

## ***Callinectes sapidus* Rathbun, 1896 (Brachyura: Portunidae): An assessment on its diet and foraging behaviour, Thermaikos Gulf, NW Aegean Sea, Greece: Evidence for ecological and economic impacts**

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**Abstract.**— The blue crab, *Callinectes sapidus* Rathbun, 1896, is native to the Atlantic coasts of the Americas and globally one of the most highly invasive marine species. In the present study, the species' diet and the foraging behaviour was studied in the Thermaikos Gulf and Papapouli Lagoon for the first time. Surveys were undertaken using fyke nets, shore surveys, scuba and snorkelling. Additional data were compiled from systematic interviews with mussel farmers, shellfish traders and fishermen. In both Thermaikos Gulf and Papapouli Lagoon *C. sapidus* was found to prey on a wide variety of species including economically important molluscs, fishes, and crustaceans, indicating a substantial potential impact on fisheries and aquaculture in the region. Observation showed that over 6 (2009–2014) years, the blue crabs became dominant in Papapouli Lagoon at the expense of the native commercially fished crab *Carcinus aestuarii* Nardo, 1847 according to fisheries data. Potential management implications are discussed.

**Key words:** blue crab, alien species, ecological imbalances, invasive species, biodiversity, East Mediterranean Sea

### ■ Introduction

According to the European Commission (2014), Invasive Alien Species (IAS) are those with 'a significant negative impact on biodiversity as well as serious economic and social consequences' and the EU Marine Strategy Framework Directive and the EU Regulation 1143/2014 on the prevention and management of the introduction and spread of invasive alien species establishes monitoring requirements that have yet to be implemented (Lehtiniemi *et al.*, 2015). In the Mediterranean Sea, IAS are a major source of biodiversity loss (Galil, 2011; Mačić *et al.*, 2018). For instance, Galil (2011) reports 100 alien crustacean species. Furthermore, Manfrin *et al.* (2018) report more than 86 non-indigenous decapod species. Also, Galil *et al.* (2015), under different criteria, indicated 91

alien decapods from the Mediterranean. Main vectors of introduction are the Suez Canal, shipping and accidental escapes from aquaculture (Galil, 2011; Katsanevakis *et al.*, 2014).

The blue crab—*Callinectes sapidus* Rathbun, 1896, is native to the Atlantic coast of the Americas and is distributed from Nova Scotia to Uruguay and Argentina including the Gulf of Mexico and the Caribbean Sea. The species inhabits a wide variety of marine, brackish and freshwater environments (Hill *et al.*, 1989; Carr *et al.*, 2004). It can be found on the continental shelf in estuaries, lagoons and near-shore waters from depths of 0 to 90 m on sandy and muddy substrates with or without vegetation (Millikin and Williams, 1984; Mizerek *et al.*, 2011).

In Europe, blue crabs were reported from 1900 from the Atlantic coast of France (Nehring, 2011). It has since been introduced to the

European North East Atlantic in Denmark, Germany, United Kingdom, Netherlands and France (Ingle, 1997; Nehring, 2011), with no clear vector of introduction (Nehring, 2011). In the Mediterranean, the blue crab appeared in 1949 or earlier (Nehring 2011; Mancinelli *et al.*, 2016) with the most recent observations recorded by Mancinelli *et al.*, (2017a, 2017b). In addition, *C. sapidus* was recored in Hawaii (Eldredge, 1995) and in Japan (Doi, et al. 2011), making it one of the world's most successful invasive species.

In their native habitats, blue crabs are among the most well studied decapods. The species is opportunistic in its feeding habits (Carrozzo *et al.*, 2014) consuming small crustaceans, molluscs, plants and fishes. Blue crabs have been shown to have important influences on American food webs (Laughlin, 1982) and can alter local benthic community structure and diversity by changing the distribution and abundance of key species (Ebersole and Kennedy, 1995). They also feed on economically important species such as the winter flounder (Collier *et al.*, 2014). The species is pliable in its feeding habits regionally and seasonally, consuming, for example, more fish prey in late autumn and early winter and more shrimp during summer and fall in Florida (Laughlin, 1982). Juvenile crabs prefer to feed during nighttime, while the adults are day-time feeders, mainly in the afternoon (Darnell, 1958). Larger crabs are active hunters, predated on mobile species (Laughlin, 1982) like fishes, prawns and crabs and cannibalism of juveniles is also a wide spread behaviour (Laughlin, 1982). Blue crabs often swim to the water surface or to the water-air interface to feed on abundant molluscs (e.g. *Littorina irrorata*; Hamilton, 1976) and on spat of small and large sized bivalves, like mussels, oysters and clams (Blundon and Kennedy, 1982; West and Williams, 1986). Blue crabs are known to scavenge on terrestrial trapped, dead or decaying animals (Darnell, 1958) and on animal tissues (e.g. skin, bones, fish re-

