

Alien fish species in the eastern Mediterranean Sea: Invasion biology in coastal ecosystems

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Doctoral Thesis



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Abstract

The spread of non-indigenous species (NIS) in the eastern Mediterranean Sea is an ongoing and accelerating process. Non-indigenous species are regularly reported from various coastal habitats in the eastern Mediterranean Sea but fundamental knowledge on the assemblage structure of coastal fish communities are lacking. This thesis aims to increase the knowledge on the fish assemblage structure and function of *Posidonia oceanica* meadows and sandy habitats in a coastal area of the eastern Mediterranean Sea and give insight into invasion biology by investigating the potential impact of introduced fish species to the local ecology and food-web of the marine systems under study.

Functional and feeding guilds were developed to investigate the fish assemblage structure and function of coastal fish communities and to assess the potential role of NIS in the food web. In addition, diet investigations were considered important first steps in order to evaluate the potential role and impact of recently established NIS in the recipient region. During the sampling campaign two species were for the first time reported in the area.

Posidonia oceanica was found to be a multifunctional habitat for fish species. It was found to be a highly important nursery habitat for several species during summer and a habitat that could under certain seasons concurrently be used by both adults and juveniles. Four functional guilds were created to describe the habitat use of *P. oceanica* meadows for each species encountered; juvenile migrants, seagrass residents, seasonal migrants and occasional visitors. Affinity of each species to *P. oceanica* was assessed in a comparison with each species distribution on open sand within the same depth range. Among the 88 species encountered, eleven were found to be non-indigenous of Indo-Pacific and Red Sea origin, three of them using seagrass mainly as juveniles, and four as residents.

In a comparison of fish assemblage structure between seagrass and sandy habitats quantitative sampling in combination with classification of fish species into six major feeding guilds revealed the position and contribution of non-indigenous species (NIS) in the food web of *Posidonia oceanica* and sandy habitats. In *P. oceanica* beds and on sandy bottoms 10 and five species, respectively, were non-indigenous of Indo-Pacific and Red Sea origin. The proportional contribution of NIS individuals on *P. oceanica* beds was lower than that of sandy bottoms (12.7 vs. 20.4 %) a pattern that also followed for biomass (13.6 vs. 23.4 %), indicating that low diverse systems may be more prone to introductions than species-rich communities. The two habitats had similar fish feeding guilds, but the biomass contribution from NIS varied within each guild, indicating different degrees of impact on the available resources. Size was considered highly important due to habitat shift of species with increased size. Two of the aspects considered in this study, the chance of establishing and the chance of being very dominant will depend upon competitive abilities strongly coupled to size and grounds for habitat shift. However, success of establishment will also depend on appropriate food resources in the recipient community as well as competitive abilities and level of competition in the food web within habitats. No support could be found for the theory that taxonomic affiliation could facilitate invasion success.

The non-indigenous bluespotted cornetfish *Fistularia commersonii* was found to be a strictly piscivore predator and the diet consisted of 96 % by number and >99 % by weight of fish. The diet of *F. commersonii* was related to time of year, and fish size. Size classification and habitat of prey groups (benthic, supra-benthic, and pelagic) showed that with increased body length it extended its diet to larger prey and more generalist feeding. *Fistularia commersonii* was found to prey on commercial

important native species (e.g. *Spicara smaris*, *Boops boops*, *Mullus surmuletus*) and the absence of NIS from its diet was mainly attributed to the absence of NIS with elongated body shape.

The feeding ecology of two common indigenous (*Sphyraena sphyraena* and *Sphyraena viridensis*) and one abundant non-indigenous barracuda, *Sphyraena chrysotaenia*, of Indo-Pacific origin, was investigated. Confamilial feeding interactions was studied to investigate overlap in feeding preferences in relation to availability of prey items. Dietary analyses revealed that all three species examined were specialized piscivores with their diet consisting to more than 90 % of fish, both by number and weight. All three predators examined showed a significant selectivity towards *Atherina hepsetus*. Diet breadth and size of prey increased with increased body size, whereas diet overlap between indigenous and NIS decreased, attributed to increased diet breadth and specific life characteristics of indigenous species developing into larger predators extending their foraging habits. During winter, condition of the NIS was significantly lower than that of the indigenous species, indicating that winter temperature in the studied area may be a limiting factor for further population growth of this Indo-Pacific species. This study filled the gap in knowledge about the feeding preferences of the most abundant piscivorous species found on the coasts of the studied area. Additionally, congeneric affiliation of fish introductions was not found to be an important factor explaining successful establishment of NIS.

The non-indigenous toxic pufferfish, *Lagocephalus sceleratus*, was reported for the first time in the Mediterranean in 2003 and two years later in the coastal habitats of Rhodes. The ecological and societal impact of the pest pufferfish was investigated in coastal habitats of Rhodes. Seasonal quantitative sampling in two common coastal habitats was used to investigate habitat use of different life-stages. Sandy areas were found to be highly important for the early life stages of *L. sceleratus*. In contrast, *Posidonia oceanica* habitats were mainly preferred by larger (> 29 cm) reproductive adults with a maximum recorded size of 64 cm. *Lagocephalus sceleratus* was found to be an invertebrate and fish feeder while size classification revealed a tendency for an ontogenetic diet shift with increased size to a molluscivore feeding. The ontogenetic diet shift is most probably attributed to a shift in habitat use with increasing size. During early life stages *L. sceleratus* inhabited sandy bottoms where it fed on various invertebrates, including the genus *Nassarius* and *Dentaliidae*. The predominant molluscan species found in the diet of larger (> 20 cm) *L. sceleratus* individuals was *Sepia officinalis* while predation of *Octopus vulgaris* was less successful. *Sepia officinalis* and *O. vulgaris* are of economic interest in the area and the impact of *L. sceleratus* on local stocks of these species is discussed. Societal impacts were also evident in the area due to increased public attention concerning the lethal effects of the toxic *L. sceleratus*, if consumed. Seasonal variations in the condition of *L. sceleratus* did not show any significance and the high conditional values together with information on high numbers caught during samplings, signifies its ability to become an important member of the coastal fish community. Combined ecological, economical and social effects clearly classify *L. sceleratus* a pest in the area.

Populärvetenskaplig sammanfattning

Jordens geologiska historia avslöjar hur kontinenterna har förflyttat sig över jordklotet och därmed skapat förbindelser eller isolerat oceaner ifrån varandra. Geologin visar också att gamla havsbottnar blivit land och landområden blivit till hav. Rörelserna i jordskorpan har lett till att djur och växter isolerats ifrån varandra men även att arter har kunnat migrera i stor skala när förbindelser uppstått mellan landmassor eller havsområden som tidigare varit isolerade. Ur ett geologiskt perspektiv är därför inte migration av främmande arter något nytt fenomen, men hastigheten med vilket det sker har mångdubblats genom mänskliga aktiviteter.. Medan många av havens arter hotas av människans överfiske och habitatförstörelse, finns det andra arter som kan invadera nya livsmiljöer med människans hjälp. Det senaste seklet har mänsklig transport (främst genom båttrafik) bidragit till att främmande arter introducerats till och från områden i alla världens hörn. Introduktioner kan antingen ske oavsiktligt (genom transport av ballastvatten eller genom att organismer sätter sig fast på fartygskrov) eller avsiktligt (främst genom arter flyttas för att odlas eller för att hållas i akvarier). Ur ett samhällsperspektiv kan främmande arter utgöra ett allvarligt hot för människans ekonomiska intressen och hälsa men också leda till negativa konsekvenser för resten av ekosystemet (konkurrens med inhemsk fauna). Hotet från främmande arter blir ofta ännu större på grund av andra mänskliga aktiviteter som rubbar ekosystemens funktioner och gör dem mer sårbara såsom habitatförstörelse, förorening och klimatförändringar. Habitatförstörelse orsakar störningar som kan öppna upp rum för invaderade arter. Föroreningar kan försvaga eller slå ut känsliga inhemska arter vilket kan gynna opportunistiska och mer tåliga främmande arter. Klimatförändringar är i sig starkt kopplade med invasionsbiologi då sydliga arter får det fysiskt lättare att anpassa sig i områden där de tidigare varit temperaturbegränsade. Å andra sidan kan främmande arter faktiskt ha positiva effekter. Detta kan ske genom att främmande arter blir kommersiellt viktiga eller förstärker befintliga ekosystemfunktioner. Främmande arter är ett omfattande och växande problem, exempelvis är 50 % av alla växtarter i Hawaii främmande, liksom 20 % av alla växter i Kaliforniens bukt och 18 % av alla fiskar i östra Medelhavet. I Medelhavet anses direkt transport från Röda Havet genom Suezkanalen som den viktigaste vektorn för introduktion av invaderade arter.

Spridning av främmande arter i östra Medelhavet är en pågående och accelererande process. Främmande arter rapporteras regelbundet från flera av kustens livsmiljöer men mycket grundläggande kunskaper om kustens djur- och växtsamhällen saknas. Avhandlingen har som syfte att öka kunskapen om fiskars struktur och funktion i sjögräsängar och på grunda sandbottnar samt ge insikter i invasionsbiologi genom att studera möjliga ekologiska konsekvenser av främmande fiskarter i näringskedjan.

