



Opinion Paper

On the Atlantic blue crab (*Callinectes sapidus* Rathbun 1896) in southern European coastal waters: Time to turn a threat into a resource?

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ABSTRACT

The blue crab *Callinectes sapidus* is native to the coastal waters of the western Atlantic Ocean, and along the US coasts the species supports an important fishery. The crab was introduced to Europe at the beginning of the 20th century. To date, the species is considered invasive and it has been extensively recorded in southern European waters (SEW), where it is starting to penetrate the shellfish market. Here, an integrated management strategy is proposed for the blue crab in SEW, including the Mediterranean and Black Sea and the eastern Atlantic coasts of the Iberian Peninsula. Taking as introductory examples two case studies represented by the red king crab *Paralithodes camtschaticus* and the green crab *Carcinus maenas*, a framework of key issues is reviewed, considering the double nature of the species as invaders and shellfish products. A SWOT analysis is eventually presented for *C. sapidus*, in order to perform a state-of-the-art synthesis of the proposed scenario, highlighting the potential opportunities as well as the weaknesses related with the limited knowledge of the ecological and economic impact of the species in invaded habitats. The review is concluded by an appraisal of the current trends in global and European crustacean fisheries. The ongoing expansion of *C. sapidus* might represent a useful management case study, where the need to control an invasive species and mitigate its ecological impact can be harmonized with the opportunity to value it as a fishery resource.

1. Introduction

Food webs of marine coastal habitats support crucial ecosystem services, and are currently experiencing a diversified spectrum of human pressures worldwide. Besides habitat loss and overfishing, the introduction of non-indigenous species is among the most pervasive stressors affecting coastal areas at every latitude, from polar to temperate and tropical regions (Molnar et al., 2008). In recent decades, the Mediterranean Sea and, in general, southern European waters (SEW hereafter) have experienced a dramatic increase in the frequency of introduction and rate of expansion of non-indigenous crustaceans (Nunes et al., 2014; Chainho et al., 2015). Several examples (e.g., see Katsanevakis et al., 2014 for a recent review) are available regarding the effects of some of these species on the delivery of goods and services (*sensu* Liqueite et al., 2013) in invaded ecosystems; in general, however, the ecological and economic impacts of crustaceans introduced in south

European coastal systems have scarcely been investigated.

An illustrative example of this knowledge void is provided by the Atlantic blue crab *Callinectes sapidus* Rathbun, 1896 (Brachyura: Portunidae). Native to the western coasts of the Atlantic Ocean, this species inhabits estuaries, lagoons and other coastal habitats, is euryhaline and eurythermal, and is characterized by a high fecundity and aggressive behaviour (Millikin and Williams, 1984). In native habitats, *C. sapidus* has long been recognized as an important functional component of coastal benthic food webs (Baird and Ulanowicz, 1989; Hines, 2007). In addition, it supports important fisheries in Northern and Central America (Fig. 1A and B; FAO, 2014; see also Fogarty and Miller, 2004; Kennedy et al., 2007; Bunnell et al., 2010 for the U.S.A.), with a capture production estimated in 2013 only in the United States at 74,495 tons, corresponding with a commercial and recreational asset valued at approximately US\$185 million (NOAA, 2014).

The blue crab was introduced in northern Europe in 1900 through

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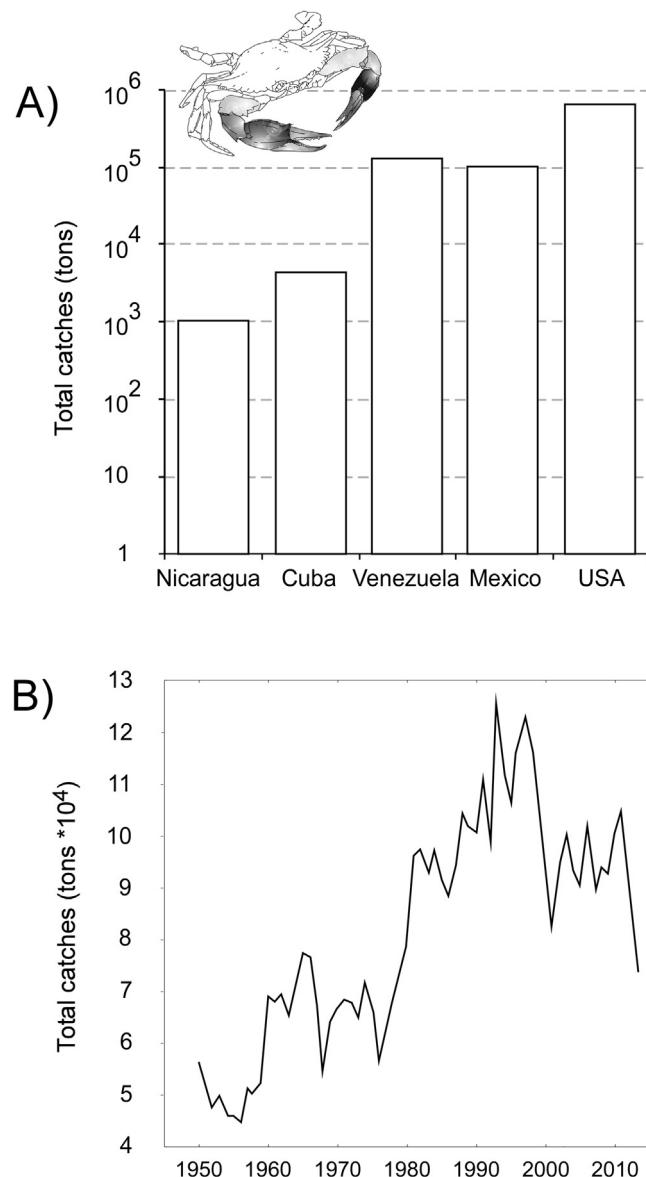


Fig. 1. Blue crab catch statistics in native areas: A) cumulative catches (in tons) of countries on the Western Atlantic in the decade 2003–2013; please note the logarithmic scale; B) temporal pattern of total catches in the same area in the period 1950–2013. Source: FAO (<http://www.fao.org/fishery/statistics/global-capture-production/en>, accessed 10/06/2016).

ballast waters; subsequently, its distribution range has progressively extended throughout the Mediterranean Sea and neighbouring waters (Nehring, 2011; Cilenti et al., 2015; González-Wangüemert and Pujol, 2016) and, to date, it is considered an Invasive Alien Species (IAS hereafter; Streftaris and Zenetos, 2006). Adverse interactions with other native crustacean species have been repeatedly suggested (Gennaio et al., 2006; Mancinelli et al., 2013a) and some negative effects on artisanal fishing activities have been episodically reported (Nehring, 2011); besides this scant information, the impact of the species on non-native coastal ecosystems is poorly known. No general capture regulations or managing strategies have been identified to date; in addition, the actual perception of fishermen and stakeholders of the impact of the species on human activities in coastal habitats has been virtually unexplored.