mains; Benedict, 1940). The species may also consume detritus and a minor proportion of the diet consists of plant matter (Darnell, 1958). Almost exclusively, the literature on the feeding behaviour and prey preferences of the blue crab *C. sapidus* is based on its native range. In the U.S.A., Brazil and in some Western European countries (e.g. UK) *C. sapidus* has a significant economic value (Stagg and Whilden, 1997; Severino-Rodrigues *et al.*, 2013). The main products are soft shell crabs or live bait. In the Mediterranean, an important fishery exists in Turkey (Tureli-Bilen and Yesilyurt, 2014) and a smaller scale fishery exists in the Adriatic Sea (Manfrin *et al.*, 2015) and Egypt (Abdel Razek *et al.*, 2016). In Greece, though that a relative fishery is developed (Perdikaris *et al.*, 2016; Mancinelli *et al.*, 2017b; Kevrekidis and Antoniadou, 2018), blue crabs have a very low commercial value and are a by-catch product, yet some quantities are exported (pers. com.). In Greece, the blue crab is not well-studied, with only a handful of published data being available (Kevrekidis et al., 2012, 2013; Perdikaris *et al.*, 2016; Kevrekidis and Antoniadou, 2018). None of them is related with the species' feeding ecology.

In the new era of science, cameras are used frequently (Struthers *et al.*, 2015), especially when scuba diving (e.g. Cook *et al.*, 2013) and along with fisheries gear (Cairns *et al.*, 2017; Merten *et al.*, 2018). Moreover, the use of underwater photography and videography has proven to be useful at detecting alien species (e.g. Marcelli *et al.*, 2016). Furthermore, photographic material and videos were used on the assessment of foraging behaviour regarding crabs (Krieger *et al.*, 2016) and turtles (Fujii *et al.*, 2018). The authors of the present study applied these methods as well as conventional traps.

The aim of the present study is to describe systematically the predation strategies and the prey preferences of the invasive blue crab, *C. sapidus*, across a wide sea area in its non-native eastern Mediterranean range for the first

time and compare this with accounts from the Americas. The dominance of blue crabs is also investigated over time in a case-study of a lagoon complex within the study area. The results are discussed in relation to the potential biodiversity impacts and economic importance of the blue crab in Thermaikos Gulf, Greek waters and the eastern Mediterranean generally.

## Material and Methods

### Study areas

Thermaikos Gulf is at the northwestern Aegean Sea (Fig. 1). It is the largest gulf (5,100 km<sup>2</sup>) in the area and is one of the most productive parts of the eastern Mediterranean basin (Sakellariou and Alexandri, 2007) supporting the most important fishing activity in the Hellenic waters (Stergiou *et al.*, 1997). Thermaikos Gulf has an extensive shelf, little depth variation and it is dominated by soft sediments -amplified by the heavy trawling activity (Dimitriadis *et al.*, 2014). The main decapod species that support the regional fisheries are the caramote prawn *Penaeus kerathurus* and the pink shrimp *Parapenaeus longirostris* (Thessalou-Legaki, 2007). Moreover, Kampoouris *et al.* (2018c) reports some fishing activity regarding *Palinurus elephas* (Fabricius, 1787). Thermaikos Gulf also receives about 120,000 m<sup>3</sup>/day of sewage from the city of Thessaloniki and 25,000 m<sup>3</sup>/day of industrial discharges (Katsikatsou *et al.*, 2011).

Papapouli Lagoon is in Thermaikos Gulf (39°58. 257'N 22°40. 204'E; Fig. 1). Is an enclosed (choked) lagoon with two points of contact with the sea: one large central canal (30 m in length and 15–45 m in width) and one small canal (15–25 m in width: Nikolopoulou *et al.*, 2013a). The small inlet is almost always closed—only under extreme conditions opens, the large inlet is periodically open (June–December). Wind direction and intensity are affecting the opening/closing of the large inlet (Paraskevopoulou *et al.*, 2015). These condi-

tions dictate a seasonality in sediment and sea water availability. The Papapouli wetland has been characterized as a wildlife refuge and it is an EU Habitat/Species Management Area IV (European Environmental Agency, 2017).