För att beskriva fisksamhällenas struktur och funktion i dessa kustekosystem kategoriserades alla fiskarter baserat på två indelningsgrunder; en för att beskriva nyttjande av kustmiljöerna och en för födoval. Dessa grupperingar användes sedan för att uppskatta de främmande arternas potentiella påverkan i de två kustmiljöerna samt för att studera deras roll i näringskedjan inom varje habitat. Flera introducerade arters dieter analyserades för att identifiera potentiella konkurrenter och bytesfiskar bland den inhemska fiskfaunan. Under provtagningarna rapporterades två nya främmande arter för första gången.

To my family and my supervisors Leif and Håkan that
made me feel like a part of their own families

LIST OF PAPERS

The doctoral thesis is based on the following publications and manuscripts:

- Paper I **Kalogirou, S.**, Corsini-Foka, M., Sioulas, A., Wennhage, H. & Pihl L. (2010). Diversity, structure and function of fish assemblages associated with *Posidonia oceanica* beds in an area of eastern Mediterranean and the role of non-indigenous species. *Journal of Fish Biology* **77**, 2338-2357
- Paper II **Kalogirou, S.**, Wennhage, H. & Pihl, L. (Manuscript) Non-indigenous species in Mediterranean fish assemblages: contrasting feeding guilds of *Posidonia oceanica* meadows and sandy habitats. Under Review in *Estuarine, Coastal and Shelf Science*
- Paper III **Kalogirou, S.**, Corsini, M., Kondilatos, G. & Wennhage, H. (2007). Diet of the invasive piscivorous fish *Fistularia commersonii* in a recently colonized area of eastern Mediterranean. *Biological Invasions* **9**, 887-896
- Paper IV **Kalogirou, S.**, Mittermayer, F., Pihl, L. & Wennhage, H. (Manuscript) Feeding ecology of indigenous and non-indigenous fish species within the family Sphyraenidae
- Paper V **Kalogirou, S.** (Manuscript) The non-indigenous invasive and pest pufferfish *Lagocephalus sceleratus* in an area of the eastern Mediterranean Sea

Related publications not included in the thesis:

Corsini-Foka, M., **Kalogirou, S.** (2008). On the finding of the Indo-Pacific fish *Scomberomorus commerson* in Rhodes (Greece). *Mediterranean Marine Science* **9/1**, 167-171

Kalogirou, S. (2010). First record of the non-indigenous fangtooth moray *Enchelycore anatina* from Rhodes Island, south-eastern Aegean Sea. *Mediterranean Marine Science* **11/2**, 357-360

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Introduction

The evolution of the Mediterranean Sea

Through most of its existence, the Mediterranean Sea has gone through striking changes in its biota. Geological history of the Mediterranean Sea is complex and it includes the break-up and then collision of the African and Eurasian plates. Mediterranean is a remnant of the Tethys Ocean (Fig. 1) and was populated by tropical biota in pre-historic times (Rilov & Galil 2009, Por 2010). During the Miocene Era, 13.65 million years ago, the Mediterranean Sea was separated from the Indian Ocean (Por 2010). Following that, approximately 7.1 million years ago, the Mediterranean Sea also lost its connection to Atlantic Ocean and was separated from the global oceanic system (Golani et al. 2006, Por 2010). The Mediterranean's present connection to the Atlantic Ocean, through the narrow Gibraltar strait, was established during the Pleistocene Era (5.32 million years ago) and resulted in a subtropical body of water. During the same Era it is also believed that the connection between the Red Sea and the Indian ocean was present (Por 2010). The time at which the Red Sea lost its connection to the Mediterranean Sea is not exactly dated (Por 2010), but it most likely occurred earlier during the Tortonian stage (7 to 11 million years ago) (Bosworth et al. 2005). During the Tortonian stage the Red Sea also lost its connection with the Indian Ocean, thus becoming a hypersaline evaporitic (Bosworth et al. 2005).

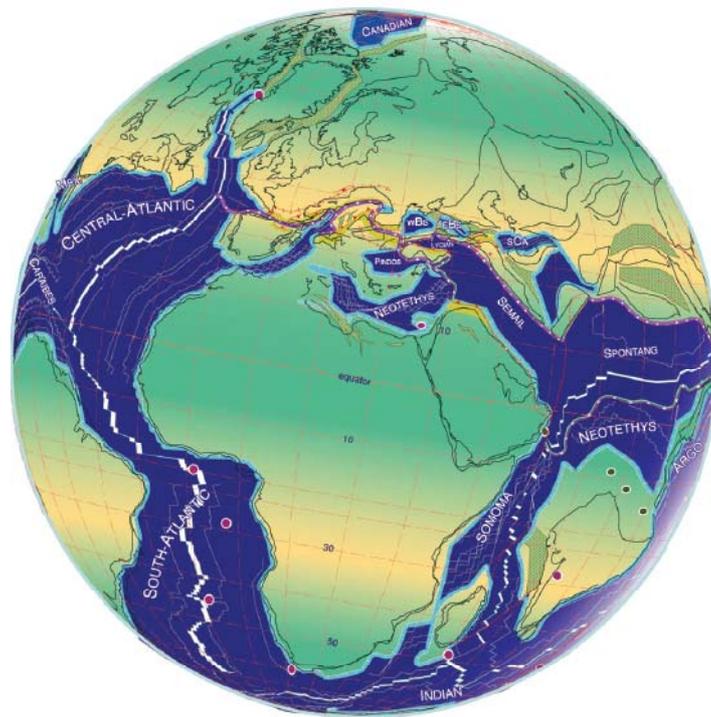


Fig. 1 The Tethys Sea ca. 70 million years ago.

Figure is kindly provided by Prof. F.D. Por, Hebrew University of Jerusalem.

Messinian salinity crisis

After the Mediterranean Sea was cut-off from the global oceanic system a long uninterrupted period with extensive evaporation followed (lasting till 5.32 million years ago), converting the Mediterranean Sea into a hypersaline basin (Por 2010). This period was called the Messinian Salinity Crisis (MSC). As Golani *et. al.* (2006) points out it was for a long time believed that the MSC led to the exclusion of most of Mediterranean's fauna and flora while at the same time losing most of its tropical characteristics. Today the ideas are quite different and it is believed that repeated incursions of Atlantic water in the Mediterranean Sea occurred (Briand 2008). During the MSC shallow water bodies with brackish, marine and hypersaline environments existed. These environments were not believed to be adverse to marine life. The idea that all marine life disappeared during the MSC does not seem to hold anymore (Por 2010). The Mediterranean's connection with the Atlantic Ocean resulted in an enrichment of temperate species.

Circulation and physical characteristics of the Mediterranean Sea

The Mediterranean is considered a semi-enclosed Sea and is divided into two basins, the western and the eastern, separated by the strait of Sicily (Fig. 2). Mediterranean's climate governs west-east differences in water temperature and salinity, and there is a net buoyancy loss due to excess evaporation. Eastern Mediterranean Sea is through extensive evaporation regulating a west-east flow of low saline surface Atlantic water (AW), which gradually becomes denser and denser until it convects downwards and becomes the Levantine intermediate water (LIW). The saltier LIW is then transported westwards and leaves the Mediterranean, thus providing the Atlantic Ocean with salt (Bergamasco & Malanotte-Rizzoli 2010) (Fig. 2). Sea surface temperature ranges between 8-24 °C and 13-31 °C in western and eastern basin, respectively. Similarly, salinity in the western basin is ca. 35 PSU while reaching ca. 39 PSU in the south-eastern Aegean, the Israeli and the Lebanese coasts. All the above-mentioned changes in environmental conditions prevailed over millions of years and significant biotic changes followed, as evident by fossil records.

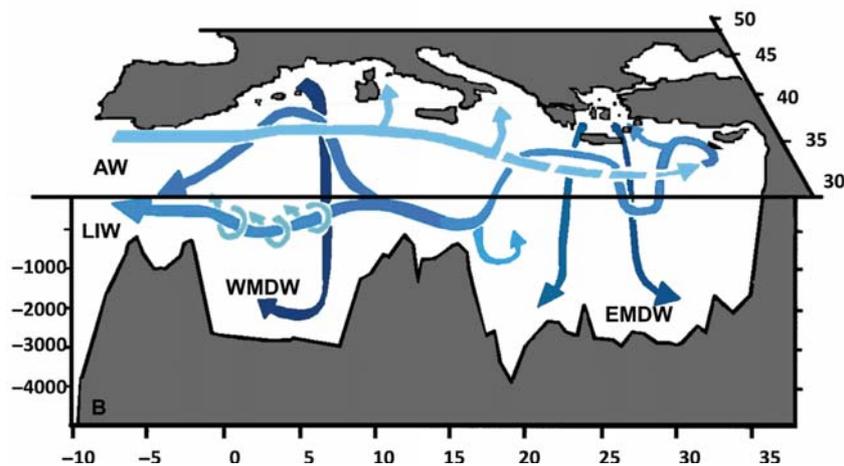


Fig. 2 General circulation of inflowing low saline surface Atlantic Water (AW) and out flowing saline Levantine Intermediate Water (LIW). Figure is kindly provided by Copyright Center of *Taylor and Francis*