Here, the overarching scope is to outline an integrated management strategy of the blue crab in invaded habitats, highlighting its potential as a shellfish product in European markets for alimentary and non-alimentary purposes. The core of the study is an analysis of the

strengths, weaknesses, opportunities, and threats (SWOT) related with a commercial exploitation of the blue crab that may simultaneously translate in an effective strategy of control and mitigation of its impacts as an invasive species. Two case studies – the red king crab *Paralithodes camtschaticus* and the green crab *Carcinus maenas* – are used to identify a spectrum of key issues directly associated with an integrated management of invasive brachyurans as shellfish products. An analysis of current and future developments of crustacean fisheries at a global and European scale is also provided, indicating how a current ecological threat may, paradoxically, foster crab fisheries in SEW in the next decade.

2. The red king crab and the green crab: two illustrative case studies

In 2011, Brockerhoff and McLay (Brockerhoff and McLay, 2011) recorded 73 species of alien marine and brackish brachyurans worldwide; currently, the number is likely to be even higher as, in 2014, Klaoudatos and Kapiris (Klaoudatos and Kapiris, 2014) listed 40 species only in the Mediterranean Sea. Among others, here we focus on the red king crab *Paralithodes camtschaticus*Tilesius, 1815 and the green crab *Carcinus maenas* Linnaeus, 1758. Even though they differ in terms of biology, invasion history, native habitats, and ecological characteristics (Table A in the online information and references cited therein), they provide two highly illustrative examples of the general convergence of strategies implemented to integrate the management of a fishery resource with effective actions of control and mitigation of an invader and vice versa. In Table A, three key points are worth highlighting:

- 1) *P. camtschaticus* was deliberately introduced from native north-western Pacific waters with the explicit aim of developing a targeted fishery. The management and exploitation of established populations started almost immediately, and only afterwards their invasive nature was acknowledged. This recognition was based on information provided by a number of field and laboratory investigations, in turn motivated by a research plan funded by the Norwegian government, allowing a quantitative assessment of the ecological and economic impact of the species, and of its overall effects on the services delivered by invaded coastal habitats. Methodological approaches originally developed to manage the populations in Norwegian waters such as the identification of free-fishing zones, or three-S (size, season, sex) procedures of stock selection, are now acknowledged as effective tools of control and mitigation (Ojaveer et al., 2015);
- 2) *C. maenas* was unintentionally introduced in North America through ballast waters, and its invasive nature was recognized as early as 1998. A thorough assessment of the negative ecological and economic impacts on invaded coastal systems has been paralleled by various attempts at control and eradication, which have only been temporarily successful. Interestingly, the huge body of information collected on the ecology of green crab populations in invaded habitats constituted a potentially useful basis for starting a fishery. Indeed, some unsuccessful attempts have been made in the past decade in the USA to develop a hard-shell fishery; more recently, the Department of Fisheries and Oceans in Canada has begun experimenting with a commercial green crab fishery. The marketing features involved to make it an alimentary asset (e.g. break-even prices) are currently under evaluation (Poirier et al., 2016; St-Hilaire et al., 2016);
- 3) regardless of the species and the sequence of events characterizing its recognition by governments and stakeholders as an invader or a fishery resource, Table A emphasizes that any action of integrated management of a marine invasive crab must necessarily rely on i) detailed information on the occurrence and abundance of populations, ii) data on their connectivity, as well as on iii) robust estimations of the ecological and economic impacts on ecosystem

Table 1
Strengths, weaknesses, opportunities, and threats (SWOT) of the management of the blue crab *Callinectes sapidus* in south European waters as a shellfish resource and as an invasive species. MSFD: Marine Strategy Framework Directive (EC, 2008a).

	Strengths	Weaknesses	Opportunities	Threats
Shellfish product	<ul style="list-style-type: none"> high alimentary value recognized in both native and invaded habitats; quality control and traceability procedures defined; alternative product market chains (hard-shell, soft-shell) identified in native habitats; the species distribution in SEW is known; the high awareness of the scientific community and the general public provides updated records almost in real time; adjustable procedures and protocols standardized in native habitats for the assessment and management of stocks; high-efficiency fishing gear identified in both native and invaded habitats (e.g., Turkey); 	<ul style="list-style-type: none"> low meat yields compared with competing shellfish products; lack of quantitative information on impacts on fishing activities and other fish and invertebrate species of economic interest; lack of regulations: the blue crab is already exported across south European countries without control; 	<ul style="list-style-type: none"> new fisheries and diversification of European shellfish product markets; development of eco-sustainable fishing practices (e.g., high efficiency, selective fishing gears, control of by-catch and discards, development of targeted fishing strategies); development of standardized stock assessment procedures for crustaceans according to ICES (2015); support to alimentary commercial sectors; support to non-alimentary commercial sectors and shellfish waste management; opportunity to capitalize on positive media coverage associated with environmental protection from IAS; 	<ul style="list-style-type: none"> by-catch of other fish and invertebrate species of economic interest; blue crab populations driven to extinction by overfishing and unregulated harvesting; shellfish alimentary product characterized by a relatively short commercial life;
Invasive species	<ul style="list-style-type: none"> reference information on the functional role available for native habitats and, to a lesser extent, for SEW; growing interest of the scientific community for the ecological and economic impact of the crab in invaded habitats; non-indigenous species are included as one the descriptors of good ecological status in the MSFD; 	<ul style="list-style-type: none"> incomplete knowledge on the biology, ecology, and connectivity of blue crab populations in SEW; incomplete quantitative information on their functional impacts on invaded ecosystems; lack of information on their impacts on economic activities; no coordination and standardization of monitoring or early detection tools and procedures; no standardization of ecological impact assessment tools; 	<ul style="list-style-type: none"> once accepted as a product in fish markets, the species is no longer considered as an invasive species to be controlled, managed, and mitigated; conversion of the blue crab to productive uses provokes contrary incentives that perpetuate and spread its distribution in SEW; increased risk of ecological impact and economic damage to the fishery sector due to the diffusion of the blue crab; 	<ul style="list-style-type: none"> rise of media interest on IAS control, management, and mitigation; support the integration and coordination among south European countries on IAS management;

services, both as a nuisance for other traditional fisheries, and as a positive element as a new shellfish product. This latter aspect also requires the identification of the actual value of the invader as an alimentary product and the most rewarding strategy to market it. For the red king crab this aspect has been explicit ever since its introduction; for the green crab previous efforts have clearly indicated that a classical hard-shell, meat-yield fishery may prove to be impractical and high-priced; alternatively, soft-shell products have been proposed, on the model of the congeneric *C. aestuarii* in Italy (Cilenti et al., 2014 and literature cited; see also Glamuzina et al., 2017) or, noticeably, of *Callinectes sapidus* in the southern USA (Poirier et al., 2016; St-Hilaire, 2016).

