



Fig. 3. Specimens of *A. foliacea* (Source: <http://www.google.gr>).

3.2 *Aristeus antennatus*: Distribution and importance

During the last twenty years a variety of aspects of the blue-red deep water shrimp (*A. antennatus* Risso, 1816) (Figure 4) have been studied in detail in the western, central and eastern Mediterranean Sea, such as fisheries (e.g. Demestre & Martín, 1993; Bianchini & Ragonese, 1994; Sardà et al., 1998; 2003; Papaconstantinou & Kapiris, 2001; D'Onghia et al., 2005), biology (e.g. Kapiris & Thessalou-Legaki, 2001a, 2006, 2009; Kapiris et al., 2002; Kapiris & Kavvadas, 2009; Matarrese et al., 1997; Sardà & Cartes, 1993; Mura et al., 1998; Follesa et al., 1998; Orsi Relini & Relini, 1998; Sardà et al., 1998), ecology (e.g. Sardà & Cartes, 1997; Cartes & Maynou, 1998; Kapiris et al., 1999; Kapiris & Thessalou-Legaki, 2011), and physiology (e.g. Company & Sardà, 1998; Puig et al., 2001).

In the Mediterranean, this important commercially and biologically species may be fished from depths of 80 m along the Algerian coast at night (Nouar, 2001), with more abundant distribution between 400 m and 800 m in Tyrrhenian waters (Aquastudio, 1996) (Figure 5). Its eurybathic distribution ranges from 100 and 150 m to nearly 1000 m in the western Ionian Sea (south Italy, Relini et al., 2000), down to 800 in the eastern Ionian (Papaconstantinou & Kapiris, 2001) and 900-1000 m off Catalonia (Demestre & Martín, 1993; Sardà et al., 1998).

Nevertheless, experimental catches (Sardà et al., 2004) have been made down to a depth of 3300 m. This broad depth distribution range for this species has led to a number of hypotheses concerning its ecology and possible relationships between the exploited populations on the upper and middle slope and the non-exploited populations dwelling deeper on the lower slope (Sardà et al., 2003). Its biology (reproduction, sex-ratio, feeding habits, and population dynamics and fisheries) is relatively well known down to 800 m, where fishery occurs.



Fig. 4. Female and male individual of *A. antennatus* (Source: <http://cobmedits2011.wordpress.com/produccion-scientifica/evaluaciones>)



Fig. 5. Geographical distribution of *A. antennatus* (Source: <http://fishbase.sinica.edu.tw/slp/SpeciesSummary.php?group=All&ID=ITS-96062>).

An increasing abundance gradient from the western to the eastern Mediterranean is confirmed by several previous works for these both deep-sea red shrimps. The abundance of *A. foliacea* increases gradually eastwards, from the Tyrrhenian Sea to the Straits of Sicily and the waters around Greece, where it becomes more abundant than *A. antennatus* (Politou et al., 2003). Different hydrological conditions (i.e. temperature and salinity) between the westernmost and the easternmost areas have been reported to affect the species distribution (Relini & Orsi Relini, 1987). *A. foliacea* is considered to be linked to warmer and more saline water masses than the other deep Sea shrimp *A. antennatus* (Ghidalia & Bourgeois, 1961). Furthermore, the eastern Mediterranean deep water transient (Klein et al., 1999) may play a role in the increased abundance of *A. foliacea* in the eastern Ionian Sea, since this event is associated with a significant upward nutrient transport, which is most pronounced in the eastern Ionian Sea, and may result in greater biological productivity.

4. Diet studies on Aristeids mainly in the E. Mediterranean – The aim of this study

Both aristeids present an increased diversity in their diet (Burukovsky, 1972; Lagardère, 1977; Relini Orsi & Wurtz, 1977; Cartes, 1994, 1995; Gristina et al., 1992; Maurin & Carries, 1968; Chartosia et al., 2005). Brian (1931), for the first time, has studied the alimentary habits of *A. foliacea* and *A. antennatus* in the Ligurian Sea and stressed the big diversity of prey types consumed by the two shrimps (e.g. pelagic, benthic and benthopelagic organisms). In the Ionian Eastern Sea the diet and the feeding habits of both aristeids have been studied in details (Kapiris & Thessalou-Legaki, 2011; Kapiris et al., 2010).