The Suez Canal-Lessepsian migration

The idea of excavating a Canal that would connect the Red with the Mediterranean Sea originates from ancient times (Galil 2006, Golani 2010). The driving force to start digging the Suez Canal came in 1852 when the French diplomat Ferdinand de Lesseps submitted a detailed plan to the Governor of Egypt, Abbas Pasha. It took 7 years of a succession of a governor and diplomatic negotiations and another 10 years of hand digging by prisoners and Egyptian fellahs before the Suez Canal was finally completed on 15 August 1869 (Fig. 3). After its completion the Canal was narrow (60-100 meters wide) and very shallow (8 meters in depth). The Canal was deepened and widened several times through time and is at present 400 meters wide and 25 meters deep and 162.5 km long (Golani 2010). In addition, the Canal passes through the high saline Timsah and Bitter Lakes. It was the high salinity levels in the Bitter Lakes that was considered the most important barrier for species attempting to migrate between the Mediterranean and Red Sea. Two years after the opening of the Canal, salinity levels in Bitter Lakes were reported to reach 70‰ (Morcos 1980). A sharp drop of salinity followed and in 1934 the salinity levels in Bitter Lakes had fallen to 40-45‰ (Morcos 1980) increasing the abilities for species to spread northwards. There is also a difference in sea level, establishing a northward current during most of the year (Golani 2010). The Suez Canal lacks rocky substrate, which could serve as stepping stones for migrating reef-associated species, and sand dominates the bottoms throughout the Canal. The construction of the Suez Canal in 1869 is the key reason for the establishment and spread of non-indigenous species (NIS) of tropical origin in the Mediterranean Sea even though other factors such as climate change and increased sea surface temperatures may recently have accelerated the establishment of new species (Raitsoos et al. 2010). This immigration of species from the Red Sea through the Suez Canal into the Mediterranean Seas was called 'Lessepsian migration' in honour of the French diplomat Ferdinand de Lesseps (Por 1990). As mentioned by Rilov and Galil (2009) the Mediterranean Sea can now be considered one of the main hotspots of marine bioinvasions on earth.



Fig. 3 Map of Suez Canal
Kindly provided by Prof. Daniel Golani, Hebrew University of Jerusalem.

Invasion Biology

Geological history of life on earth reveals that continents have been isolated for long periods. It also reveals that sea bottoms were exposed through lower sea levels and that land masses collided allowing for migration (Stachowicz & Tilman 2005). Life in today's seas is altering at an alarming high rate unprecedented in the records of natural changes over geological time-scales. While many species are dwindling due

to overfishing and habitat destruction (Jackson et al. 2001), others invade new areas through anthropogenic vectors (Carlton 1985, Galil 2006, Galil et al. 2007). During the last centuries, human transport has increased the number of NIS introductions. For example, half of the plant species of Hawaii are exotics (Sax et al. 2002) as are about 20% of plants in California bay (Sax 2002) and about 18% of fish species in the eastern Mediterranean Sea (Golani et al. 2002, Golani et al. 2006, EastMed 2010, Golani 2010).

Understanding invasion ecology requires a good knowledge of ecological processes in the systems under study, prior to invasion. Diversity, structure, and function of natural communities would give insights into fundamental ecological processes which could in turn give a better understanding of potential effects following the introduction of NIS.

From a societal perspective, species invasions might pose serious threats to human economic interests and health (Yang et al. 1996, Sabrah et al. 2006, Katikou et al. 2009). Species invasions have also been considered to have negative impacts on native biodiversity (Streftaris & Zenetos 2006, Galil 2007, Lasram & Mouillot 2008, Zenetos et al. 2009). Conflicting studies shows that NIS generally do not impair biodiversity and ecosystem functioning but more often expand ecosystem functioning by adding new ecological traits, intensifying existing ones and increasing functional redundancy (Reise et al. 2006). For most of the occasions, NIS does not have serious effects on ecosystems but there are examples where effects can be severe. Invasions interacts with other factors disturbing marine ecosystem functioning including habitat destruction, pollution and climate change (Rilov & Crooks 2009). Habitat destruction causes disturbance, which opens up space for invaders. Space can also be released by invaders. Consider the example given by Rilov and Galil (2009) where two non-indigenous siganids might have reduced the competition between algae and mussels through intensive grazing, thus providing space for a non-indigenous mussel. Pollution can make environmental conditions less tolerable for native species, and perhaps provide opportunities for opportunists, among which non-indigenous could be found (Occhipinti-Ambrogi & Savini 2003, Wallentinus & Nyberg 2007). Climate warming is predicted to be the driving force for species extending their biographical range northwards in the northern hemisphere and southwards in the southern hemisphere (CIESM 2008), a tendency that is particularly observed in the Mediterranean Sea (Bianchi 2007, Raitsos et al. 2010). This phenomenon has been called "meridionilization" to explain the distributional extension of typical southern thermophilous "meridional" species to the northern parts of the Mediterranean Sea. This phenomenon might enhance the spread of NIS of tropical origin.

Theories and conceptual models of Invasion Biology

The main research in invasion biology has been on temporal and spatial spread of NIS (Golani 1998a, Corsini-Foka & Economidis 2007, Bilecenoglu 2010, Corsini-Foka 2010, Zenetos 2010), conditions facilitating invasions and biological impacts caused by invasions. Conditions facilitating invasions are often of physical (e.g. climate change and increased seawater temperatures) and biological (e.g. traits of species, invisable habitats, pollution) nature. Biological impacts caused by invasions include mostly those of economic interests (e.g. fisheries) (Streftaris & Zenetos 2006), human health (e.g. toxic species) (Yang et al. 1996, Bentur et al. 2008, Katikou et al. 2009) and biodiversity (e.g. competition with indigenous species or habitat modifiers) (Golani 1993a, Golani 1994, Azzurro et al. 2007a, Kalogirou et al. 2007, Wallentinus

& Nyberg 2007, Bariche et al. 2009). A lot of research has also focused on the factors controlling success or failure of invasive species by considering mechanisms of interactions between indigenous and NIS. There is no simple theory for the mechanisms controlling the success or failure of an invading species (Stachowicz & Tilman 2005). Important mechanisms include competition for resources or space (Kalogirou et al. 2007), top-down forces (Goldschmidt et al. 1993), herbivory (Lundberg & Golani 1995, Galil 2007), and parasites (Diamant 2010).

A widely cited theory in invasion ecology is about the relationship between diversity and invasibility of an ecosystem (i.e. more diverse communities should be more resistant to invasion) (Leppäkoski & Olenin 2000). The mechanism explaining it is that as species accumulate the competition intensifies and fewer resources remain available for new colonizers (MacArthur 1955, Levine & D'Antonio 1999). On the other hand, less diverse ecosystems possessing fewer species and simpler food-web interactions would therefore provide empty niches for the establishment of NIS. This hypothesis is often referred as the "biotic resistance hypothesis" (Levine & Adler 2004). As an aid to understand this mechanism both observational and experimental approaches have been applied with conflicting results (Levine & D'Antonio 1999). Stachowicz and Tilman (2005) stated that studies that employ both observational and experimental approaches show that diversity does reduce invasion success. There is a long history of theoretical discussions about the relationship between species richness and productivity or stability of a system. Threats to global species diversity caused by human activities have raised concern on the consequences of species losses to the functioning of ecosystems. In ecology, this concern has received a lot of attention. During the last 20 years, experimental tests of the relationship between species richness and ecosystem processes such as productivity, stability and invasibility have increased rapidly (Stachowicz & Whitlatch 1999).

Another two theories goes back to the work of Darwin. Darwin's "naturalization hypothesis" predicts that NIS tends not to invade areas where closely related species are present because they would compete with their relatives and would encounter predators and pathogens that would attack them. An opposing view is the "pre-adaptation" hypothesis predicting that NIS should succeed in areas where indigenous closely related species are present because they are more likely to share traits that pre-adapt them to their own environment. Since most studies have focused on plant species, Ricciardi and Mottiar (2006) tested these hypotheses on fish species and could not find any support for either hypothesis. Ricciardi and Mottiar (2006) agreed with Moyle and Light (1996) that success is primarily determined by competitive interactions (e.g. "biotic resistance" hypothesis), propagulae pressure and environmental abiotic factors (i.e. the degree to which NIS physiological tolerances are compatible to local physical conditions).

Rapid changes in environmental conditions, caused by human activities, have also been mentioned as to increase invasibility (Occhipinti-Ambrogi & Savini 2003). Habitats that lack predators are also suggested to be more prone to introductions of NIS (Moyle & Light 1996).

There is also a higher risk of further establishment of species in habitats that have already been invaded, referred as the "invasional meltdown" (Simberloff & Von Holle 1999, Ricciardi 2001). In a study from Great Lakes, Ricciardi (2001) found support for the "invasional meltdown" hypothesis by showing that positive interactions (mutualistic) among NIS are more common than negative (competitive). In further

support of the "invasional meltdown" hypothesis, Ricciardi (2001) shows that exploitative interactions (e.g. predator-prey) among NIS are strongly asymmetrical.

Defining introductions and their status

Several definitions are used to describe the invasion status of NIS. A common general definition used is *Introduced*, a definition misleadingly also often referred as alien, exotic, non-native or novel species. *Introduced* is referred to as a species that has been transported by human activity across a geographical barrier from a native donor region to a new recipient region. When evaluating the introduction status of species, five common non-exclusive definitions are used; *Established* or *naturalized* is referred as a species being able to reproduce and maintain a population in its new recipient region, *casual* when failing to reproduce and are only occasionally found, *invasive* when it occurs in high abundances and have a negative impact on native biodiversity, *pest* when a species is unwanted by humans in a specific area (e.g. have a social or economical impact), and *transformer* when a species is able to change ecosystem functioning (Richardson et al. 2000).