3. Pros and cons of a blue crab management strategy: a SWOT analysis

Taking the issues highlighted for the red king crab and the green crab as guidelines (Table A), an integrated management strategy of *Callinectes sapidus* in SEW as both a shellfish product and an invasive species is proposed. Its strengths, weaknesses, opportunities, and threats (SWOT) are summarized in Table 1. In recent years, SWOT analyses have been repeatedly applied to marine fisheries (e.g., Panigrahi and Mohanty, 2012; Glass et al., 2015); criticisms have been raised since no implementation procedures are generally identified (Helms and Nixon, 2010; Clardy, 2013). Here, an effort is made to go beyond the analysis itself and propose, as far as possible, effective follow-up approaches and methodologies.

In general, the notion that, by eating invasive species humans can effectively control their abundance and mitigate their impacts, has only recently gained popularity (Clark et al., 2009; Nuñez et al., 2012). However, the assumption that the commercial exploitation of the blue crab may ultimately help in the control of its distribution and abundance – the concept at the core of the proposed strategy – has in effect already been demonstrated: human activities have strongly impacted Atlantic populations, as the considerable decline in catch observed in the period 1995–1999 (Fig. 1B) has been ascribed to overfishing (Sharov et al., 2003; Hewitt et al., 2007; Huang et al., 2015). Similarly, the reduction in the abundance of commercial stocks of the red king crab in the Barents Sea has been related with overharvesting (Table A).

A number of strengths and opportunities characterizing the proposed strategy are listed in Table 1; although, we first focus on the most unwanted, threatening consequence that may derive from starting a *Callinectes sapidus* fishery. Once accepted in south European fish markets, the crab may no longer be considered an invasive species threatening the biodiversity and stability of invaded ecosystems. The occurrence of the species may be legitimized, and the risk it represents overlooked or even ignored (Pasko and Goldberg, 2014). Furthermore, the establishment of an economically important blue crab fishery may motivate illegal efforts to set up an uncontrolled export of live specimens at a national and international scale, ultimately promoting invasion (Nuñez et al., 2012). Unfortunately, this is already a major threat at present, since Greek blue crabs are currently being exported alive and sold in Italian and Portuguese fish markets (Ribeiro and Veríssimo, 2014; Mancinelli, personal observation). Thus, even though recognized as invasive by European environmental regulations (e.g., EU, 2014), the blue crab is not subject to any control, as it is not included in the list of species of Union concern (EU, 2016). As indicated by Nuñez et al. (2012; see also Conde and Domínguez, 2015 for an example on the freshwater crayfish *Procambarus clarkii*), the effectiveness of a strategy avoiding the cultural incorporation of an IAS may depend on how the species is presented. An explicit reminder to entrepreneurs and consumers that the goal is to control the spread of an invasive species may be the key to avoiding negative consequences. To date, such an approach has been totally neglected; on the other hand, the implementation within south European countries of an

integrated management plan may provide the opportunity for the identification and standardization of marketing and export strategies for the blue crab, including, in addition, common quality control and traceability procedures.

Of the major points listed in Table 1, the most significant is related with the alimentary value of the species. As a shellfish product, the blue crab has long been valued in native areas (among others, Farragut, 1965; Thompson and Farragut, 1982), and its high alimentary quality is, to date, also acknowledged in SEW (e.g., Küçükgülmez and Çelik, 2008; Zotti et al., 2016a, 2016b). A potential weakness for the European hard-shell market may be the species total meat yield (14–16%; Mancinelli, unpublished data; Desrosier and Tressler, 1977), lower than that characterizing other crab species of economic interest such as *Paralithodes camtschaticus* (Table A, online information) or *Cancer pagurus* (25–30%; Barreto et al., 2009). A soft-shell blue crab fishery may alternatively be developed (see previous paragraph); however, it may be economically unrewarding to start a blue crab market chain – either hard-shell or soft-shell – centred on alimentary uses only. In addition, the local extinction of the species – a positive event from a conservation point of view – may represent a threat for the sustainability of the market demand (Table 1). The extraction of chitosan and astaxanthin from crabs' shells may represent an opportunity to i) support the on-going global shellfish market shift (see further in the last paragraph); ii) increase the efficiency of waste management in agreement with current European regulations (EC, 2008b) and with global trends (Ravindran and Jaiswal, 2016); iii) reduce the species-specificity of the market chain (i.e., other crustacean species of economic interest may support the demand) and iv) produce valuable compounds with wide applications in pharmaceutical, biomedical, cosmetic, agricultural, and biotechnological fields (Ambati et al., 2014; see also Demir et al., 2016; Baron et al., 2017 for recent examples on *C. sapidus*).

In SEW, the number of records of *C. sapidus* have boosted in the past few years (Mancinelli et al., 2017b), testifying its range expansion along with a growing interest from the scientific community and the general public. Overall, this information provides an advanced resolution of the current distribution of the species, constituting a preliminary, yet essential support to the implementation of a blue crab fishery. A huge body of studies from native habitats are available on the species regarding methodological approaches, field protocols, and procedures of catch data analysis for stock assessment and management, as well as on its functional role and ecology. The book by Kennedy and Cronin, (2007) represents an outstanding example of the vast literature dedicated to the species. This knowledge basis may constitute, given the appropriate adjustments and complemented with the necessary biological and ecological information, a robust support for starting management actions of blue crab stocks in SEW, as well as for integrating these efforts within a wider, environmental framework fully consistent with current EU legislation on invasive species (e.g., EC, 2008a; EU, 2014).

It is worth noting that a considerable number of quantitative studies have already been carried out on populations from Turkish waters and other invaded habitats of the Aegean and Ionian Sea (Atar et al., 2002; Atar and Seçer, 2003; Gökçe et al., 2007; Gökçe et al., 2006; Sumer et al., 2013; Türel et al., 2016; Özdemir et al., 2015; Katselis and Koutsikopoulos, 2016) providing useful information for stock management as well as on fishing gears efficiency, tailored for reducing by-catch and other negative impacts on local traditional fisheries. Indeed, small-scale, local blue crab fisheries are currently located only in these areas; for example, annual landings of 17–77 tons of blue crabs were recorded in Turkey in 2008 and 2009, respectively (Ayas and Ozogul, 2011) while 50–80 tons were landed in 2010 and 2011 in northern Greece (Kevrekidis et al., 2013).