The object of this chapter is to provide a detailed description of the feeding habits of both deep-water red shrimps in the Eastern Ionian, in relation to Season, size and sex. New information concerning its feeding patterns provides greater insight concerning the population ecology of these important and unexploited resources of the Greek Seas. In addition, such data could serve in the comparison of its life history traits along the Mediterranean.

4.1 The study area

Few studies have been carried out about the dominant demersal fish species found on the upper-middle slope (between 473 and 603 m) in the Ionian Sea (e.g. D'Onghia et al., 1998; Kallianiotis et al., 2000; Labropoulou & Papaconstantinou, 2000; Madurell et al., 2004). The results of those studies indicated that the Ionian demersal ichthyofauna is similar to the other eastern Mediterranean areas. Dominant species in the eastern Mediterranean, such as *H. mediterraneus*, and *C. agassizi* which are plankton feeders, are rare (or absent) in the Catalan Sea (Stefanescu et al., 1994). Macrofauna from the eastern Mediterranean decrease in biomass below 400m and there is a significantly lower biomass of meiofauna than in the Western Basin (Tselepides & Eleftheriou, 1992; Danovaro et al., 1999). These low levels of benthos biomass may reinforce the dominance of top predators feeding on planktonic resources in the Ionian Sea.

Exploratory sampling of *A. foliacea* and *Aristeus antennatus* took place along the south coast of the Greek Ionian Sea, between Zakynthos Island and Peloponnisos Peninsula (Figure. 6). A total of 92 hauls were taken during 12 experimental trawl survey cruises on a monthly

basis (December 1996–November 1997). Samples were collected by the commercial trawler Panagia Faneromeni II (26 m in length, 450 HP) using a net with a cod-end mesh size of 18 mm from knot to knot. The results of the feeding habits and diet of both aristeids in the Eastern Ionian are given below.