### Survey methods

*Underwater and shore surveys.*—Eleven scuba diving surveys were conducted in six different locations from 14 September to 9 November 2014 (Fig. 1): two at Plaka Beach (40°05'49.4"N, 22°34'07.7"E), two at Neoi Poroï Beach (39°58'40.6"N, 22°39'22.5"E), one at Pineios River estuaries (39°56'11.8"N 22°43'07.3"E). Six more surveys were conducted at the east shores of Thermaikos Gulf: four at Potamos Beach (40°22'32.8"N 22°53'49.9"E) (ship wreck area), two at the saltworks of Epapanomi (40°26'17.1"N 22°51'47.6"E). All scuba dives were performed in morning hours from 09:00 to 12:30, standard protocols were followed with two divers working together, freely searched foraging *C. sapidus*. The depth range was 2–20 m. Additionally, 24 snorkel diving and beach surveys (09:00–14:00) were conducted at the aforementioned areas from 1 June to 20 July 2014 and following the same protocol. The depth range was 2–10 m. During scuba, snorkel and beach surveys videography and photography were used to record encounters with blue crabs (Midland XTC 300VP4, PENTAX K-5 camera, Sony Cyber-shot DSC-W70) over a 60-minute period. Prey items were visually identified to the lowest taxonomic level possible. Video footage was subsequently reviewed and feeding encounters categorised per prey type and behaviour.

*Fyke net surveys.*—Fyke nets were deployed on a weekly basis at Papapouli Lagoon from May 2009 to September 2014 at four sampling stations and under a salinity gradient and ( $B \geq C \geq D$ ) with a reference station (A). Fyke nets had a 20 mm mesh opening and were equal in length (300 m). The central leader net was 3.5 m long and the mesh size was 30 mm. Fyke nets

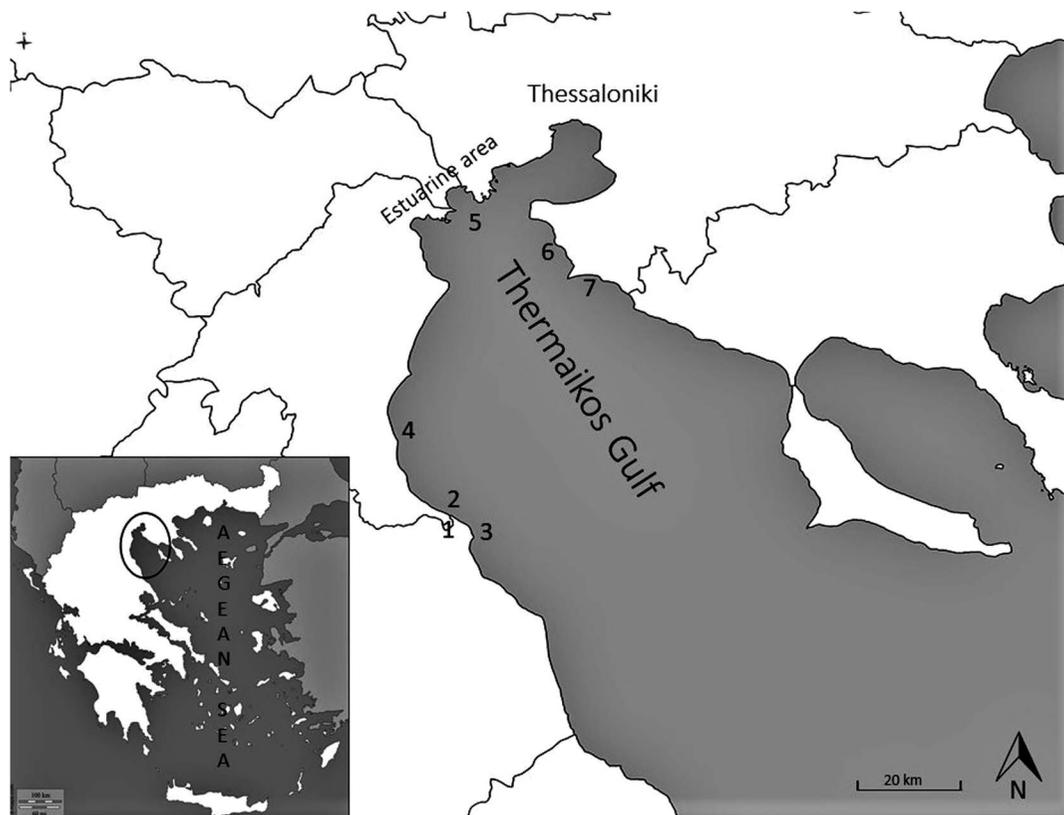


Figure 1. Thermaikos Gulf, North Aegean Sea, Greece with the sampling sites marked. (1) Papapouli Lagoon, (2) Neoi Poroï beach, (3) Pineios River estuaries, (4) Plaka beach, (5) Mussel farms, (6) Saltworks, (7) Potamos. Source: Ministry of Environment & Energy, modified. Inlaid map: d-maps.com, modified.

were equipped with inner chambers (22 mm mesh size). Both chambers were framed with plastic tubes of 0.5 cm in width and of horse-shoe shape. The frame's dimensions were 0.6 m in height and 0.7 m in width. The ends of cod-end were fastened before deployment. During fyke net deployments (approximately 60 minutes at each location) blue crab feeding encounters were regularly recorded.