The challenge for an effective management of the blue crab in SEW as a shellfish product is to build on these experience, expanding them at a whole-basin scale, with the strong co-operation of Mediterranean

countries (such as that initiated between Norway and Russia for the management of the red king crab) in a perspective of standardization of methods and approaches, as implemented in the past years for the EU Water Framework Directive (EC, 2000).

Of the weak points reported in Table 1, the most relevant regards the paucity of biological and ecological data on blue crab populations. Indeed, with the exception of the Mediterranean Levantine sector, a low number of studies are available that provide quantitative data on the abundance and biology of established populations. In addition, only scant attempts have been made to implement practices and approaches such as high efficiency fishing gears, or capture strategies tailored in space and time to the biological cycle of the species (e.g., selective for females: Cilenti et al., 2016).

Specifically, while data on maturity and fecundity are diverse (e.g., see Dulčić et al., 2011 for Croatia, Cilenti et al., 2015 for SE Italy), other crucial biological information on populations necessary for stock assessment, such as abundance or natural mortality are lacking, in particular outside the eastern sectors of the Mediterranean Sea (but see Mancinelli et al., 2013a and Carrozzo et al., 2014 for studies providing quantitative information on seasonal abundance patterns).

These knowledge voids currently hinder the development of selective capture procedures (e.g., 3-S strategies), as well as the identification of areas characterized by specific capture regimes that may respond to the market demand and, as already tested with the red king crab (Table A), contribute towards reducing the spread of the species.

The scarcity of biological data is echoed by a paucity of quantitative information on the ecological and economic impacts on the goods and services of invaded ecosystems. Table A clearly suggests that for both the red king crab and green crab a wealth of biological and ecological data have been collected on invasive populations in order to identify and refine effective management (as shellfish products) and control (as invasive species) actions. No similar data are available for the blue crab in SEW. Only recently, an estimation of its invasion potential based on decision support tools has provided a retrospective assessment of its high risk of invasiveness (Perdikaris et al., 2016), while stable isotope studies have only indirectly suggested a significant impact on the trophic structure of invaded benthic communities (Mancinelli et al., 2013a, 2016, 2017a).

In addition, preliminary information (period July–October 2015) on the impact on fisheries perceived by Ionian and Aegean Greek fishermen has been assessed by means of a questionnaire, indicating that where blue crab populations have reached maximum abundances in the last decade (i.e., Vistonida lagoon in North Aegean Sea), considerable negative effects on fishing activities are recognized by local populations (Katselis, unpublished data).

Independently of whether the blue crab is considered as a product or an invader, a further weakness is represented by the lack of information on connections between populations. The spatial and genetic structure of blue crab populations in native Atlantic habitats has been widely investigated (McMillen-Jackson and Bert, 2004; Yednock and Neigel, 2014; Lacerda et al., 2016), indicating a generally low inter-population gene flow and high variability in genetic composition at extremely small spatial and temporal scales. However, these issues have been completely overlooked in SEW. A further unexplored aspect regards parasites and pathogens. Infectious disease agents can magnify or buffer the impact of an IAS depending on their relative effects on its fitness and on that of indigenous competitors (Dunn and Hatcher, 2015; Goedknegt et al., 2015). In the USA the green crab has been demonstrated to experience reduced parasite diversity and prevalence in its invasive range, and the greater biomass density seen in invasive populations has been attributed to an “enemy-release” effect (Torchin et al., 2001; see also references in Table A). In fact, given its economic value, great attention has been given to the identification of pathogens in the blue crab in the USA (Messick, 1998; Nagle et al., 2009; Flowers et al., 2015). In SEW information is scant, being mostly limited to epiparasites (i.e., cirripedia: Zenetos et al., 2005), while there have

been unconfirmed claims regarding the occurrence of parasitic dinoflagellates of the genus *Hematodinium* in blue crabs from the Ionian Sea (Mancinelli et al., 2013b). Future research is needed to specifically address the analysis of epi- and endoparasites and pathogens in SEW blue crabs, and to clarify the potential for transmission to native crustacean species.

4. Opportunities and future prospects in crab fisheries

The opportunities listed in Table 1 indicate that the implementation of a management plan of the blue crab in invaded habitats may provide an unprecedented support to the integration and coordination of common policies focused on both fisheries and IAS management among south European countries.

In 2011, the European Union adopted a new strategy to halt the loss of biodiversity and degradation of ecosystem services by 2020, to restore them as far as possible, and to contribute to averting global biodiversity loss (EC, 2011). Among the six main targets of the strategy, target 4 commits the EC to reform the Common Fisheries Policy (CFP) so that ecological impacts are reduced, including impacts on marine ecosystems, while target 5 commits the EC to combat invasive alien species through preventing their establishment and through control and eradication. Regarding target 4 it is worth noting that in the CFP the management of alien species is addressed only for aquaculture (EU, 2011; see also EU, 2013) and no other related issues are considered further. As outlined in Table 1, the implementation of the management strategy herein proposed may constitute an outstanding opportunity to i) widen the aims and the spectrum of practical policy actions of the CFP in terms of alien species, and to ii) provide a bridging framework of methodologies, procedures, and protocols with other EU environmental legislations focused on invasive alien species (e.g., Regulation 1143/2014, EU, 2014).

The most unique opportunity, however, may be related with the current and future shifts in European and global shellfish markets. The exploitation of crustacean fisheries has gained in relevance worldwide (Fig. 2; FAO, 2014; see also Anderson et al., 2011). It is worth noting that the exploitation of European crustacean fisheries has not varied accordingly: in the Mediterranean Sea, for example, total captures almost doubled in the period from 1970 through 1990; subsequently, however, negligible increases occurred (Fig. 2). Cultural reasons, local dietary habits, and market strategies have contributed to maintaining finfish species as the favoured seafood when compared to shellfish (Vasilakopoulos and Maravelias, 2015). Additional limitations are represented by the lack of attractive and valuable large-sized species, in particular for brachyurans: among the species considered in Green et al. (2014) the edible crab *Cancer pagurus* is the only valuable species found in European fish markets. Future developments of the Mediterranean demersal and coastal fisheries are nonetheless expected to mirror the shifts already observed on a European scale; given the current critical conditions of most of the stocks of crustacean species of commercial interest (Vasilakopoulos and Maravelias, 2015), new fishing grounds are needed and new species are to be exploited.

The current invasion of the blue crab offers the possibility of identifying successful policies of exploitation and marketing for a shellfish product whose economic value has already been recognized outside Europe. The management and control costs in invaded habitats may ultimately be reverted into profits for local populations, while the ecological impact of the invader may be greatly reduced, and partially converted into an enhancement of the ecosystem goods and services provided by coastal habitats.