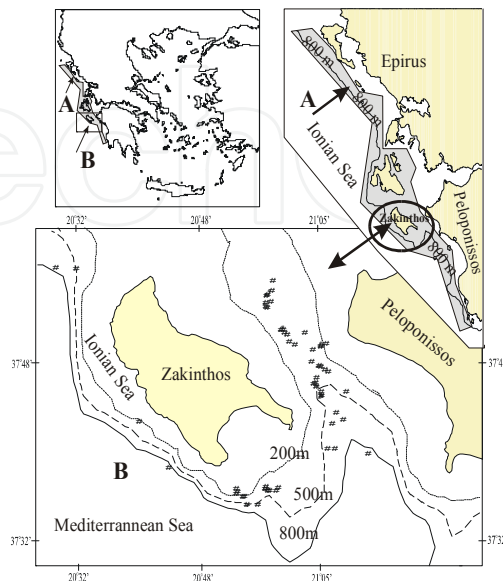


Fig. 6. Study area in the Eastern Greek Ionian Sea

4.2 *foliacea's* feeding habits

4.2.1 Feeding activity and food quality

The highly diversified diet observed in *A. foliacea* is typical of bathyal penaeoideans in the Western Mediterranean (Cartes, 1995). The feeding activity of *A. foliacea* in the Eastern Ionian Sea was examined studying the stomach fullness according the equations (i) wet food weight (g) per 100 g shrimp wet weight [% body weight (BW) Wet = (SWW/BW) x 100] and (ii) dry food weight (g) per 100 g wet weight [%BWDry = (SWD/BW) * 100] (Héroux & Magnan, 1996). The nutritional quality (food quality) of the preys has been estimated by two ways: (a) % dry weight (DW) = (SWD/SWW) 100 and (b) % ash free dry weight (AFDW) = (AFDW/SWD) x 100, where SWW=stomach wet weight, g, SWD= stomach dry weight, gr after 24 h of oven drying at 70° C), ash-free dry weight (AFDW; as loss on ignition at 450° C for 3 h) and BW is the body weight. All the weights were measured to an accuracy of 0.0001 g). The food quality indices are a measure of total organic matter and form a better estimation of food value than wet weight, which includes substantial amounts of inorganic material (Hiller-Adams & Childress, 1983). The stomach fullness of *A. foliacea* varied seasonally in both sexes and both fullness indices (%BW Wet, %BW Dry) were significantly higher in females than in males for each Season. The maximum values of %BW Wet in both sexes occurred in winter and the minimum in spring.

Diet quality (%BW Dry and %AFDW) also differed significantly among Seasons for both sexes of *A. foliacea*. In general, few significant differences in food quality were detected between males and females for each Season. Males and females of *A. foliacea* presented the highest values of both quality indices in spring and the minimum in winter.

The feeding habits of this decapods identified in the Ionian Sea are generally comparable to those reported in other regions of the Mediterranean, such as in the Catalan Sea (Cartes, 1995), Sicilian Channel (Gristina et al., 1992) and Aegean Sea (Chartosia et al., 2005). Any difference observed in the whole Mediterranean, such as food diversity, different food categories and mean number of prey could be due to bottom morphology (Cartes 1995) and to the oligotrophic conditions of the Eastern Mediterranean. This characteristic of the Eastern Mediterranean could also explain the increased number of pelagic prey consumed by *A. foliacea* compared to the western part of the basin (Cartes, 1995). The considerably higher water temperature of the Eastern Mediterranean (Politou et al., 2004) may also play a role, resulting in a higher metabolic rate of this species, in comparison with those from the western part of the basin.

Trophic diversity (H' , Shannon-Wiener index) varied slightly among Seasons in both sexes (Figure 7) and no statistically significant differences were established between sexes. The maximum diversity (3.00 and 3.04 for males and females, respectively) and mean number of prey items (2.9 and 3.1 for males and females, respectively) were found in summer for both sexes of *A. foliacea*.

The observed low number of empty stomachs [(number of empty stomachs per number of stomachs examined) * 100] (Hyslop, 1980) in the present study, ranging from 4,5 to 18,1%, indicating either a high feeding rate or slow digestion rate, could be explained by their high metabolic rates. The lowest proportion of empty stomachs of *A. foliacea* was found in spring for both sexes, followed by summer. In contrast, the highest number of empty stomachs was found in autumn for females and summer for males.