Additional data on the foraging behaviour and diet of the species obtained by interviewing professional fishermen, traders and mussel farmers in Thermaikos Gulf. Crab fisheries raw data (2008–2013) from Papapouli Lagoon were provided by a consultancy company (fisheries-aquaculture).

Food items were identified to species level,

where possible. They were also classified as species with Commercial Value (CV), species with Potential Commercial Value (PVC) and species with No Commercial Value (NCV) (pers. comm. with Dimitrios Argyriadis and Giorgos Dimoudis).

## ■ Results

After a total of 36 hours of diving, snorkelling and shore survey, the following feeding strategies of blue crab were observed mainly on soft-bottom, but also on hard-bottom (ship wreck) habitats.

### *Predation strategies*

Blue crabs demonstrated similar foraging be-

haviour and strategies to those described from the US Atlantic coasts and the Gulf of Mexico. They actively preyed on mobile species like fishes and decapods or they searched, dug out and consumed clams. The crabs used their walking legs to detect prey in the substrate by either sensing changes at the substrate material (sand—fish flesh) or by sensing vibrations. In this way, blue crabs fed on flatfishes (*Solea solea*) (juveniles and adults) firstly by spearing their flesh with their walking legs and secondly by using their claws like scissors (Fig. 2a). Scavenging was also observed throughout the study area. At Papapouli Lagoon between May 2014 and August 2014 male blue crabs were observed to move across the lagoon's shores (Fig. 2b) and feed on any possible prey. Blue crabs moved individually or in small groups of two to four individuals. Also, at Papapouli Lagoon blue crabs were attracted to traps, fyke nets and other fishing gear (*cf* Benedict 1940) to feed on trapped fish and prawns (Fig. 2c). Further observations were made of them scavenging decaying animals like a snake (*Malpolon monspessulanus*) and a dead seagull (*Ichthyetus melanocephalus*). Some blue crabs were observed to be cannibalistic on juvenile or sub-adults. On one occasion a male crab was observed to consume a similar sized male crab in Papapouli Lagoon (Fig. 2d). Blue crabs were recorded consuming mussels (*Mytilus galloprovincialis*) near to the water surface and to the air-water interface at the mussel farming units using the pickets as a feeding base. Lastly, blue crabs include plant matter originating from halophytes (*Salicornia sp.*) in their diet.

Despite similarities with previously described foraging behaviour, blue crabs also exhibited other feeding behaviours in the present study:

**Ambush.**— Blue crabs were observed to ambush fishes or other decapods in Thermaikos Gulf and at Papapouli Lagoon. In the first method blue crabs buried themselves at the sandy or muddy bottom (Fig. 2e) and then

waited for the prey (e.g. *Mullus surmuletus*) to come closer. The above method was observed at the west coasts, Papapouli Lagoon and at Potamos Beach at the east shores of Thermaikos Gulf. The second method, meaning blue crabs hanging at weirs, was observed only at Papapouli Lagoon, several times from 2010 to 2014 and specifically at the weirs that operating as fish traps when the seawater retreats.

**Seaweed sifting.**— Seaweeds in Papapouli Lagoon support a variety of taxa, such as amphipods and isopods (Paraskevopoulou *et al.*, 2015), mysids (Nikolopoulou *et al.*, 2013b), and larvae and sub-adult decapods (Nikolopoulou *et al.*, 2013a). Blue crabs were observed to prey on these invertebrates using a sifting strategy: holding seaweeds to their mandibles and systematically manipulating the material (Fig. 2f).

#### **Prey items**

Overall, there were 13 prey species recorded in Thermaikos Gulf (Table 1): 10 of which were molluscs, 2 crustaceans and 1 fish (Fig. 3a). Almost all the species, 12 of 13, were classified as species with commercial value, one as species with potential commercial value -mollusc species that are domestically exploited. Species with no commercial value were not recorded (Fig. 3a). Blue crabs had similar feeding patterns at Papapouli Lagoon. Their prey items included 35 different species (Table 1), including fish (16 species), molluscs (eight species), and crustaceans (nine species). The remaining four species were belonging in other miscellaneous taxa (Fig. 3b). Many of the prey species had commercial value (25), or potential commercial value (six). Of the commercially important species 15 were fish, 7 were bivalves and gastropods molluscs and three were crustaceans. Species with potential commercial value were mainly crustaceans (four species). The remaining six were two different taxa and two species (Fig. 3b).