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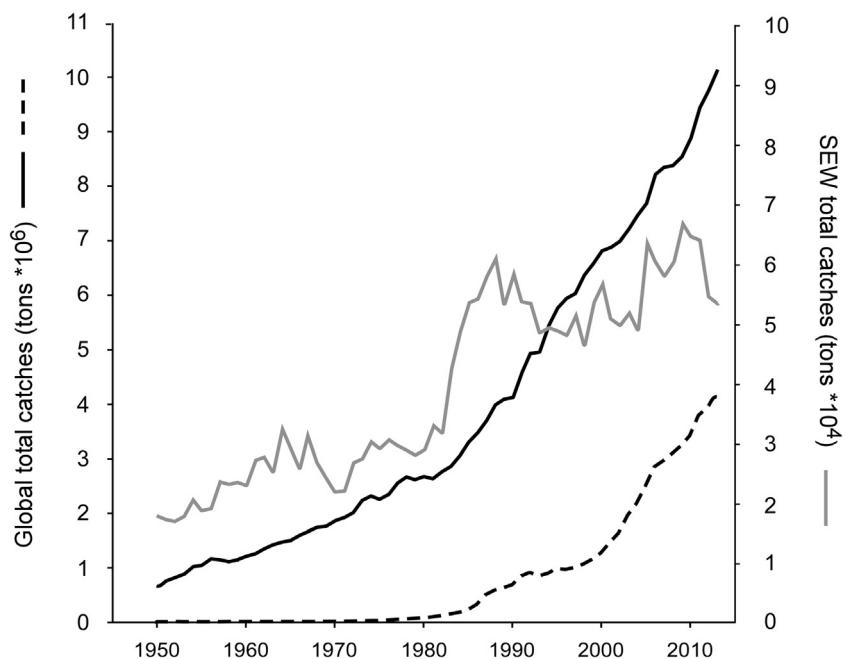


Fig. 2. Temporal patterns of variations in crustacean fishery catches: data on global wild catches (continuous line), global aquaculture (dashed line) and total catches in south European waters (including Portugal, and the Mediterranean and Black Sea: grey line) are reported. Please note the different scales on y-axes. Data cover the period 1950–2013.

Source: FAO (<http://www.fao.org/fishery/statistics/global-capture-production/en>, accessed 10/06/2016).

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.fishres.2017.05.002>.

References

- Ambati, R.R., Phang, S.M., Ravi, S., Aswathanarayana, R.G., 2014. Astaxanthin: sources, extraction, stability, biological activities and its commercial applications – a review. *Mar. Drugs* 12, 128–152.
- Anderson, S.C., Flemming, J.M., Watson, R., Lotze, H.K., 2011. Rapid global expansion of invertebrate fisheries: trends, drivers, and ecosystem effects. *PLoS One* 6, e14735.
- Atar, H.H., Seçer, S., 2003. Width/length-weight relationships of the blue crab (*Callinectes sapidus* Rathbun 1896) population living in Beymelek lagoon lake. *Turk. J. Vet. Anim. Sci.* 27, 443–447.
- Atar, H.H., Ölmez, M., Beckan, S., Seçer, S., 2002. Comparison of three different traps for catching blue crab (*Callinectes sapidus* Rathbun 1896) in Beymelek Lagoon. *Turk. J. Vet. Anim. Sci.* 26, 1145–1150.
- Ayas, D., Ozogul, Y., 2011. The effects of sex and seasonality on the metal levels of different muscle tissues of mature Atlantic blue crabs (*Callinectes sapidus*) in Mersin Bay, north-eastern Mediterranean. *Int. J. Food Sci. Technol.* 46, 2030–2034.
- Baird, D., Ulanowicz, R.E., 1989. The seasonal dynamics of the Chesapeake Bay ecosystem. *Ecol. Monogr.* 59, 329–364.
- Baron, R.D., Pérez, L.L., Salcedo, J.M., Córdoba, L.P., Sobral, P.J.d.A., 2017. Production and characterization of films based on blends of chitosan from blue crab (*Callinectes sapidus*) waste and pectin from Orange (*Citrus sinensis* Osbeck) peel. *Int. J. Biol. Macromol.* 98, 676–683.
- Barrento, S., Marques, A., Teixeira, B., Anacleto, P., Vaz-Pires, P., Nunes, M.L., 2009. Effect of season on the chemical composition and nutritional quality of the edible crab *Cancer pagurus*. *J. Agric. Food Chem.* 57, 10814–10824.
- Brockhoff, A., McLay, C., 2011. Human-mediated spread of alien crabs. In: Galil, S.B., Clark, F.P., Carlton, T.J. (Eds.), *In the Wrong Place – Alien Marine Crustaceans: Distribution, Biology and Impacts*. Springer, Netherlands, pp. 27–106.
- Bunnell, D.B., Lipton, D.W., Miller, T.J., 2010. The bioeconomic impact of different management regulations on the Chesapeake Bay blue crab fishery. *N. Am. J. Fish Manag.* 30, 1505–1521.
- Carrozzo, L., Potenza, L., Carlino, P., Costantini, M.L., Rossi, L., Mancinelli, G., 2014. Seasonal abundance and trophic position of the Atlantic blue crab *Callinectes sapidus* Rathbun 1896 in a Mediterranean coastal habitat. *Rend. Lincei Sci. Fish Nat.* 25, 201–208.
- Chainho, P., Fernandes, A., Amorim, A., Ávila, S.P., Canning-Clode, J., Castro, J.J., Costa, A.C., Costa, J.L., Cruz, T., Gollasch, S., Grazziotin-Soares, C., Melo, R., Micael, J., Parente, M.I., Semedo, J., Silva, T., Sobral, D., Sousa, M., Torres, P., Veloso, V., Costa, M.J., 2015. Non-indigenous species in Portuguese coastal areas, coastal lagoons, estuaries and islands. *Estuar. Coast. Shelf Sci.* 167, 199–211.
- Cilenti, L., D'Errico, G., Scirocco, T., Manzo, C., Fabbrocini, A., 2014. Spatial variability in the population structure of the *Carcinus aestuarii* in Varano lagoon. *Transit. Water Bull.* 8, 24–31.
- Cilenti, L., Pazienza, G., Scirocco, T., Fabbrocini, A., D'Adamo, R., 2015. First record of ovigerous *Callinectes sapidus* (Rathbun, 1896) in the Gargano Lagoons (south-west Adriatic sea). *Bioinvasions Rec.* 4, 281–287.
- Cilenti, L., Scirocco, T., Mancinelli, G., D'Adamo, R., 2016. Controllo biologico del Decapode Portunide *Callinectes sapidus* Rathbun, 1896, nelle lagune di Lesina e Varano, attraverso la pesca selettiva alle foci. *Lagunet* 2016 31.
- Clardy, A., 2013. Strengths vs. strong position: rethinking the nature of SWOT analysis. *Mod. Manag. Sci. Eng.* 1, 100–122.
- Clark, P.F., Mortimer, D.N., Law, R.J., Averns, J.M., Cohen, B.A., Wood, D., Rose, M.D., Fernandes, A.R., Rainbow, P.S., 2009. Dioxin and PCB contamination in Chinese mitten crabs: human consumption as a control mechanism for an invasive species. *Environ. Sci. Technol.* 43, 1624–1629.
- Conde, A., Domínguez, J., 2015. A proposal for the feasible exploitation of the red swamp crayfish *Procambarus clarkii* in introduced regions. *Conserv. Lett.* 8, 440–448.
- Demir, D., Öfkeli, F., Ceylan, S., Bölgön, N., 2016. Extraction and characterization of chitin and chitosan from blue crab and synthesis of chitosan cryogel scaffolds. *J. Turk. Chem. Soc. Sect. Chem.* 3, 131–144.
- Desrosier, N.W., Tressler, D.K., 1977. *Fundamentals of Food Freezing*. The AVI Publishing Company, Inc.
- Dulčić, J., Tutman, P., Matić-Skoko, S., Glamuzina, B., 2011. Six years from first record to population establishment: the case of the blue crab, *Callinectes sapidus* Rathbun, 1896 (Brachyura, Portunidae) in the Neretva river delta (South-Eastern Adriatic Sea, Croatia). *Crustaceana* 84, 1211–1220.
- Dunn, A.M., Hatcher, M.J., 2015. Parasites and biological invasions: parallels interactions, and control. *Trends Parasitol.* 31, 189–199.
- EC, 2000. Directive 2000/60/EC of the European Parliament and of the Council of 23 October 2000 establishing a framework for Community action in the field of water policy. *Off. J. Eur. Union Lex* 327, 1–82.
- EC, 2008a. Directive 2008/56/EC of the European Parliament and of the Council of 17 June 2008, establishing a framework for community action in the field of marine environmental policy (Marine Strategy Framework Directive). *Off. J. Eur. Union Lex* 164, 19–40.
- EC, 2008b. Directive 2008/98/EC of 19 november 2008 on waste and repealing certain directives. *Off. J. Eur. Union Lex* 312, 1–28.
- EC, 2011. Our Life Insurance, Our Natural Capital: an EU Biodiversity Strategy to 2020. COM/2011/244. European Commission.
- EU, 2011. Regulation (EU) No 304/2011 of the European Parliament and of the Council of 9 March 2011 amending Council Regulation (EC) No 708/2007 concerning use of alien and locally absent species in aquaculture. *Off. J. Eur. Union Lex* 88, 1–4.
- EU, 2013. Regulation (EU) no 1380/2013 of the european parliament and of the council of 11 december 2013 on the common fisheries policy, amending council regulations