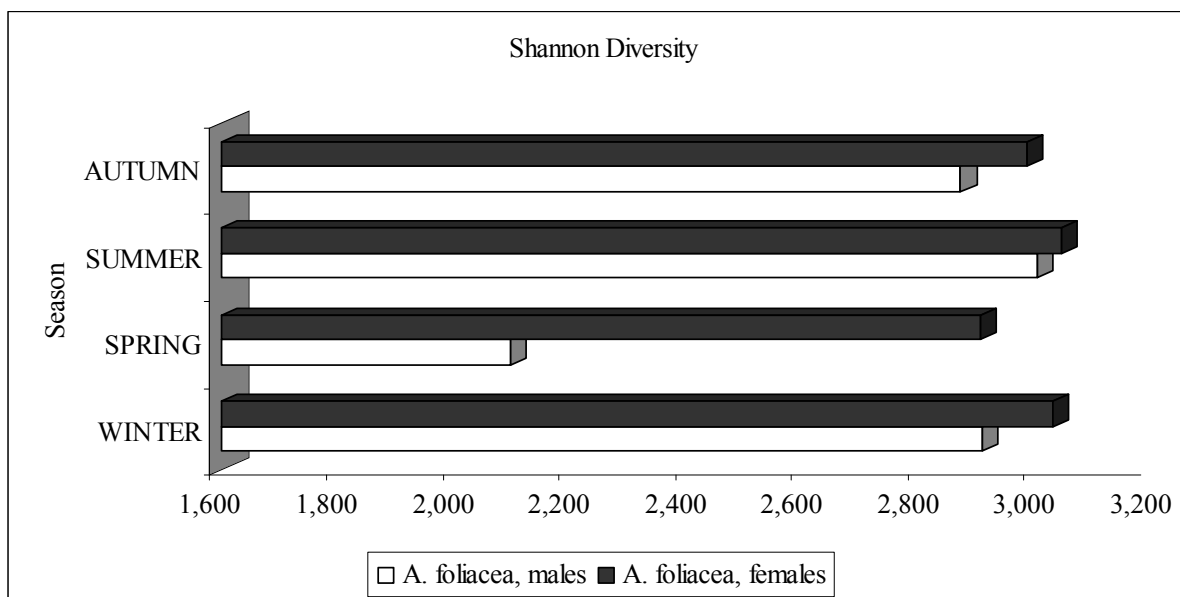


Fig. 7. Diversity index (H' , Shannon-Wiener index) values for *A. foliacea* per sex and season in the Ionian Sea.

In general, a decrease in diversity and mean prey items with increasing overlap was observed. In the Eastern Ionian Sea, the giant red shrimp fed on a greater proportion of pelagic resources and prey with a good swimming ability, such as the natantian decapods,

and to a lesser extent on benthic prey, indicating that this shrimp is an active and effective predator of the bathyal zone in the Eastern Mediterranean. The characteristic of its active predation could be also confirmed by the very low abundance of infaunal and epibenthic prey (e.g. polychaetes, bivalves and gastropods) in the stomachs of this species. The increased abundance of fishes and cephalopods in their foreguts most probably reflects the great scavenging ability of this species. In any case, this does not exclude the possibility that this species feeds actively upon fishes and cephalopods.

4.2.2 Food habits in relation to sex, season and size

The diets of both sexes of *A. foliacea* consisted of 60 different prey categories (most as species-level prey categories). The preys belonged chiefly to three major groups: (i) crustaceans – particularly decapods, reptantia (anomurans, brachyurans), amphipods, euphausiids, ostracods, copepods, mysids, tanaidaceans, cumaceans, (ii) cephalopods and (iii) fishes. These three prey categories constituted 72–82% of the relative abundance and total occurrence for males and 70–88% of the relative abundance and the total occurrence in females. The most dominant natantians found were the nektobenthic *Plesionika martia*, *Plesionika heterocarpus* and *Plesionika giglioli*, followed by *Pasiphaea sp.*, *Sergestes sp.* and *Solenocera sp.* Some appendages from *Aristeus antennatus* were also found mainly in female *A. foliacea*. These findings could be accidental, as they were found in the sampling stations where both species coexisted and, thus, some body appendages could have been destroyed and mixed during the net tow (net feeding). It is also possible that the smaller individuals of each species were consumed by larger adults of the other, due to their voracious character, but further study of this hypothesis is required. Among cephalopods, the dominant species were *Abraliopsis pfefferi*, *Pyroteuthis margarifera* and *Abralia veranyi*. For fishes, specimens of Myctophidae and Macrouridae were the most abundant in the foreguts.

Only a partial differentiation in the feeding behaviour, in terms of both diet composition and feeding activity, was observed between sexes of *A. foliacea*. In general, both sexes fed upon natantian decapods, particularly *Plesionika spp.*, *Sergestes sp.*, *Pasiphaea sp.*, and fishes throughout the year, while ‘other crustaceans’ and polychaetes were ingested on a secondary basis. The consumption of the same prey items, but in different abundance and occurrence, may be attributed to sexual dimorphism and to size difference between the sexes.