Fisheries data (2009–2014) (Fig. 4) from the small-scale fishery off Papapouli Lagoon, sug-

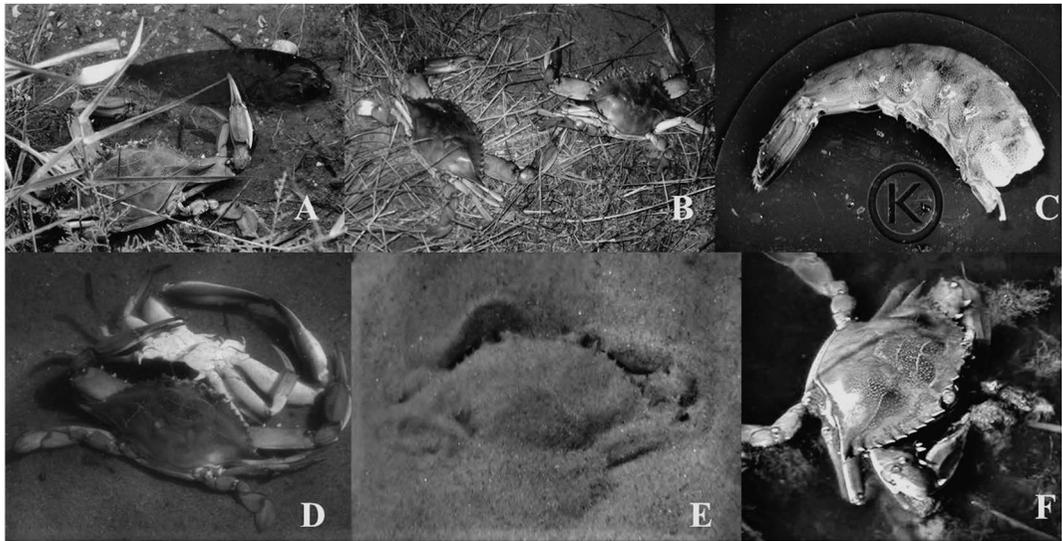


Figure 2. Predation strategies and diet of the blue crab at Thermaikos Gulf. A: a male blue crab feeding on *Solea solea*. B: male blue crabs patrolling and scavenging at the shores C: a juvenile individual of *P. aztecus* sliced in half by blue crabs at Papapouli Lagoon. D: Cannibal blue crab feeding on a male of similar size, Papapouli Lagoon. E: blue crab setting an ambush, Potamos beach Epanomi. F: female blue crab sifting seaweeds.

gest an influence of the established blue crab population on the native green grab *Carinus aestuarii* Nardo, 1847, since the latter species is listed among the prey items of the former (Table 1). Furthermore, the two-co-occurring species demonstrate significant differences in their mean abundances between years (one-way ANOVA,  $P=0.0494$ ). The mean abundances for the green crab are constantly decreasing, the maximum value was observed in 2009 (211) and the minimum in 2014 (one). The annual mean abundance of the blue crab has a different pattern with maximum value in 2011 (277) and minimum value in 2009 (44) (Fig. 4).

## Discussion

The blue crab is a very adaptable species which has several predation strategies and has been observed to consume a broad range of prey items. Data resulting from this study suggest that the species has not changed its general foraging behaviour, or its prey in terms of broad taxonomic groups between native habi-

tats (e.g. Laughlin, 1982) and the Eastern Mediterranean. Nevertheless, prey species between the West Atlantic Ocean and Thermaikos Gulf invariably differ. Common predation strategies were found in both America and Thermaikos Gulf. Namely, predation on small bivalves (cf. Juanes, 1992) such as *Gari depressa*, *Tellina tenuis* and *T. incarnata*.

The previously described predation strategies from the U.S.A vary from active predation on smaller invertebrates like polychaetes, (Darnell, 1958; Millikin & Williams, 1984) mobile molluscs and crustaceans (Mascaro *et al.*, 2003) and even adult flatfishes like the common sole, to scavenging on dead, trapped or decaying animals or even to cannibalism, a feeding strategy that occurs in many decapod species (e.g. Long *et al.*, 2012). In the present study, these strategies were also seen, as well as *Ambush* and *Seaweed sifting* behaviour for the species. In this study, the species appears to have a strong feeding plasticity and there were many similarities in its predation strategies compared to those demonstrated in American

Table 1. List of blue crab prey items list at Thermaikos Gulf and Papapouli Lagoon.