- (EC) no 1954/2003 and (EC) no 1224/2009, and repealing council regulations (EC) no 2371/2002 and (EC) No 639/2004, and council decision 2004/585/EC. Off. J. Eur. Union Lex 354, 22–60.
- EU, 2014. Regulation (EU) No 1143/2014 of the European Parliament and of the Council of 22 October 2014 on the prevention and management of the introduction and spread of invasive alien species. Off. J. Eur. Union Lex 317, 35–55.
- EU, 2016. Commission implementing regulation (EU) 2016/1141 of 13 July 2016 adopting a list of invasive alien species of Union concern pursuant to Regulation (EU) No 1143/2014 of the European Parliament and of the Council. Off. J. Eur. Union L 189, 4–8.
- FAO, 2014. The State of World Fisheries and Aquaculture. FAO.
- Farragut, R.N., 1965. Proximate composition of Chesapeake Bay blue crab (*Callinectes sapidus*). J. Food Sci. 30, 538–544.
- Flowers, E.M., Simmonds, K., Messick, G.A., Sullivan, L., Schott, E.J., 2015. PCR-based prevalence of a fatal reovirus of the blue crab, *Callinectes sapidus* (Rathbun) along the northern Atlantic coast of the USA. J. Fish Dis. 39, 705–714.
- Fogarty, M.J., Miller, T.J., 2004. Impact of a change in reporting systems in the Maryland blue crab fishery. Fish. Res. 68, 37–43.
- Gökçe, G., Erguden, D., Sangun, L., Gekic, M., Alagoz, S., 2006. Width/length-weight and relationships of the blue crab (*Callinectes sapidus* Rathbun, 1986) population living in Camlik Lagoon Lake (Yumurtalı) Pak. J. Biol. Sci. 9, 1460–1464.
- Gökçe, G., Gekic, M., Metin, C., Özbilgin, H., 2007. Size selectivity of square mesh barriers for *Callinectes sapidus* Rathbun, 1896 (Brachyura, Portunidae). Crustaceana 80, 277–284.
- Gennaro, R., Scordella, G., Pastore, M., 2006. Occurrence of blue crab *Callinectes sapidus* (Rathbun, 1986, Crustacea, Brachyura), in the ugento ponds area (Lecce, Italy). Thalassia Salentina 29, 29–39.
- Glamuzina, L., Conides, A., Mancinelli, G., Dobroslavić, T., Bartulović, V., Matić Škoko, S., Glamuzina, B., 2017. Population dynamics and reproduction of the Mediterranean green crab in the Parila lagoon (Neretva Estuary, Adriatic Sea) as fishery management tools. Mar. Coast. Fish. (accepted).
- Glass, J.R., Kruse, G.H., Miller, S.A., 2015. Socioeconomic considerations of the commercial weathervane scallop fishery off Alaska using SWOT analysis. Ocean Coast. Manag. 105, 154–165.
- Goedknegt, M.A., Feis, M.E., Wegner, K.M., Luttikhuijzen, P.C., Buschbaum, C., van der Meer, J., Thieltges, D.W., 2015. Parasites and marine invasions: ecological and evolutionary perspectives. J. Sea Res. 113, 11–27.
- González-Wangüemert, M., Pujo, J.A., 2016. First record of the atlantic blue crab *Callinectes sapidus* (Crustacea: Brachyura: Portunidae) in the Segura river mouth (Spain, southwestern mediterranean sea). Turk. J. Zool. 40, 1–5.
- Green, B.S., Gardner, C., Hochmuth, J.D., Adrian, L., 2014. Environmental effects on fished lobsters and crabs. Rev. Fish Biol. Fish. 24, 613–638.
- Helms, M.M., Nixon, J., 2010. Exploring SWOT analysis—where are we now? A review of academic research from the last decade. J. Strat. Manag. 3, 215–251.
- Hewitt, D.A., Lambert, D.M., Hoenig, J.M., Lipcius, R.N., Bunnell, D.B., Miller, T.J., 2007. Direct and indirect estimates of natural mortality for Chesapeake Bay blue crab. Trans. Am. Fish. Soc. 136, 1030–1040.
- Hines, A.H., 2007. Ecology of juvenile and adult blue crabs. In: Kennedy, V.S., Cronin, L.E. (Eds.), The Blue Crab: *Callinectes Sapidus*. Maryland Sea Grant College, pp. 565–654.
- Huang, P., Woodward, R.T., Wilberg, M.J., Tomberlin, D., 2015. Management evaluation for the Chesapeake Bay blue crab fishery: an integrated bioeconomic approach. N. Am. J. Fish Manag. 35, 216–228.
- ICES, 2015. Interim Report of the Working Group on the Biology and Life History of Crabs (WGCRAB). 3–5 November 2015, Brest, France. ICES CM 2015/SSGEPD:11, p. 43.
- Küçükünlmez, A., Çelik, M., 2008. Amino acid composition of blue crab (*Callinectes sapidus*) from the North Eastern Mediterranean Sea. J. Appl. Biol. Sci. 2, 39–42.
- Katsanevakis, S., Wallentinus, I., Zenetos, A., Leppäkoski, E., Çınar, M.E., Oztürk, B., Grabowski, M., Golani, D., Cardoso, A.C., 2014. Impacts of invasive alien marine species on ecosystem services and biodiversity: a pan-European review. Aquat. Invasions 9, 391–423.
- Katselis, G., Koutsikopoulos, C., 2016. The establishment of blue crab *Callinectes sapidus* Rathbun, 1896 in the lagoon pogonitsa (Amvrakikos gulf, western Greece). HydroMedIT 2016 – Proceedings of the 2nd International Congress on Applied Ichthyology & Aquatic Environment 530–532.
- Kennedy, V.S., Cronin, L.E., 2007. The Blue Crab: *Callinectes sapidus*. Maryland Sea Grant College.
- Kennedy, V.S., Oesterling, M., Van Engel, W.A., 2007. History of blue crab fisheries on the US atlantic and gulf coasts. In: Kennedy, V.S., Cronin, L.E. (Eds.), The Blue Crab: *Callinectes Sapidus*. Maryland Sea Grant College, pp. 655–710.
- Kevrekidis, K., Antoniadou, C., Avramoglou, K., Efstratiadis, J., Chintiroglou, C., 2013. Population structure of the blue crab *Callinectes sapidus* in Thermaikos Gulf (Methoni Bay). In: 15th Pan-Hellenic Congress of Ichthyologists. 10–13 October 2013. pp. 113–116.
- Klaoudatos, D., Kapiris, K., 2014. Alien crabs in the Mediterranean Sea: current status and perspectives. In: Ardvini, C. (Ed.), Crabs: Global Diversity, Behavior and Environmental Threats. NOVA Publishers, pp. 101–159.
- Lacerda, A.L.F., Kersanach, R., Cortinhas, M.C.S., Prata, P.F.S., Dumont, L.F.C., Projetti, M.C., Maggioni, R., D'Incao, F., 2016. High connectivity among blue crab (*Callinectes sapidus*) populations in the Western South Atlantic. PLoS One 11, e0153124.
- Liquete, C., Piroddi, C., Drakou, E.G., Gurney, L., Katsanevakis, S., Charef, A., Ego, B., 2013. Current status and future prospects for the assessment of marine and coastal ecosystem services: a systematic review. PLoS One 8, e67737.
- Mancinelli, G., Carrozzo, L., Marini, G., Costantini, M.L., Rossi, L., Pinna, M., 2013a. Occurrence of the Atlantic blue crab *Callinectes sapidus* (Decapoda, Brachyura, Portunidae) in two Mediterranean coastal habitats: temporary visitor or permanent resident? Estuar. Coast. Shelf Sci. 135, 46–56.