In general, the existence of regular Seasonal rhythms in the feeding activity of deep water species is related mainly to Seasonal fluctuations in various factors including the abundance of their prey, depth, local geographical characteristics, submarine canyons, bottom type, Seabed features, Seasonal horizontal or diurnal vertical migrations, etc. (Cartes 1993, 1998). In the Eastern Ionian Sea the Seasonal feeding habits of the giant red shrimp seem to be related to reproduction, and perhaps to other biological processes, and food availability.

High observed values of trophic overlap between Seasons for both sexes indicated that Season is not the main factor affecting the diet of deep-water shrimps in the Eastern Ionian Sea. In spite of this, most feeding activity values (empty stomachs, quality indices, mean number of prey items found into the stomachs, diversity index) support the finding that feeding activity increased during spring-summer for both sexes. This increase could be attributed to the increased reproductive activity (gonad maturity, egg-laying) observed in this period (Papaconstantinou & Kapiris 2001, 2003). In addition, copulation begins at the

end of winter and by spring almost all females are inseminated (Kapisiris, 2004). The minimum value of the stomach fullness in spring, in combination to the highest food quality value and the lowest vacuity index in females in the same Season, suggests that egg maturation is connected to the feeding habits of *A. foliacea*. During winter, *A. foliacea* had the highest stomach fullness, but with decreased food quality. This increase of food consumption by the giant red shrimp of the Ionian Sea during the pre-reproductive period has also been observed in *A. antennatus* off the Balearic Islands. Increased feeding rates could be the main reason for its egg development and could allow earlier gonad maturity (Cartes et al., 2008a).

Besides the Seasonal feeding adaptation to the biological requirements (reproductive process), food availability also plays an important role for these species in the Eastern Ionian Sea. The highest densities in the suprabenthic fauna (mysids, cumaceans, amphipods, isopods, tanaidaceans) have been observed during spring, but zooplankton (chiefly copepods, ostracods and chaetognaths) were more abundant in summer and autumn. Such fluctuations in food availability have also been shown in the diets of both sexes of *A. foliacea* in this study. Thus, the diet of the giant red shrimp probably reflects localized forage assemblages rather than a preference for specific items.

The size-related changes in diet composition are an important factor in determining ecological relationships of marine organisms during their life span. Comparison of diet composition, dietary diversity, and feeding activity among small, medium and (only for females) large individuals reveals that this decapod undergoes slight changes in feeding habits with increasing body size, as well as gonad maturity, in the Eastern Ionian Sea. Small males and females (immature individuals) consumed fewer prey due to their smaller stomachs, with more frequent occurrence of epibenthic prey in their foreguts. Larger, mature individuals of both sexes are more efficient predators due to their greater swimming ability and larger mandibles. A positive trend of ingesting larger prey with increased size was observed only for females. This is the first time where this gradation, probably due to the population structure and to morphological variation among size classes and sexes, has been observed for *A. foliacea*. In general, somatic growth and gonad development induce a change in this species' feeding behavior as the body grows an increase in the mean weight of prey and a decrease in the mean number of prey items per stomach was obvious. However, almost the same prey occurred in the stomachs of small, medium and large specimens, but in different proportions

4.3 *Aristeus antennatus*' feeding habits

4.3.1 Feeding activity and food quality

A differentiation has been presented in *A. antennatus* diet according to the depth in the western Mediterranean (Cartes, 1994), the feeding time (Cartes, 1993a) and the daily consumption of food (Maynou & Cartes, 1997, 1998; Cartes & Maynou, 1998). The diet of *A. antennatus* changed as a function of depth at around 1000 m depth in the Catalan Sea, as a function of Seasonality influences by planktonic prey in deeper zones and by possible nocturnal movements upward along the slope canyons (Cartes, 1993a, 1994; Cartes et al., 2010). The importance of spatial patterns in its diet and feeding habits and the main environmental variables controlling these trophic aspects has been studied by Cartes et

al.(2008b) in Western Mediterranean. In the whole E. Mediterranean, the feeding habits of *A. antennatus* have been studied in detail in the Ionian (Kapiris & Thessalou-Legaki, 2011) and the Aegean Sea (Chartosia et al., 2005).