In the Mediterranean Sea, the general term *Lessepsian migration* have been widely used to define the influx of Red Sea biota into the Mediterranean Sea via the Suez Canal (Por 1978). Nevertheless, the term non-indigenous species (NIS) will be used throughout this thesis to identify a species that is introduced by man, regardless of date and origin.

Vectors of introductions

The vectors of introductions can be divided into two main categories, namely *accidental* and *intentional*.

Accidental introductions include the well known ballast water transportation which is considered the most important mode of unintentional dispersal of aquatic species worldwide. Other important modes of unintentional introductions are transport of sessile species on ship hulls, unintentional releases of aqua-culture organisms and associated species, species related to the aquarium trade and species immigrating through the constructions of new waterways. Probably, the most striking example of accidental vector is the construction of the Suez Canal in the Mediterranean Sea where direct transport (i.e. through the channels water) is considered the most important vector for the introduction of new species into the Mediterranean Sea (Rilov & Galil 2009).

Intentional introductions are mainly related to human consumption and thus mainly concerns fish and mollusca species. However, species that accompany the intentionally introduced species (e.g. parasites, epiphytes) is by far outnumbering the intentionally introduced species. Most work concerning the decisions made to introduce or not a NIS, has so far mainly been taken into account in the North America (Thomas & Randall 2000). Decisions have considered gaining benefits without disrupting the ecological balance or facing an ecological devastation.

The invasion process

The invasion of an introduced species can be divided into four main steps, as described by Heger and Trepl (2003). These steps includes: the *arrival* phase when a species is introduced by humans regardless of mode; the *establishing* phase, when a species is able to reproduce both in the biotic (e.g. competition for food resources,

predation) and abiotic (e.g. salinity, temperature) conditions of its new region; the *integration* phase when the introduced species is able to build up new ecological links in its new environment and the *dispersal* or *spreading* phase when a species is able to extend its distribution within its new environment (e.g. other habitats).

An invading species might sometimes go to a peak of density and then decline, a path often called boom and bust. This path followed the NIS bluespotted cornetfish *Fistularia commersonii* in the area under study (Kalogirou, pers. obs.). When a NIS is transported into waters where its preferred food is under-utilized by indigenous species the resulting population explosion is later brought into equilibrium with available resources. Even though this dynamic leads to the significant reduction of the invading species population size, only very few studies have reported subsequent extinction of the NIS. Competition, despite strong advocacy (Moulton 1993), seems to be the least likely explanation for most of the examples (Williamson & Fitter 1996). Decline and extinction from a build-up of enemies (predators and pathogens) and lack of sufficient resources is more likely to be important explanations in failure of invading animals to establish permanent populations (Williamson & Fitter 1996).

Biological Invasions in the Mediterranean Sea

For the past two centuries the biodiversity in the Mediterranean Sea has been altering at an alarmingly high rate due to human mediated arrival of new species. Mediterranean Sea is considered to be one of the main hotspots of marine bio-invasions on earth (Rilov & Galil 2009), and is by far the major recipient of NIS among European seas including macrophytes, invertebrates and fish (Streftaris et al. 2005). Mediterranean is unique due to the route of immigration via the Suez Canal, the so called Lessepsian immigration (Por 1978). The rate of this immigration has increased in recent decades and has ecological, social and economical impacts (Streftaris & Zenetos, 2006). Eastern Mediterranean basin is potentially more prone to introductions of subtropical and tropical NIS via the Suez Canal than western basin is. This has been attributed to different physical and biological conditions between the basins. Eastern Mediterranean possesses more subtropical physical conditions (i.e. arid nature) and maintains lower number of species (i.e. leaving empty niches). It is to mention that the construction of the Aswan Dam in 1966 in Nile River reduced the freshwater flood into the Mediterranean Sea. This led to increased salinities of 2-3% in Egyptian coasts while reducing one of the most important sources of nutrients in the Mediterranean Sea (Galil 2006). The Nile Damming might have positively influenced the westward dispersion of NIS immigrating through the Suez Canal along the North African coasts (Ben-Tuvia 1973).

Two main terms have been recently added in invasion biology studies of the Mediterranean Sea: Tropicalization and Meridionalization. The "tropicalization" of the Mediterranean Sea refers to the augmented influx of thermophilous species throughout the Mediterranean Sea (Bianchi & Morri 2003) and is described as a combined effect of four different phenomena: introduction of NIS of tropical Atlantic origin, lessepsian immigration, man-made introductions and sea-water warming. With "meridionalization" we mean the homogenization of fauna and is described as the northward extension of thermophilous species distribution and the recession of boreal ones (Massuti et al. 2010).

In a recently published book on biological invasions the history, distribution and ecology of marine bioinvasions in the Mediterranean Sea is discussed (Rilov & Galil 2009). The authors divided the Mediterranean into three regions; western, central and

eastern. At the same time the authors used current temporal, spatial and ecological data on fish, crustacea and mollusca from CIESM (International Commission for the Scientific Exploration of the Mediterranean Sea). The data was used to analyze the contribution of NIS origin for each region and taxa (Fig. 4).

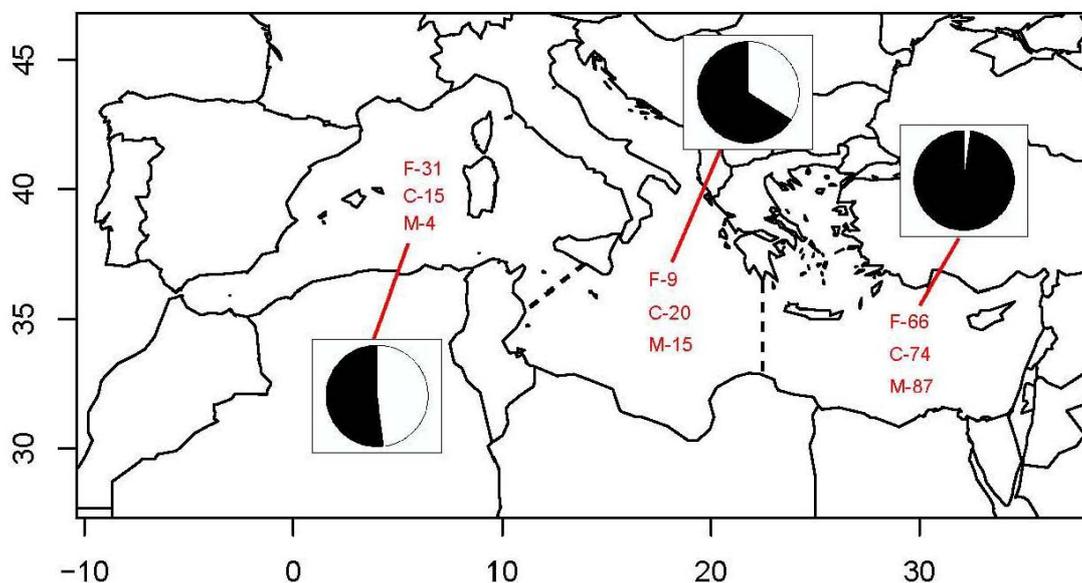


Fig. 4. Spatial patterns of NIS in the Mediterranean. Numbers indicate the percentage of each taxa (F: Fish; C: Crustacea; M: Mollusca) in each region of the Mediterranean. Pie charts indicate the percentage (all taxa pooled) with either Pacific (black) or Atlantic (white) origin. *Redrawn* from Rilov and Galil (2009).

Non-indigenous fish species in the Mediterranean Sea

Approximately 716 fish species inhabit the whole Mediterranean Sea (Froese & Pauly 2011) with a general decrease in number of species moving eastwards (Golani et al. 2006). Among these, 80 are non-indigenous of Indo-Pacific and Red Sea origin (Cicek & Bilecenoglu 2009, Bariche 2010, EastMed 2010, Golani 2010).

There is lack of information on ecological effects of many NIS introduced through the Suez Canal and it is apparent and that no general conclusions can be drawn (Rilov & Galil 2009). It is at the same time obvious that the ecological effects of some species are strong (Kalogirou et al. 2007, Bariche et al. 2009). Competitive exclusion and displacement of native species are often potential expectations in ecological studies (Galil 2007).

Several indigenous species such as *Sparisoma cretense* and *Thalassoma pavo* have been regarded as "meridional" (CIESM 2008) since they have been found to reproduce and maintain naturalized populations in the coldest part of the Mediterranean Sea (Ligurian Sea) (Guidetti et al. 2002). Additionally, a reduction of temperate species followed the increase of tropical species in the Ligurian Sea (Bianchi & Morri 2003).