- Mancinelli, G., Carrozzo, L., Marini, G., Pagliari, P., Pinna, M., 2013b. The co-occurrence of *Callinectes sapidus* Rathbun, 1896 (Brachyura: Portunidae) and the parasitic dinoflagellate *Hematodinium* sp. (Dinoflagellata: Syndinidae) in two transitional water ecosystems of the Apulia coastline (South-Italy). Transit. Water Bull. 7, 32–42.
- Mancinelli, G., Glamuzina, B., Petrić, M., Carrozzo, L., Glamuzina, L., Zotti, M., Raho, D., Vizzini, S., 2016. The trophic position of the Atlantic blue crab *Callinectes sapidus* Rathbun 1896 in the food web of Parila Lagoon (South Eastern Adriatic, Croatia): a first assessment using stable isotopes. Mediterr. Mar. Sci. 17, 634–643.
- Mancinelli, G., Alujević, K., Guerra, M.T., Raho, D., Zotti, M., Vizzini, S., 2017a. Spatial and seasonal trophic flexibility of the Atlantic blue crab *Callinectes sapidus* in invaded coastal systems of the Apulia region (SE Italy): a stable isotope analysis. Estuar. Coast. Shelf Sci. <http://dx.doi.org/10.1016/j.ecss.2017.1003.1013>. in press.
- Mancinelli, G., Chainho, P., Cilenti, L., Falco, S., Kapiris, K., Katselis, G., Ribeiro, F., 2017b. The Atlantic blue crab *Callinectes sapidus* in southern European coastal waters: distribution, impact and prospective invasion management strategies. Mar. Pollut. Bull. <http://dx.doi.org/10.1016/j.marpolbul.2017.1002.1050>. in press.
- McMillen-Jackson, A.L., Bert, T.M., 2004. Mitochondrial DNA variation and population genetic structure of the blue crab *Callinectes sapidus* in the eastern United States. Mar. Biol. 145, 769–777.
- Messick, G.A., 1998. Diseases, parasites, and symbionts of blue crabs (*Callinectes sapidus*) dredged from Chesapeake Bay. J. Crust. Biol. 18, 533–548.
- Millikin, M.R., Williams, A.B., 1984. Synopsis of biological data on blue crab. FAO Fisheries Synopsis. pp. 38.
- Molnar, J.L., Gamboa, R.L., Revenga, C., Spalding, M.D., 2008. Assessing the global threat of invasive species to marine biodiversity. Front. Ecol. Environ. 6, 485–492.
- NOAA, 2014. National oceanographic and atmospheric administration, national marine fisheries service, office of science and technology, commercial fisheries. Annual Commercial Landing Statistics.
- Nagle, L., Place, A.R., Schott, E.J., Jagus, R., Messick, G., Pitula, J.S., 2009. Real-time PCR-based assay for quantitative detection of *Hematodinium* sp. in the blue crab *Callinectes sapidus*. Dis. Aquat. Org. 84, 79.
- Nehring, S., 2011. Invasion history and success of the american blue crab *Callinectes sapidus* in European and adjacent waters. In: Galil, B.S., Clark, P.F., Carlton, J.T. (Eds.), In the Wrong Place – Alien Marine Crustaceans: Distribution, Biology and Impacts. Invading Nature – Springer Series in Invasion Ecology. Springer, Netherlands, pp. 607–624.
- Nuñez, M.A., Kuebbing, S., Dimarco, R.D., Simberloff, D., 2012. Invasive species: to eat or not to eat, that is the question. Conserv. Lett. 5, 334–341.
- Nunes, A.L., Katsanevakis, S., Zenetos, A., Cardoso, A.C., 2014. Gateways to alien invasions in the European seas. Aquat. Invasions 9, 133–144.
- Özdemir, S., Gökçe, G., Çekiç, M., 2015. Determination of size selectivity of traps for blue crab (*Callinectes sapidus* Rathbun, 1896) in the Mediterranean Sea. Tarım Bilimleri Dergisi 21, 256–261.
- Ojaveer, H., Galil, B.S., Campbell, M.L., Carlton, J.T., Canning-Clode, J., Cook, E.J., Davidson, A.D., Hewitt, C.L., Jelmert, A., Marchini, A., McKenzie, C.H., Minchin, D., Occhipinti-Ambrogi, A., Olenin, S., Ruiz, G., 2015. Classification of non-indigenous species based on their impacts: considerations for application in marine management. PLoS Biol. 13, e1002130.
- Panigrahi, J.K., Mohanty, P.K., 2012. Effectiveness of the Indian coastal regulation zones provisions for coastal zone management and its evaluation using SWOT analysis. Ocean Coast. Manag. 65, 34–50.
- Pasko, S., Goldberg, J., 2014. Review of harvest incentives to control invasive species. Manag. Biol. Invasion 5, 263–277.
- Perdikaris, C., Konstantinidis, E., Gouva, E., Klaoudatos, D., Nathanaelides, C., Paschos, I., 2016. Occurrence of the invasive crab species *Callinectes sapidus* Rathbun, 1896 in NW Greece. Walailak J. Sci. Technol. 13, 1–12.
- Poirier, L.A., Mohan, J., Speare, R., Davidson, J., Quijón, P.A., St-Hilaire, S., 2016. Moulting synchrony in green crabs (*Carcinus maenas*) from Prince Edward Island, Canada. Mar. Biol. Res. 12, 969–977.
- Ravindran, R., Jaiswal, A.K., 2016. Exploitation of food industry waste for high-value products. Trends Biotechnol. 34, 58–69.
- Ribeiro, F., Veríssimo, A., 2014. A new record of *Callinectes sapidus* in a western European estuary (Portuguese coast). Mar. Biodivers. Rec. 7, e36.
- Sharov, A.F., Vølstad, J.H., Davis, G.R., Davis, B.K., Lipcius, R.N., Montane, M.M., 2003. Abundance and exploitation rate of the blue crab (*Callinectes sapidus*) in Chesapeake Bay. Bull. Mar. Sci. 72, 543–565.
- St-Hilaire, S., Krause, J., Wight, K., Poirier, L., Singh, K., 2016. Break-even analysis for a green crab fishery in PEI, Canada. Manag. Biol. Invasion 7, 297–303.
- St-Hilaire, S., 2016. Assessing the Potential for a Soft-shell Green Crab Industry in PEI. MBA Thesis, University of Prince Edward Island.
- Streftaris, N., Zenetos, A., 2006. Alien marine species in the Mediterranean – the 100 ‘Worst Invasives’ and their impact. Mediterr. Mar. Sci. 7, 87–117.
- Sumer, C., Teksal, I., Karatas, H., Beyhan, T., Aydin, C.M., 2013. Growth and reproduction biology of the blue crab, *Callinectes sapidus* rathbun, 1896, in the beymelek lagoon (Southwestern coast of Turkey). Turk. J. Fish. Aquat. Sci. 13, 675–684.
- Türeli, C., Miller, T.J., Gündogdu, S., Yesilyurt, I.N., 2016. Growth and mortality of blue crab (*Callinectes sapidus*) in the north-eastern Mediterranean Sea. J. FisheriesSciences.com 10, 55–62.
- Thompson, M.H., Farragut, R.N., 1982. Amino acid composition of the chesapeake bay blue crab *Callinectes sapidus*. Comp. Biochem. Physiol. 17, 1065–1078.
- Torchin, M.E., Lafferty, K.D., Kuris, A.M., 2001. Release from parasites as natural enemies: increased performance of a globally introduced marine crab. Biol. Invasions 3, 333–345.
- Vasilakopoulos, P., Maravelias, C.D., 2015. A tale of two seas: a meta-analysis of