The observed low number of empty stomachs in the Greek Ionian (mean value of the empty stomachs in males was 6,53 and for females was 8,54) could be explained by their high metabolic rates (Company, 1995). Significant statistical differences amongst the Seasonal medians of both fullness indices were found [%BW Wet (for both sexes) and %BW Dry (only in females)]. The maximum values of %BW Wet were determined in winter in both sexes and the minimum in spring. Both fullness indices were statistically higher in females than those of males (Figure 8).

Significant statistical differences amongst the Seasonal medians of both indices of food quality (%DW, %AFDW) were established only for females. Females presented a lower value of %DW and higher of %AFDW than males, in spring, while their highest values of both quality indices were found in spring (Figure 8).

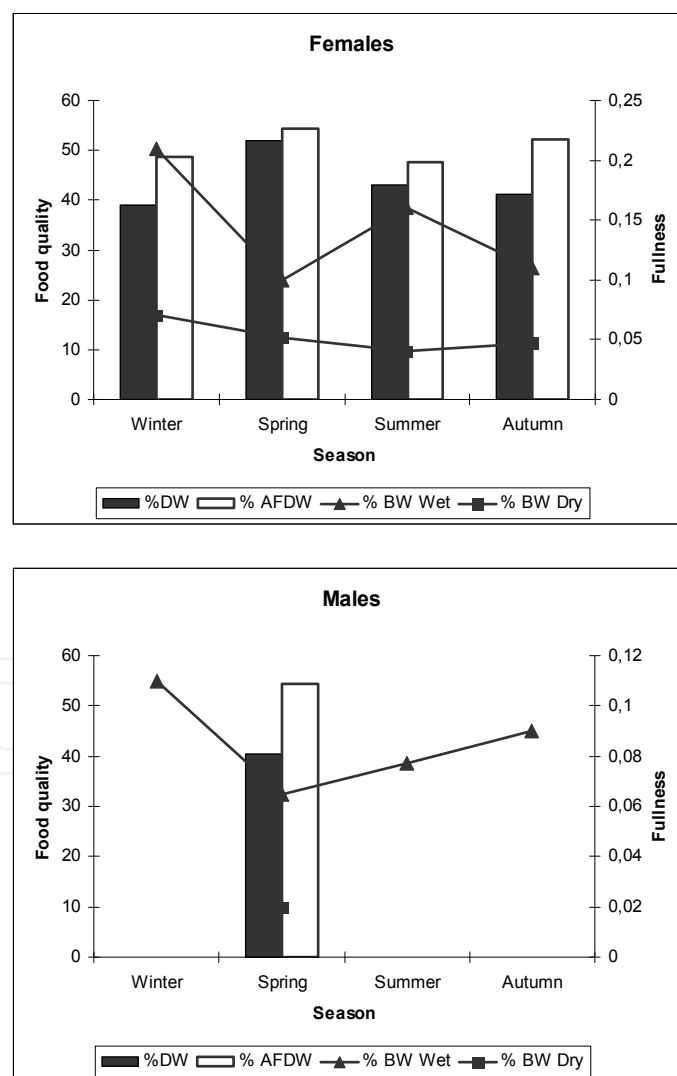


Fig. 8. Seasonal values of stomach fullness and food quality of both sexes of *A. antennatus* in the Greek Ionian Sea.