Taxonomic group/species	Location	Survey methodology	Observation date/period
<b>MOLLUSCA</b>			
<i>Acanthocardia tuberculata</i> (Linnaeus, 1758)	Platamonas beach/Papapouli Lagoon	SCUBA/snorkelling/shore	July 2011/19 July 2014
<i>Arca noae</i> (Linnaeus, 1758)	Axios-Loudias River estuaries mussel farming units	Video	May 2008*
<i>Bittium reticulatum</i> (da Costa, 1778)	Papapouli Lagoon	Shore	From 2009 to 2014*
<i>Callista chione</i> (Linnaeus, 1758)	Neoi Poroï beach	SCUBA/snorkelling	17 August 2013
<i>Cerastoderma glaucum</i> (Bruguère, 1789)	Papapouli Lagoon	Shore	From 2008 to 2010*
<i>Chamelea gallina</i> (Linnaeus, 1758)	Neoi Poroï beach	SCUBA/snorkelling	5 July 2014
<i>Gari depressa</i> (Pennant, 1777)	Papapouli Lagoon	Shore	From 2008 to 2014*
<i>Mactra stultorum</i> (Linnaeus, 1758)	Plaka beach	SCUBA/snorkelling	June 2010*
<i>Modiolus barbatus</i> (Linnaeus, 1758)	Axios-Loudias River estuaries/Epanomi saltworks	SCUBA/snorkelling	2008*/7 September 2014
<i>Mytilus galloprovincialis</i> (Lamarck, 1819)	Axios-Loudias River estuaries mussel farming units	Fishermen interviews	May 2008*
<i>Ostrea edulis</i> (Linnaeus, 1758)	Epanomi Potamos Beach, shipwreck	SCUBA/snorkelling	14 September 2014
<i>Ruditapes decussatus</i> (Linnaeus, 1758)	Papapouli Lagoon	Shore	From 2008 to 2014*
<i>Solen marginatus</i> (Pulteney, 1799)	Papapouli Lagoon	Shore	From 2008 to 2014*
<i>Tellina incarnata</i> (Linnaeus, 1758)	Thermaikos Gulf, west coasts	Shore	From 2010 to 2012*
<i>Tellina tenuis</i> (da Costa, 1778)	Thermaikos Gulf, west coasts	Shore	From 2010 to 2012*
<b>CRUSTACEA</b>			
<i>Callinectes sapidus</i> (Rathbun, 1896)	Papapouli Lagoon	Shore/Video/Fyke	21 June 2014
<i>Carcinus aestuarii</i> (Nardo, 1847)	Papapouli Lagoon	Shore	From 2008 to 2014*
<i>Corophium orientale</i> (Schellenberg, 1928)	Papapouli Lagoon	Shore	From 2009 to 2014*
<i>Gammarus aequicauda</i> (Martynov, 1931)	Papapouli Lagoon	Shore	From 2009 to 2014*
<i>Gammarus</i> sp.	Papapouli Lagoon	Shore	From 2009 to 2014*
Isopoda sp.	Papapouli Lagoon	Shore	From 2009 to 2014*
<i>Mesopodopsis slabberi</i> (Van Beneden, 1861)	Papapouli Lagoon	Shore	From 2013 to 2014*
<i>Penaeus aztecus</i> (Ives, 1891)	Pineios River estuaries/Papapouli Lagoon	Fyke	20 September 2014/21 June 2014
<i>Penaeus kerathurus</i> (Forskål, 1775)	Papapouli Lagoon	Fyke	2012*
<b>POLYCHAETA</b>			
<i>Hediste diversicolor</i> (O. F. Müller, 1776)	Papapouli Lagoon	Shore	2009*
<b>PISCES</b>			
<i>Chelon labrosus</i> (Risso, 1827)	Papapouli Lagoon	Fyke	From 2008 to 2014*
<i>Dicentrarchus labrax</i> (Linnaeus, 1758)	Papapouli Lagoon	Fyke	From 2008 to 2014*
<i>Diplodus annularis</i> (Linnaeus, 1758)	Papapouli Lagoon	Fyke	From 2008 to 2014*
<i>Diplodus sargus sargus</i> (Linnaeus, 1758)	Papapouli Lagoon	Fyke	From 2008 to 2014*
<i>Diplodus vulgaris</i> (Geoffroy Saint-Hilaire, 1817)	Papapouli Lagoon	Fyke	From 2008 to 2014*
<i>Gambusia affinis</i> (Baird & Girard, 1853)	Papapouli Lagoon	Fyke	From 2008 to 2014*
Gobiidae	Papapouli Lagoon	Video	4 May 2015
<i>Lithognathus mormyrus</i> (Linnaeus, 1758)	Papapouli Lagoon	Fyke	From 2008 to 2014*
<i>Liza aurata</i> (Risso, 1810)	Papapouli Lagoon	Fyke	From 2008 to 2014*
<i>Liza ramada</i> (Risso, 1827)	Papapouli Lagoon	Fyke	From 2008 to 2014*
<i>Liza saliens</i> (Risso, 1810)	Papapouli Lagoon	Fyke	From 2008 to 2014*
<i>Mugil cephalus</i> (Linnaeus, 1758)	Papapouli Lagoon	Fyke	From 2008 to 2014*
<i>Mullus surmuletus</i> (Linnaeus, 1758)	Epanomi Potamos Beach	SCUBA	14 September 2014
<i>Solea solea</i> (Linnaeus, 1758)	Papapouli Lagoon	Video	From 2008 to 2014*
<i>Sparus aurata</i> (Linnaeus, 1758)	Papapouli Lagoon	Fyke	From 2008 to 2014*
<i>Umbrina cirrosa</i> (Linnaeus, 1758)	Papapouli Lagoon	Fyke	From 2008 to 2014*
<b>CARYOPHYLLALES</b>			
<i>Salicornia</i> sp.	Papapouli Lagoon	Shore	2014*
<b>TRAPED, DEAD OR DECAYING ANIMALS</b>			
<i>Ichthyæus melanocephalus</i> (Temminck, 1820)	Papapouli Lagoon	Fyke	2010
<i>Malpolon monspessulanus</i> (Hermann, 1804)	Papapouli Lagoon	Fyke	27 July 2014

\*More than one observation or continuous observations during specific period.