A noteworthy example from the Mediterranean Sea was the appearance of two herbivorous fish species *Siganus rivulatus* and *Siganus luridus* (fam. Siganidae), which entered the Mediterranean through the Suez Canal and were believed to have affected the ecosystem resilience. Recently, these two siganid species impact on indigenous species communities received a lot of scientific attention and

contradiction, and were studied by several authors (Bariche et al. 2004, Azzurro et al. 2007a, Galil 2007, Golani 2010). These two species were for the first time recorded off the coasts of Palestine in 1924 and Israel in 1955 (Rilov & Galil 2009). Since then, these herbivorous species have spread westwards and are today found as far as Sicily and Tunisia. Goren & Galil (2001) showed that these two species approximately made up one third of the total fish biomass in the vermetid reef of Shiqmona (Israel) while Bariche *et al.* (2004) showed that the contribution of Siganidae to the guild of herbivorous fish species in shallow coastal areas of Lebanon reached 80%. Additionally, Bariche *et al.* (2004) and Galil (2007) showed that these two species not only out-competed native herbivorous fish such as *Boops boops* and reduced their abundance but even replaced the native herbivorous species *Sarpa salpa*. In contradiction, Golani (2010) finds the replacement of *S. salpa* suspicious since Bariche (2004) relied on the abundance description, prior to colonization, given by Gruvel (1931) who were not an ichthyologist and who might easily have confused *S. salpa* with *B. boops* together with information given by Gruvel (1931) that *B. boops* was not captured by trawl. Moreover, Lundberg & Golani (1995) compared the feeding of siganids relative to food availability in the source (Red Sea) and recipient area (Mediterranean Sea) and found that in comparison algae are highly abundant in eastern Mediterranean. This reveals lack of data to postulate that NIS are better competitors than indigenous ones until it is proven that trophic resources constitute the most important limiting factor (Golani 2010). Nevertheless, negative consequences of fish invasions are not only restricted to native fish communities. As showed by Rilov *et al.* (2009), grazing of macroalgae by these Siganidae species released space on rocky shores along the Lebanese coast. The space released is believed to have been overtaken by a non-indigenous mussel, *Brachiodontes pharaonis*, most likely transported with hull fouling through the Suez Canal. It is to be mentioned that the two siganids are commercially important in the eastern Mediterranean Sea.

Aims of the Thesis

This thesis aims to increase the knowledge on the fish assemblage structure and function of *Posidonia oceanica* and sandy habitats in a coastal area of the eastern Mediterranean and give insight to invasion biology by investigating the potential impact of introduced fish species to the local ecology and food-web of the marine systems concerned. Analysis of functional and feeding groups as well as diet descriptions were considered important first steps in order to evaluate the potential role and impact of recently established NIS in the recipient region. During the sampling campaign two species were for the first time reported in the area.

One of the fundamental aspects in ecology is the explanation of temporal and spatial distribution patterns of organisms. An invasive species can become dominant in an ecosystem displacing and/or even replacing native species. This is due to the fact that a species invading a new environment and consequently establish in it, use both space and food. The impact may not be of “a first order” to humans, but can affect the biodiversity dramatically. Most of the work done so far, in the marine area of concern, only takes into account the presence of new species but neither their distribution nor their ecology. The need to characterize, both quantitatively and qualitatively the fish diversity associated within different habitats is of major interest and importance in order to determine the structure of ecological communities as well as understanding the role of NIS. For that reason I begun with describing the fish assemblage structure associated with *Posidonia oceanica* habitat by classifying species into functional guilds, followed by investigations of the role of NIS in the food-web of two important coastal habitats by categorizing species into feeding guilds. In addition, the distribution and feeding ecology of invaders in new areas were investigated to assess the ecological impacts of NIS to native biodiversity and to assess their social impacts.

The specific aims of this thesis are:

1. To quantitatively assess the fish assemblages associated with *Posidonia oceanica* meadows and to develop a system for classifying the fish fauna into functional guilds. In addition, the role of NIS in this habitat was studied. **(Paper I)**

In **Paper I**, temporal variation in density and body size of fishes was used to assess the seasonal and ontogenetic habitat use of each species, with their affinity to seagrass assessed by comparing their respective distribution on sand. Four functional guilds were created (juvenile migrants, seagrass residents, seasonal migrants and occasional visitors) to describe the habitat use of *Posidonia oceanica* meadows by each species.

2. To investigate the role of non-indigenous fish species in the food web of two common coastal habitats in an area of the eastern Mediterranean. Specifically, we tested if there is a significant higher proportion of non-indigenous fish species on sandy bottoms compared to *Posidonia oceanica* meadows. Seasonal dynamics in the proportion of NIS within and between the two habitats was also investigated. **(Paper II)**

In Paper II, we designed the study to investigate the fish assemblages associated with *Posidonia oceanica* and sandy bottoms, two dominating coastal habitats in the eastern Mediterranean. Through quantitative sampling, the objective of this study was to assign fish species to a feeding guild, in order to investigate the contribution and position of NIS in the food-web contrasting the two habitats.

3. To describe the feeding habits of the invasive piscivorous fish *Fistularia commersonii* from a recently invaded area. (**Paper III**)

In **Paper III**, the feeding ecology of a recently introduced NIS, *Fistularia commersonii* was described during fall and winter. Size-related differences between prey items and their contribution in number and weight to the diet were assessed. The feeding habits determined were also used to evaluate the potential impact of this NIS on the native food web. One of the most important aspects of the ecology of an invasive species is the diet that it assumes after colonisation and how this may affect native competitors and prey.

4. To study the feeding ecology of indigenous and non-indigenous fish species of the barracuda family Sphyraenidae (**Paper IV**)

In **Paper IV**, the diet composition of the two common indigenous (*Sphyraena sphyraena* and *Sphyraena viridensis*) and one abundant non-indigenous sphyraenid species, *Sphyraena chrysotaenia*, was investigated in an area of the eastern Mediterranean Sea. Different sizes, collected during the period February 2008 to December 2009, were examined. This was the first study to analyse the feeding habits of the most common species within the Sphyraenidae family in the eastern Mediterranean Sea. Confamilial overlap in feeding preferences was investigated to assess any possible competition between indigenous and NIS, accounting for differences in size distribution among the species. The feeding habits were used to assess the potential role of the NIS *S. chrysotaenia* in the food web. Additionally, the condition for each of the predator species were seasonally analysed to assess the potential negative effect of NIS on indigenous species.

5. To investigate the role of the non-indigenous pest pufferfish, *Lagocephalus sceleratus* in *Posidonia oceanica* beds and on sandy bottoms.

The aim of Paper V was to quantitatively study the size distribution of *Lagocephalus sceleratus* in *Posidonia oceanica* beds and on sandy bottoms. By quantitatively investigating the habitats used during the life cycle ontogenetic habitat shift was identified. Further, through dietary analyses the aim was to assess possible interactions in the food web and to discuss its potential impact on commercial fisheries.

General Methods

Study area

The shoreline of Rhodes Island is characterized by a mixture of rocky- and sediment-bottom areas. Mean surface water temperature ranges between 16 and 18 °C in winter, 21 and 23 °C in autumn and spring respectively, reaching 28 °C in summer. Surface salinity is constant throughout the year and is between 39.3 and 39.7. Five of the selected coastal locations in the studied area were typical *Posidonia oceanica* habitats (locations 1, 2, 3, 4, 5; Fig. 1) while the remaining two were sandy habitats (locations 6 and 7; Fig. 1). *Posidonia oceanica* is distributed over sediment bottoms between the water depths of 5 to 35 m. The study of **Paper I** included five locations (1, 2, 3, 4 and 5; Fig. 1). The study of **Paper II** was performed on two *P. oceanica* (locations 1 and 2; Fig. 1) and two sandy habitats (locations 6 and 7; Fig. 1). For **Paper III** all samples were collected from sampling location 1 (Fig. 5). For **Paper IV** and **V** all samples were collected from locations 1, 2, 6 and 7.

Sampling

The Danish seine fishing method was used to sample fishes from two coastal habitats (*Posidonia oceanica* and sandy habitats) with the help of a local fishing boat. The design of the seine used in this study consisted of a set of long warps (400 m), brails (connecting the lines with the wings), a net panel of various mesh-sizes with a codend in the centre. The operating procedure was first to anchor and buoy the end of the start warp, usually 70 meters from the shoreline. After the start warp was set out, the boat was headed *c.* 45° from the shoreline. The first wing, followed by the net, the codend and the other wing had a total length of 350 m and were laid parallel to the shoreline before the boat headed back to the buoy with the back warp. The track of the boat thereby formed a triangle. Once both warps were onboard and attached to winches the seine was hauled at a constant speed of *c.* 0.3 m s⁻¹. The total time elapsing from deployment of the start line with an anchor to the time the seine was taken onboard was *c.* 35 min. Mesh-size decreased from the outer end of the wing towards the centre in the sequence 500, 180, 32–34, 12 and 11 mm, with a minimum mesh-size of 8 mm in the codend. For **Paper I** and **II** three sweeps with the seine were randomly taken at each location and sampling occasion, covering a total area of 0.12 km² (0.04 km² per

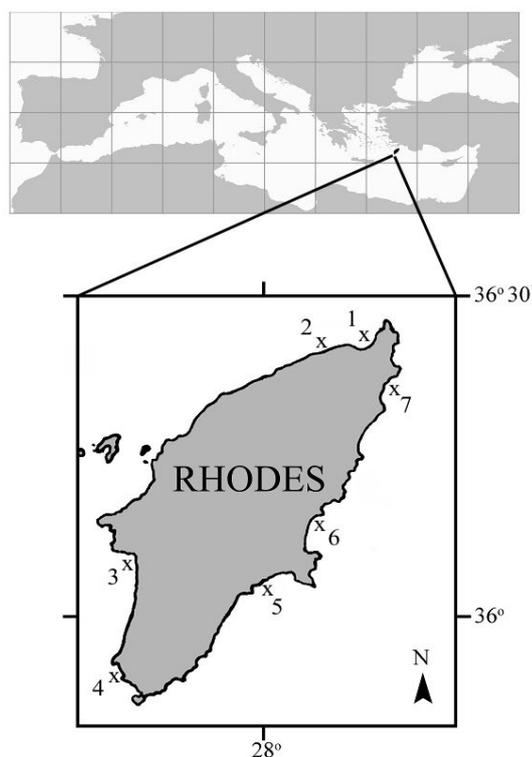


Fig. 5 Map of Rhodes Island with sampling locations.

seining). In Hellenic waters, fishing with the Danish/boat seine was banned from 1st of April till 31st of September according to national legislation, and the method was totally banned according to EC in May 2010.