The diet of *A. antennatus* both sexes consisted of 54 prey categories. These prey items belonged mainly to smaller crustaceans (e.g. natantian decapods, *Plesionika sp.*, *Sergestes sp.*, euphausiids, tanaidaceans), molluscs primarily gastropods, bivalves, polychaetes (Eunicidae, Spionidae, and Nereididae), chaetognaths and, to a lesser extent, fishes. The above prey categories consisted of 71–82% of the relative abundance and total occurrence for males and 61–81% of the relative abundance and the total occurrence in females. Its diversified diet in the present study area consists of increased endobenthic and epibenthic invertebrates and includes organisms that are related with the Seabed, nekton and decapods. This species is among the few megabenthic predators whose diet is mainly based on benthos in the deep Mediterranean (Cartes & Carrassón, 2004). The increased abundance of gastropods, echinoderms, polychaetes – chiefly Eunicidae, sipunculans and chaetognaths in the stomachs, confirms that this species in the Greek Ionian Sea could be considered a “slow hunter”, foraging mainly on organisms that live completely or partially buried in the substratum. The macrophyte consumption was rare in both sexes and probably reflects availability in the marine environment.

The data of the present study confirm that *A. antennatus* could be considered a less active and slower hunter than the other aristeid species (*A. foliacea*) found in the same area (Kapiris et al., 2010) and preys on detritivores or small predators occupying a lower position in the benthopelagic food chain (Maynou & Cartes, 1997). The feeding activity patterns of *A. antennatus* in the Greek Ionian Sea are, more or less, comparable to those reported in other geographical regions, such as the central (e.g. Relini & Orsi Relini, 1987; Follesa et al., 2009) or in the western Mediterranean (Cartes & Sardà, 1989; Maynou & Cartes, 1998). Apparent differences in the activity patterns should be attributed to the more oligotrophic character of the Ionian Sea (E. Mediterranean) in relation to the western one and to the bottom morphology (Cartes, 1995). The above mentioned oligotrophic character of the eastern Mediterranean could explain the presence of the increased number of some pelagic preys in its stomachs, in comparison to the western one (Cartes, 1995), but – as we said before – these preys constitute the minority comparing to the benthic ones. Some remains of the sympatric *A. foliacea* in the stomachs of *A. antennatus* and vice versa could be accidental, since they have been found in the sampling stations where both species coexisted and, thus, some body appendages were destroyed and mixed during the net tow (net feeding). It is possible that the smaller individuals of each species, due to their voracious character, can be fed by the adults of the other one. In any case, further study is necessary.

Only a partial differentiation in the feeding behaviour between sexes, in terms of both diet composition and feeding activity, is observed. Males exhibit lower values of fullness, food quality indices and evenness than females. Both sexes consume the same prey items, but in different abundance and occurrence. From the above results, a slightly higher predatory ability of females is shown. These differences could also be attributed to sexual dimorphism and to size difference between the sexes.

4.3.2 Seasonal differences

Taking into consideration the narrow depth sampling range, the estimated values of the trophic overlap indicate that, Season could not be considered as the main factor affecting the diet of blue-red shrimp in the Greek Ionian Sea, like in *A. foliacea*. Notwithstanding, some particular topics are analyzed below. The existence of regular Seasonal rhythms in the

feeding activity of deep-water species is mainly related to the Seasonal fluctuations of abundance of prey they consume, the depth, the local geographical characteristics, the submarine canyons, the type of bottom, the Seabed, the Seasonal horizontal and diurnal vertical migrations, etc. (Cartes, 1993a, 1998). In addition to this, the Seasonal changes in stomach fullness of blue-red shrimp could be possibly linked to the oceanographic processes and to the several water masses, at least in the W. Mediterranean (Cartes et al., 2008b; Maynou, 2008).