Atlantic populations. It seems that adult individuals are daytime feeders, juveniles were not observed foraging during day. Noteworthy, blue crabs exhibited a “relaxed” behaviour during diver’s presence that might be associated

with the establishment success of this species in the study area.

In the present study, the blue crab in the wide area of Thermaikos Gulf feeds on a broad variety of organisms that can include terrestrial an-

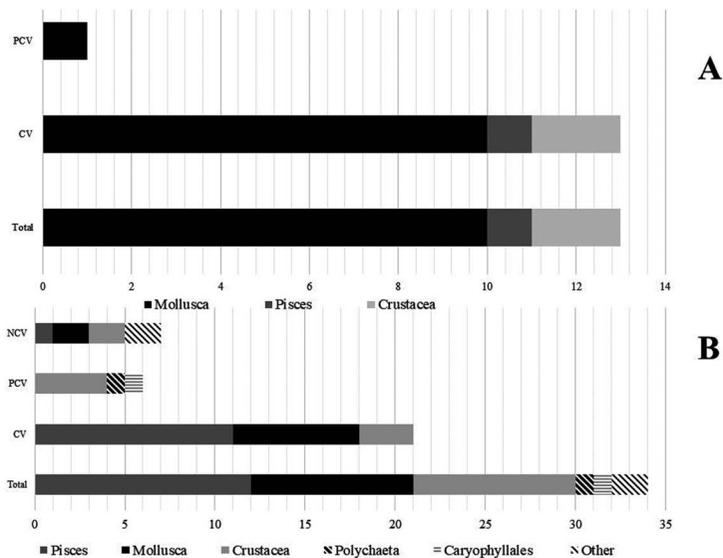


Figure 3. (A) Prey items of *C. sapidus* and their taxa (species number), in total, species with Commercial Value (CV), species with Potential Commercial Value (PCV) at Thermaikos Gulf. (B) Prey items of *C. sapidus* and their taxa (species number), in total, species with Commercial Value (CV), species with Potential Commercial Value (PCV) and species with no commercial value (NCV) at Papapouli Lagoon.

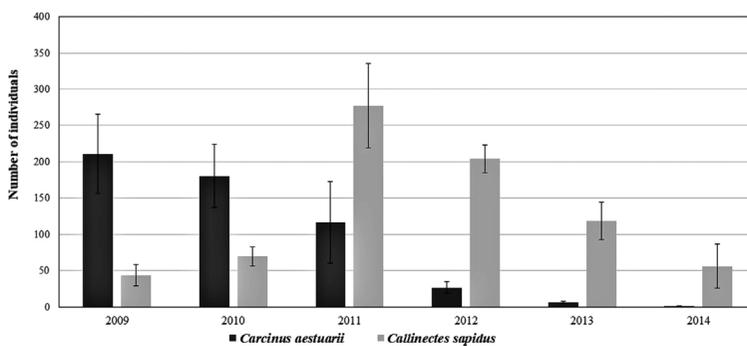


Figure 4. Mean annual catches (number of individuals) of green and blue crabs from Papapouli Lagoon (average  $\pm$  SD) by using fyke nets at the same sampling stations. Source (raw data): Nearchus G. P.

imals that are already dead or decaying or even offered as bait (chicken shanks with claws) by amateur fishermen. The species shows similar behaviour to that observed in the areas of its natural distribution. It is reported that blue crabs had been observed feeding on animal by-products from abattoirs (animal offal) (Darnell, 1958) or baits like raw meat, skin and bones (Benedict, 1940).

As in United States blue crabs fed on mobile

prey including the decapods *Penaeus aztecus*, *P. kerathurus* and *C. aestuarii* in Papapouli Lagoon. At Papapouli Lagoon the proportion of blue crabs also increased as the population of green crabs (*C.aestuarii*) became extirpated (Fig. 4) and, anecdotally, the population of the lagoon cockle (*Cerastoderma glaucum*) became virtually extinct at the same time (Kampouris, personal observations). The population of blue crabs dwelling in the estuarine area of

the four rivers seems to be substantially unchanged and therefore is an important problem for professional fishermen and mussel farmers of the region. In the present study, throughout the Thermaikos Gulf, blue crabs were found feeding on economically important species like the Mediterranean seabream (*Sparus aurata*) and seabass (*Dicentrarchus labrax*), mussels and prawns. For all the above-mentioned reasons, *C. sapidus* contributes negatively to the ecological balance of the area and has a significant impact on the Greek national fisheries and aquaculture.