In **Paper I**, temporal and spatial variations in fish assemblages associated with *Posidonia oceanica* beds were investigated through daylight sampling at five localities (1, 2, 3, 4 and 5) on four occasions over the year 2008: February (winter), May (spring), August (summer) and December (autumn).

In **Paper II**, temporal and spatial variations in fish assemblages associated with two coastal habitats were investigated through daylight samplings on four locations where two represented *Posidonia oceanica* (1 and 2) and two sandy habitats (6 and 7) on four occasions over the years 2008-2009: December 2008 (Autumn), March (winter), May (spring) and August (summer).

In **Paper III, IV and V** a total of 245 *Fistularia commersonii*, 738 sphyraenid (*Sphyraena viridensis*, *Sphyraena sphyraena* and *Sphyraena chrysotaenia*) and 290 *Lagocephalus sceleratus* individuals were analyzed.

Statistical analyses

This thesis included analyses of fish assemblage structure, function of ecological communities and diet descriptions. For parametric tests, XLSTAT (Ver. 2010.05.08) was used to perform single- and multifactorial- analysis of variance (ANOVA) (Quinn & Keough 2002) while pair-wise tests were performed with Tukey's Honest Significant Difference tests (HSD). Non-parametric tests were performed in PRIMER 6 (Ver. 6.1.12) and PERMANOVA + (Ver 1.0.2) from PRIMER-E (Plymouth Routines In Marine Ecological Research) (Clarke & Gorley 2006). From PRIMER, multidimensional scaling (MDS) similarities percentages (SIMPER) and analyses of similarities (ANOSIM) were used (Clarke & Gorley 2006). Affinity, diet electivity (Chesson 1978), diet breadth (Smith & Zaret 1982) and diet overlap indices were also used in this thesis.

Diversity, structure and function of fish assemblages associated with *Posidonia oceanica* and sandy habitats. Functional and Feeding Guilds (Paper I, II)

Studies that describe and compare the structure of fish assemblages in different habitats commonly do so through the analysis of several components. i.e. presence/absence, abundance and/or biomass of species (Guidetti 2000). Spatial and temporal measurements of species density and/or biomass are important in order to understand habitat use of fish species.

When evaluating fish function and habitat use, functional guilds are valuable complements to the use of taxonomic groups. Habitats have several ecological roles for species and can serve as spawning grounds, nursery areas, and feeding grounds. The functional guilds developed in **Paper I** were defined using the approach described by Elliot and Dewailly (1995), although the guilds were modified according to the local ecosystem and the ecology of the fish species. Functional guilds were defined for all fish species as: SR – Seagrass residents, species which are stationary and highly dependent on *Posidonia oceanica* meadows and where both juveniles and adults can co-occur seasonally; JM – juvenile migrants, species which use seagrass primarily as a nursery ground; SM – seasonal migrants, species which seasonally visit seagrass, usually as adults for spawning or feeding and OV – occasional visitors, species that appear in low abundances or in low association to this habitat. Non-

indigenous species were identified and their distribution among functional groups investigated.

Statistical analyses of **Paper I** included temporal variations in density, biomass and number of fish species with one-way ANOVA (Underwood 1997). All data were examined for normality and homoscedasticity *via* histograms, Q-Q plots and residuals *v.* fitted plots. Tukey's honest significant difference (HSD) test was used to identify temporal density variation in pair-wise comparisons between seasons. Temporal and spatial variation in assemblage structure based on density was investigated using the Bray–Curtis similarity index (Field et al. 1982). Nonmetric multidimensional scaling (MDS) was produced using Primer for Windows (version 6) (Clarke & Gorley 2006). Dispersion weighting (Clarke et al. 2006) was applied to reduce the contribution of schooling species in separating samples. Additionally, analysis of similarity (ANOSIM) was used to determine if there was a difference in fish assemblage structure between seasons.

Two picarel species, *Spicara smaris* (L.) and *S. maena*, were excluded from measurement of seasonal variation in total density and biomass, since they are strictly planktivorous and are rather more a part of the water column than associated with *P. oceanica* beds. These species were also excluded from ANOSIM when investigating seasonal differences in assemblage structure. Two of the schooling species, the bogue *Boops boops* (L.) and the damselfish *Chromis chromis* (L.), were highly associated with *P. oceanica* beds and were therefore not excluded from the analysis despite their high contribution to the variability among samples.

In **Paper II** the position and contribution of NIS in the food web of the fish assemblage of *Posidonia oceanica* and sandy habitats was investigated by categorizing each species into feeding guilds, based on a review of the feeding habits of Mediterranean fish by Stergiou and Karpouzi (2002). For fish species not included in this review additional information was obtained from Bell & Harmelin-Vivien (1983) Whitehead *et al.* (1986), Cardinale *et al.* (1997) as well as own dietary analyses (Kalogirou, unpublished). Primary information on the diet of each species was used to construct the following feeding guilds: herbivorous (H), zooplanktivorous (Z), invertebrate feeders (I), piscivorous (P), invertebrate and fish feeders (IF) and omnivorous (O). To be classified to the feeding guild H, Z, I and P, 90% of the diet had to belong to the respective food category. Further, to be classified as IF, invertebrates and fish together had to add up to 90 % of the total diet while when vegetation together with invertebrates and/or fish were among the food categories and contributed to 90 % of the total diet it was classified as O. The purpose of this classification was to reveal new interactions in the food web and give insights on the impact on food resources and potential competitors, following the introduction of non-indigenous fish species.

Statistical analyses of **Paper II** included temporal and spatial variations in density, biomass and number of fish species, analyses that were investigated with a three-way nested ANOVA. Habitat (*Posidonia* beds or sandy bottoms) and season (winter, spring, summer or autumn) were fixed factors with localities (1-4) nested in habitats. No transformation was applied for absolute values of density, biomass and number of fish species while arcsine transformation was applied to test differences in the proportions of NIS (Sokal & Rohlf 1995). Normality and homoscedasticity assumptions were met for both absolute and transformed data (Underwood 1997, Quinn & Keough 2002). Tukey's HSD (Honest Significant Difference) test was used to discriminate seasonal variations within each habitat. In addition, fish assemblage

structure was compared among seasons and between habitats using non-parametric multivariate analysis. A Bray-Curtis similarity matrix based on fish biomass was used to produce a non-metric Multi Dimensional Scaling ordination (MDS) (Clarke & Gorley 2006) in order to 2-D visualize differences in the fish assemblages between habitats and seasons. The biomass data had been log-transformed prior to analysis. A bubble-plot was superimposed on the MDS to show patterns in the proportions of non-indigenous species that could be attributed to habitat and season. The similarity matrix was also used to perform an ANOSIM in order to discriminate seasonal and habitat differences in the fish assemblages (Anderson 2001a, b, McArdle & Anderson 2001). In addition, a SIMPER analysis (Clarke & Gorley 2006) was performed to identify the species mainly responsible for similarities and differences in fish assemblage structure between habitats.

Dietary analysis (Paper III, IV and V)

Each specimens were thawed, measured (total length: TL, standard length: SL, accuracy of 0.01 cm), and wet weighed (accuracy of 0.01 g). Prey items were counted by number and identified to the lowest taxonomical level possible, depending on the extent of digestion (well digested, partially digested, or fresh). Prey species were identified accordingly (Fischer 1973, Smith & Heemstra 1986, Whitehead et al. 1986). After identification, each prey was wet weighted with an accuracy of 0.01 g and the SL was measured, with 0.001 cm accuracy, by use of a caliper. The by-number (% N) and by-weight (% W) composition was determined for all identified prey, to quantify and evaluate their contribution to the diet.

In **Paper III** investigation of the feeding habits included pooling prey species into taxonomic (i.e. families) and functional groups—benthic, supra-benthic, and pelagic fishes, following Goren and Galil (2001), depending on their habitat use stated in the literature (Fischer 1973, Smith & Heemstra 1986, Froese & Pauly 2005). Additionally, predators were pooled into three size classes (SL): 0–350 mm (class 1), 351–700 mm (class 2), and 701–1050 mm (class 3). Fish length was plotted against prey length to assess any relationship between predator size and prey size, for benthic, supra-benthic, pelagic prey and for all prey combined.

In **Paper IV**, diet composition was investigated by calculating each prey species, percentage by number (%N), occurrence (%O) and weight (% W) in the stomachs of each of the predators examined.