The above slight Seasonal changes in the feeding dynamics of this aristeid in the Greek Ionian Sea seem to be related mainly to their biological processes (e.g. mating and reproduction) and to the food availability. The increased values of food quality indices and diversity support the finding that feeding activity seemed to increase qualitatively – in the period spring–summer, mainly for females. In addition to this, the observed highest empty stomachs found in these Seasons, mainly for females, could be attributed to the increased volume of the gonads which press the stomach. This increase of the highly energetic diet could be attributed to the increased pre- and reproductive activity observed in this period (Kapiris and Thessalou-Legaki, 2006, 2009). As Cartes et al. (2008a) noted *A. antennatus* seemed to increase the energy intake in its diet from February to April–June in the western Mediterranean. During winter both sexes of *A. antennatus* in Greek Ionian Sea consume an increased number of prey items, having as a result the highest stomach fullness, but of decreased quality. This phenomenon could be related to the mating period which takes place in this Season (Kapiris & Thessalou-Legaki, 2006, 2009). Besides the Seasonal feeding adaptation to the biological requirements, the food availability also plays an important role for this species in the Greek Ionian Sea. Madurell & Cartes (2005) point out that, in the same study area, the suprabenthos fauna (mysids, cumaceans, amphipods, isopods, and tanaidaceans) showed the highest densities in spring, while the zooplankton fauna (chiefly copepods, ostracods and chaetognaths) was more abundant in autumn and summer. In agreement with the results of the present study, the above fluctuations of food availability are also shown in the diet of *A. antennatus*. Thus, the diet of the blue-red shrimp probably reflects localized forage assemblages rather than a preference for specific items. In addition to this, these results reinforce the opinion concerning the “accidental hunting” of *A. antennatus*.

4.3.3 Ontogenetic differences

Comparison of the diet composition, dietary diversity and feeding activity between the small size, medium size and – only in females – large size individuals reveals that this species undergoes changes in feeding habits with increasing body size and gonad maturity in the Greek Ionian Sea. Small immature individuals consume less prey, mainly epibenthic, – but of increased quality – due to their smaller stomach. Larger mature specimens of both sexes are more efficient predators because of their greater swimming ability and their larger mandibles. The positive trend between increasing females' body size and consumption of larger prey is observed could be attributed to the population structure and to the morphological characteristics of the different size classes and sexes. In general, somatic growth and gonad development induce a change of *A. antennatus* feeding behaviour in the Greek Ionian Sea: as the body grows, an increasing mean weight of prey and mean number of prey items per stomach was obvious. However, almost the same prey occurred in the stomachs of small, medium and large specimens, but in different proportions.

5. Conclusions

Our results on the feeding ecology of both deep water shrimps could be considered as primary importance for the future management of deep water assemblages, since they play an important role. Since the deep waters in the E. Ionian Sea are almost unexploited, the present data could elucidate the relationships between species in this ecosystem improving, thus, the knowledge and the trophic relationships among the species helping in their integrated management in the future.

According all the studies carried out on both decapods feeding habits, *A. foliacea* exploits different resources from those used by *A. antennatus* and, despite both shrimps have similar morphologies and size ranges, the exploitation of different resources probably both species to coexist in the same areas (Cartes, 1995). In addition to this, since both deep-sea red shrimps belonging in the same family, have an almost similar depth distribution It is expected that they have similar energy values (in terms of wet mass), water body content (K. Kapiris unpublished observations) and oxygen consumption rates (Company & Sardà 1998).

Concluding, the increased demand of the large energetic content and the food availability in the same period make us suggest that both facts could stimulate fecundity in the deep-sea blue-red shrimp in the E. Mediterranean. A similar trend has been shown for the same species in the western Mediterranean (Cartes et al., 2008a, b). Generally, energy reserves strongly affect fecundity and reproduction in fishes (e.g. Lloret et al., 2005) and have been also observed in deep-water decapods (Fanelli & Cartes, 2008).

6. References

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The book discusses the novel scientific approaches for the improvement of the food quality and offers food scientists valuable assistance for the future. The detailed methodologies and their practical applications could serve as a fundamental reference work for the industry and a requisite guide for the research worker, food scientist and food analyst. It will serve as a valuable tool for the analysts improving their knowledge with new scientific data for quality evaluation. Two case study chapters provide data on the improvement of food quality in marine and land organisms in the natural environment.

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