One management solution could be to slurry the crabs, to create organic food pellets that will be sold in lower prices at aquaculture units: experimental trials on octopus (*Octopus vulgaris* Cuvier, 1797) farming with crab pellets (Estefanell *et al.*, 2014) had given increased growth rates and lower mortality. Moreover, citizen-science has been proven as a reliable monitoring tool on alien species detection and range expansion (e.g. Kampouris *et al.*, 2018a, 2018b, 2018d). The present proposals could be developed in parallel with those proposed by Mancinelli *et al.* (2017a, 2017b).

Elsewhere in the Mediterranean, there is limited information on the biology, ecology and population dynamics of *C. sapidus* (Manfrin *et al.*, 2015). The only available data on foraging behaviour and prey are from Italy (Carrozzo *et al.*, 2014) and Croatia (Mancinelli *et al.*, 2016) where, as seen in the present study, *C. sapidus* predation has a negative impact on the, green crab, other fish, and the species that they feed upon. The study of Mancinelli *et al.* (2016) classifies the blue crab as a 'fully carnivorous predator' species and that adult individuals could decrease their trophic position. The findings of the current study are in accordance with Mancinelli *et al.* (2016) and Carrozzo *et al.* (2014). Also, the observed decrease of the trophic position as described in Mancinelli *et al.* (2016) in adult blue crabs could be explained by the findings of this study, since blue crabs

were observed feeding systematically on riparian vegetation (Table 1).

Generally, aquatic fauna tends to become invasive more easily than the terrestrial fauna (e.g. *Procambarus clarkii*; Di Leo *et al.*, 2014). Often, besides environmental impacts, they tend to negatively affect economies and societies affecting sectors like fisheries and tourism but see Galil *et al.* (2009) and supplementary material for details. The EU Biodiversity Strategy (European Union, 2011) states that: 'By 2020, invasive alien species and their pathways are identified and prioritized, priority species are controlled or eradicated, and pathways are managed to prevent the introduction and establishment of new invasive alien species. However, the blue crab establishment and spreading in the Mediterranean is a challenge to the EU Biodiversity Strategy.

The fish listed as prey items of blue crab in this work, were often juvenile individuals that were captured by active hunting or with the -Ambush- method. In other cases, adult trapped individuals were captured by blue crabs in fyke nets at Papapouli Lagoon. Adults of shrimp and crabs were also captured and eaten within the fishing gear used at Papapouli Lagoon. All of these observations imply commercial impact on targeted fisheries. Many species of molluscs that have been included at the category of species with Commercial Value (CV) are exported to other countries. These include the following: *Modiolus barbatus*, *Chamelea gallina*, *Tellina tenuis*, *Tellina incarnata*, *Arca noae*, *Cerastoderma glaucum* and *Ruditapes decussatus*.

Species with Potential Commercial Value (PCV) include Amphipods and Mysids that have economical value elsewhere (e.g. pet food) are listed but are not currently exploited in the region. Also, the halophyte *Salicornia sp.* has the potential to be farmed (e.g. Ventura & Sagi, 2013) and therefore exploited. Furthermore, some mollusc species were included since they are being sold in local markets, but not in large quantities. Also, the polychaete

species *Hediste diversicolor* was included since it is one of the marine worms that supports the live bait industry (Gillet & Torresani, 2003).

Currently, cameras and other electronic means are considered as important tools of passive monitoring in many cases and behavioural observations are widely used either in terrestrial or aquatic environments, for instance, in conservation assessments (Cairns *et al.*, 2017), behavioural ecology (Fujii *et al.*, 2018) among others. Moreover, the in-depth knowledge and experience of fishers should be further acknowledged and utilized, and wider collaborations should be established among scientists and policy makers (Azzuro *et al.*, 2018).

Overall, the present study presents evidence that the invasive blue crab *C. sapidus* preys on a wide range of species, including economically important fish, molluscs and crustaceans. Noteworthy, is that the present study revealed blue crabs predated upon the invasive prawn *P. aztecus* firstly reported in the area in 2012 (Nikolopoulou *et al.*, 2013a) but further and systematic research is required to assess this complex phenomenon. Blue crab was using a variety of feeding strategies, some of which have not been reported for the species. The survey methodologies in the present study were diverse, allowing robust data collection. The present study though that presents novel data it sets the basis on the blue crab's feeding ecology. Further laboratory-based research can improve our conducted knowledge on the species diet and foraging preferences. There are potential economic and ecological consequences such as ecological imbalance at the food-web changes as described in the blue crab native range (Laughlin, 1982), or financial difficulties of the mussel farmers, due to the invasion of *C. sapidus* in the eastern Mediterranean and Thermaikos Gulf that warrants further investigation and management.

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