To investigate feeding selectivity, we included density in fish resource availability following Manly-Chesson's alpha (α) selectivity index (Chesson 1978, Krebs 1989). A selectivity index value (α) greater than $1/n$ indicates selection for a prey species and a value less than $1/n$ indicates avoidance of a prey species while n is the number of prey species available (e.g. $n=20$ and the critical value is $1/n=0.05$). Manly-Chesson's α represents the value of each prey in relation to its density in its natural environment (Lechowicz 1982).

Diet breadth was investigated by the use of Smith's measure (Smith & Zaret 1982). Smith's measure of niche breadth varies from 0 (minimal) to 1.0 (maximum). This measure was preferred, among others available in the literature, since it takes into account the proportions of fish species in the environment and it is less sensitive to selectivity of rare resources (Krebs 1989). The proportion of each prey species in the environment were based on a quantitative fish study performed over *Posidonia oceanica* meadows in the studied area (**Paper I**). It is to be mentioned that presence of predators and prey was concurrently found during the same season (summer). To

investigate diet breadth, each species was grouped as pelagic, supra-benthic and demersal. Being in awareness of the high mobility of the predators examined, we presumed that their feeding capabilities were limited to pelagic and supra-benthic living prey (Golani et al. 2006, Froese & Pauly 2011). For that reason, the potential feeding was investigated including only pelagic and supra benthic species. The high amount of fresh or partially digested fish prey was assumed to a feeding mainly over the same habitat.

Diet overlap between species was investigated by the use of Schoener's index of overlap (Schoener 1974). Schoener's index was calculated for occurrence of prey items identified to species level. The index was calculated to test inter-specific overlap in feeding preferences but also to investigate potential intraspecific competition by classifying species into three size classes according to Allam *et al.* (2004a). To separate juveniles from adults, border values were set to 18cm. Index values range from 0 to 1; approaching 0 for species that share no prey and approaching 1 for species pairs that have identical prey utilizations. Values exceeding 0.6 have been considered to represent "biologically significant" overlap in resource use (Wallace 1981).

In addition, each predator's length was plotted against the total length of its prey to investigate predator-prey length-length relationships. Spearman's nonparametric correlation was used to examine the significance of the correlation.

Condition of each species was temporarily examined where seasons were classified accordingly: January-March representing winter, April-May representing spring, June-September representing summer, and October-December representing autumn. The condition factor was calculated according to Le Cren (1951) and recommendations given by Froese (2006). Due to differences in sample size between size class and season, ten fish were randomly selected and used to test seasonal differences in condition for each of the predators by the use one-way ANOVA.

In **Paper V**, identification of prey items was limited to higher taxonomic levels since the beak-like jaws of *Lagocephalus sceleratus* crush food items to the extent that prey could not be identified to species. However, cephalopod beaks found in the stomachs could easily be identified to species level according to Clarke (1986). Due to differences in level of taxonomic classification, prey items were arranged into three major groups as Mollusca, Crustacea and Fish. In this study only an indication of the prey families and species identified were given with no quantitative measurement on percentage prey by number or by weight.

Thus, the description of *Lagocephalus sceleratus* diet was limited to percentage frequency of occurrence of each taxa. Additionally, to investigate ontogenetic diet shift with increased fish size, *L. sceleratus* individuals were categorized into seven size classes accordingly: 0-10, class 1; 10.1-20, class 2; 20.1-30, class 3; 30.1-40, class 4; 40.1-50, class 5; 50.1-60, class 6 and 60.1-70 to class 7.

Reproduction

Maturity stage and sex was macroscopically examined only for **Paper V**. Stages of maturity were classified as I, immature; II, developing; III, mature; IV, ripe; V, running; and VI, spent. With this information, length at first maturity was estimated as length at which 50% of the fish had become mature. Sampling design performed in **Paper II** helped to investigate temporal and size variations in the occurrence of *Lagocephalus sceleratus* contrasting two coastal habitats (*Posidonia oceanica* meadows and sandy habitats).

Main Results and Discussion

Diversity, structure and function of fish assemblages associated with *Posidonia oceanica* meadows in an area of the eastern Mediterranean and the role of non-indigenous species

Several studies have focused on the fish fauna of *Posidonia oceanica* meadows in western Mediterranean (Bell & Harmelin-Vivien 1982, Francour 1997, Guidetti 2000, Moranta et al. 2006, Deudero et al. 2008), while the information is scarce for the eastern part of the Mediterranean as most studies on littoral fishes concerns rocky substratum (Goren & Galil 2001, Harmelin-Vivien et al. 2005, Golani et al. 2007). Therefore, the diversity, structure and function of fish assemblages in *P. oceanica* meadows of the eastern Mediterranean are largely unknown.

Posidonia oceanica meadows play an important ecological role and provide benefits to humans that rank among the highest of all ecosystems on earth. *P. oceanica* produce oxygen and organic material while at the same time provides a habitat for food, shelter and breeding for several species. Leaves and rhizomes provide a surface for sessile species and shelter for mobile species, thus sustaining a highly diverse ecosystem. *Posidonia oceanica* meadows are especially valuable in providing a nursery habitat for several commercial fish species (Bell & Harmelin-Vivien 1982, Francour 1997).

This study showed that *Posidonia oceanica* meadows from the eastern Mediterranean sustain a diverse fish community including 88 species within 34 families, a number that accounts for 19% of the total number of fish species inhabiting the eastern Mediterranean (Papakonstantinou 1988, Golani et al. 2006). Even though the total number of fish species recorded during this study was higher than the total number of species recorded in the same habitat in western Mediterranean (Francour 1997, Moranta et al. 2006, Deudero et al. 2008), several species were only occasionally found and their role could not be fully addressed. The mean number of species varied among localities between 23 and 28 in spring and summer and between 17 and 23 in autumn. The high mean species richness found on *P. oceanica* meadows during this study is in accordance with several studies performed in western Mediterranean (Francour 1997, Guidetti 2000), indicating that physical structure of habitats is an important factor affecting near-shore fish assemblages (Bell & Harmelin-Vivien 1982, Guidetti 2000). Mean number of fish caught per location with boat seining was highest during samplings in summer (August) with *c.* 13000 individuals. The three times higher values of mean fish density in summer were attributed both to increased densities of fish species and to the recruitment of juveniles, a pattern that is in accordance with *P. oceanica* habitats in western Mediterranean (Deudero et al. 2008). Several authors from western Mediterranean have emphasized the important role of seagrass as nursery areas for many fish species (Bell & Harmelin-Vivien 1982, García-Rubies & Macpherson 1995, Francour 1997, Pihl & Wennhage 2002, Moranta et al. 2006, Deudero et al. 2008). Food and shelter are referred to as the main factors for juvenile and adult fish species, and thus vegetated habitats play a crucial role in providing these requirements (Guidetti 2000). Temperature is often considered as a major factor for the dynamics of fishes and water temperature may trigger migrations of fish species within the shallow coastal zone and/or offshore waters (Pihl & Wennhage 2002). However, the lack of tides, constant salinity regime, low temperature range, and depth range of *Posidonia oceanica* may be responsible for the stable community structure observed, that was

also concluded by Bell and Harmelin-Vivien (1982). In addition, the similarity in assemblage structure and lack of evident difference observed in mean fish biomass and numbers of species among seasons in this study indicate a stable community structure with little variation in production over the year. The obvious peak in recruitment of several fish species during summer could probably explain the observed seasonal pattern in fish species composition.

Labridae and Sparidae were found to be the two most diverse fish families, which is in accordance with previous studies from western Mediterranean (Bell & Harmelin-Vivien 1982, Francour 1997, Moranta et al. 2006, Deudero et al. 2008). The high abundance of Labridae in *Posidonia oceanica* meadows may be attributed to greater availability of their prey items (amphipods and gastropods) which benefit from higher primary production due to increased nutrient levels (Bell & Harmelin-Vivien 1982).

Functional or eco-trophic guilds have been widely used in European seas (Elliott & Dewailly 1995, García-Rubies & Macpherson 1995, Francour 1997, Deudero et al. 2008) to indicate fish species use of different habitats. The high proportion of seagrass resident species in this habitat indicates the important role of this habitat both for adults and juveniles as also observed by Francour (1997) and Bell and Harmelin-Vivien (1982). The majority of the species within this guild showed a high affinity to seagrass. Several authors have mentioned that members of the Labridae family recruit in *Posidonia oceanica* meadows (García-Rubies & Macpherson 1995, Francour 1997). In addition, Bussotti and Guidetti (1999) showed that juveniles of several species of the family Labridae were occupying the same habitat occupied by adults, a pattern that is consistent with the results from this study where most of the Labridae species were classified as seagrass residents. Several species of commercial value were found to be residents in *P. oceanica* meadows (e.g. *Spicara smaris*, *Spicara maena*, *Boops boops*, *Sphyræna viridensis* and *Sphyræna sphyraena*) although without neglecting the fact that several of these pelagic fishes may also be distributed over coastal rocky and sandy bottoms (Fig. 6). The high contribution of juvenile migrants indicated the use of this habitat as a nursery ground during summer, a pattern that is consistent with studies of fish assemblages in western Mediterranean (García-Rubies & Macpherson 1995, Francour 1997). As pointed out by several authors studying seagrass systems in western Mediterranean (Bell & Harmelin-Vivien 1982, García-Rubies & Macpherson 1995) the families Sparidae and Mullidae contained several members of the guild juvenile migrants. Several species return to seagrass as adults due to the high productivity and food supply as well as for reproduction (Deudero et al. 2008). Even though several species (e.g. *Diplodus sargus*, *Diplodus vulgaris*, *Oblada melanura*, *Sparisoma cretense*) within the juvenile migrant guild were occasionally observed as adults, their contribution to the total abundance represented only a small fraction, designating the main use of this habitat to early life stages. Among the 10 most numerous species found in seagrass, five species (*Sardina pilchardus*, *Siganus rivulatus*, *Sphyræna chrysotaenia*, *Mullus surmuletus* and *Sparisoma cretense*) were classified as juvenile migrants of commercial value indicating the important nursery function of this habitat for the replenishment of exploited fish stocks. High densities of spawning adults were observed for *Thalassoma pavo* and *Chromis chromis* during samplings in May, signifying this habitat as essential for reproduction of the species. Juveniles of *C. chromis* have been mentioned to occur over rocky-algal habitats (García-Rubies & Macpherson 1995) indicating that the species is probably spawning over the seagrass meadows, while spending its juvenile stages on rocky-algal habitats rich in small

crevices. Occasional visitors were found to be a major group in terms of number of species, although represented only a fraction in terms of density and biomass. This was attributed either to an affinity for sandy or rocky habitats in several species, but could also simply reflect that some of the species are naturally rare in this region.