- crustacean stocks in the NE Atlantic and the Mediterranean Sea. Fish 17, 617–636.
- Yednock, B.K., Neigel, J.E., 2014. Detecting selection in the blue crab, *Callinectes sapidus*, using DNA sequence data from multiple nuclear protein-coding genes. PLoS One 9, e99081.
- Zenetas, A., Çınar, M.E., Pancucci-Papadopoulou, M.A., Harmelin, J.G., Furnari, G., Andaloro, F., Bellou, N., Streftaris, N., Zibrowius, H., 2005. Annotated list of marine alien species in the Mediterranean with records of the worst invasive species. Mediterr. Mar. Sci. 6, 63–118.
- Zotti, M., De Pascali, S.A., Del Coco, L., Migoni, D., Carrozzo, L., Mancinelli, G., Fanizzi, F.P., 2016a. ^1H NMR metabolomic profiling of the blue crab (*Callinectes sapidus*) from the Adriatic Sea (SE Italy): a comparison with warty crab (*Eriphia verrucosa*), and edible crab (*Cancer pagurus*). Food Chem. 196, 601–609.
- Zotti, M., Del Coco, L., De Pascali, S.A., Migoni, D., Vizzini, S., Mancinelli, G., Fanizzi, F.P., 2016b. Comparative analysis of the proximate and elemental composition of the blue crab *Callinectes sapidus*, the warty crab *Eriphia verrucosa*, and the edible crab *Cancer pagurus*. Heliyon 2, 1–15.