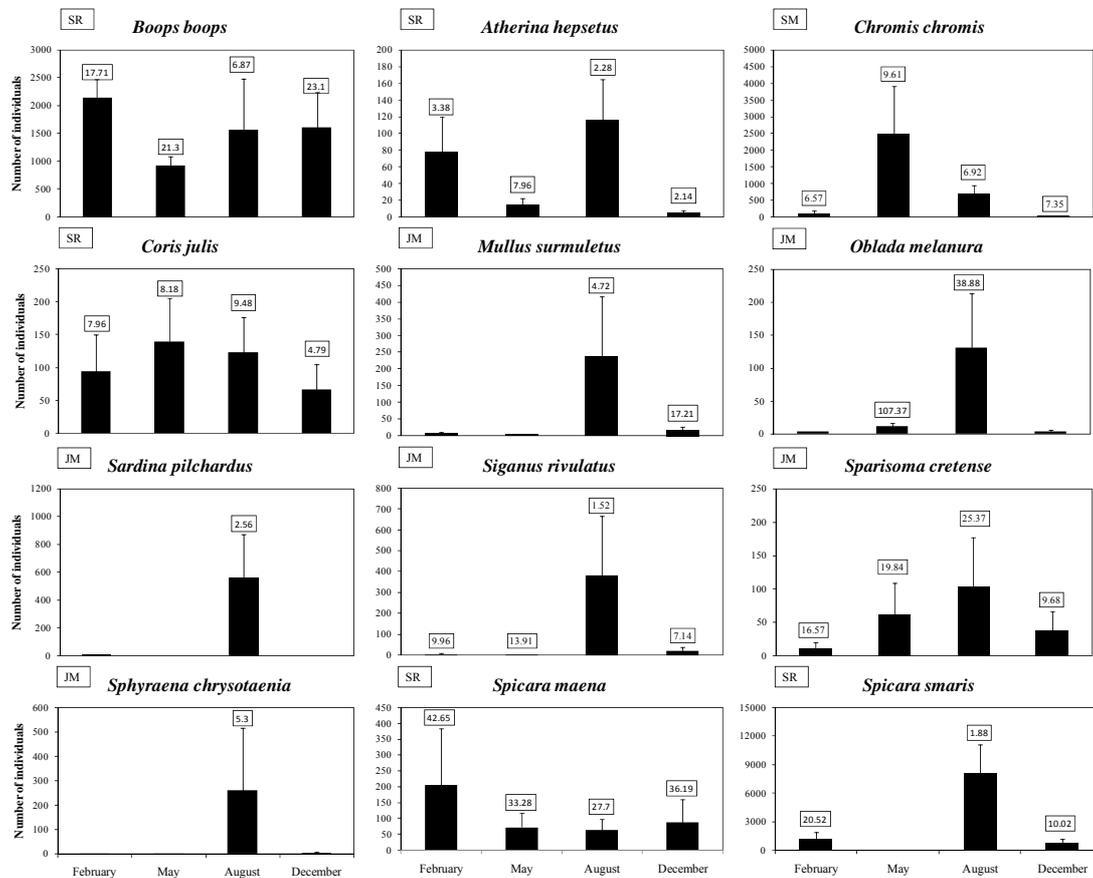


Fig. 6 Mean density + SE per season for each of the 12 most abundant species. Mean weight per individual and season is indicated in boxes above each bar plot. Functional groups are indicated for each species on the left upper box according to classification in the study.

The results of this study show the successful establishment and habitat use of several NIS in eastern Mediterranean. The majority of NIS was found to use *Posidonia oceanica* meadows during their early life stages indicating the importance of this habitat during arrival, temporary and permanent establishment stages during their invasion process. Classification of fish species into functional guilds revealed three juvenile migrants and four seagrass residents. It is to be noticed that only four NIS recorded during this study (*Stephanolepis diaspros*, *Upeneus moluccensis*, *Siganus luridus* and *Siganus rivulatus*) are established colonizers (Galil 2006), while the remaining seven have recently appeared in the area (Corsini-Foka & Economidis 2007). The number of fish species inhabiting eastern Mediterranean has increased to approximately 470 species, due to the influx of more than 80 NIS of Indo-Pacific and Red Sea origin, contributing with 18% to the total ichthyofauna (Golani et al. 2006, EastMed 2010).

The recently introduced species *Pteragogus pelycus* was one of the NIS found to be a seagrass resident, belonging to the most diverse fish family in seagrasses, namely Labridae. Another two seagrass residents were *Fistularia commersonii* and the tetrodotoxin-containing *Lagocephalus sceleratus*, where high densities of young

individuals were caught during samplings in August. Several studies have shown that *F.commersonii* undergo ontogenetic shift towards a more generalistic feeding and habitat selection (Bilecenoglu et al. 2002, Takeuchi et al. 2002, Kalogirou et al. 2007, Bariche et al. 2009, Takeuchi 2009). Moreover, *L. sceleratus* ranked among the 10 most dominant fish species in terms of biomass a pattern that could be attributed to the capture of few but large specimens during samplings in winter. *L. sceleratus's* socio-economical impact on the local fishery is obvious both due to the presence of tetrodotoxin and to the increased effort introduced to the local fishery for cleaning the fishing gears (Streftaris & Zenetos 2006).

Juvenile migration was found to be a common feature for three NIS when functional classification was possible. *Posidonia oceanica* was found to be an important habitat for the successful introduction and establishment of the recently introduced yellow-striped barracuda (*Sphyræna chrysotaenia*), and the two earliest NIS, *Siganus rivulatus* and *Siganus luridus*. Their classification as juvenile migrants was attributed to the high densities of juveniles observed during summer. *Siganus luridus* and *S. rivulatus* are well established in the area and are of high commercial value for the local fishery (Papaconstantinou 1990, Corsini-Foka & Economidis 2007). In this study, the two siganids made up 56 % of the abundance of herbivorous fishes over *P. oceanica*, a number slightly lower than previous studies from Lebanon (Bariche et al. 2004). Further, the study showed that the nine times higher abundance of *S. rivulatus* compared to *S. luridus*, is in accordance to previous studies in Lebanon waters (Bariche et al. 2004). Another two NIS, *Upeneus pori* and *Upeneus moluccensis*, were found to be less associated with *P. oceanica* meadows than their other two native con-familial mullet species.

In a time of an alarming high introduction rate of NIS, essential information on the arrival process is highly important. Tracking the invasion process from temporary to permanent establishment is thus considered crucial to understand basic invasion processes. At the same time, the integration of indigenous species with newcomers results in new ecological links. The need to continuously monitor a changing assemblage structure of fish species is evident.

Non-indigenous species in Mediterranean fish assemblages: contrasting feeding guilds of *Posidonia oceanica* meadows and sandy habitats

This investigation was designed to study the fish assemblages associated with seagrass and sandy substratum, two dominating coastal habitats in the eastern Mediterranean. To our knowledge this is the first study in the eastern Mediterranean to quantitatively compare the density and biomass of fish species in the two habitats under the influence of NIS. The objective of this study was to assign fish species to a feeding guild, in order to investigate the contribution and position of non-indigenous species in the food-web contrasting the two habitats. Absolute contra proportional values of NIS density and biomass give different results but since the objective of this study was to investigate the potential impact on the food web, proportional biomass values were considered most relevant. In perspectives of investigating essential fish habitats for NIS, potential impacts of NIS on fisheries or recruitment, contrasting different habitats, absolute density and biomass values can be more important.

The proportion of non-indigenous fish species was 13% in *Posidonia oceanica* meadows and 16 % on sandy substrata. However, NIS made up a significantly higher proportion of fish biomass on sandy bottoms (23%) compared to *P. oceanica* meadows (13%) (Fig. 7). Both in terms of density and biomass, the highest

contribution of NIS to the fish assemblage in *Posidonia oceanica* occurred during the summer, whereas during this season the contribution of NIS on sand was at the lowest. Instead, the highest contribution of NIS on sandy bottoms was encountered during spring and autumn and these seasons were significantly higher compared to the other two seasons.

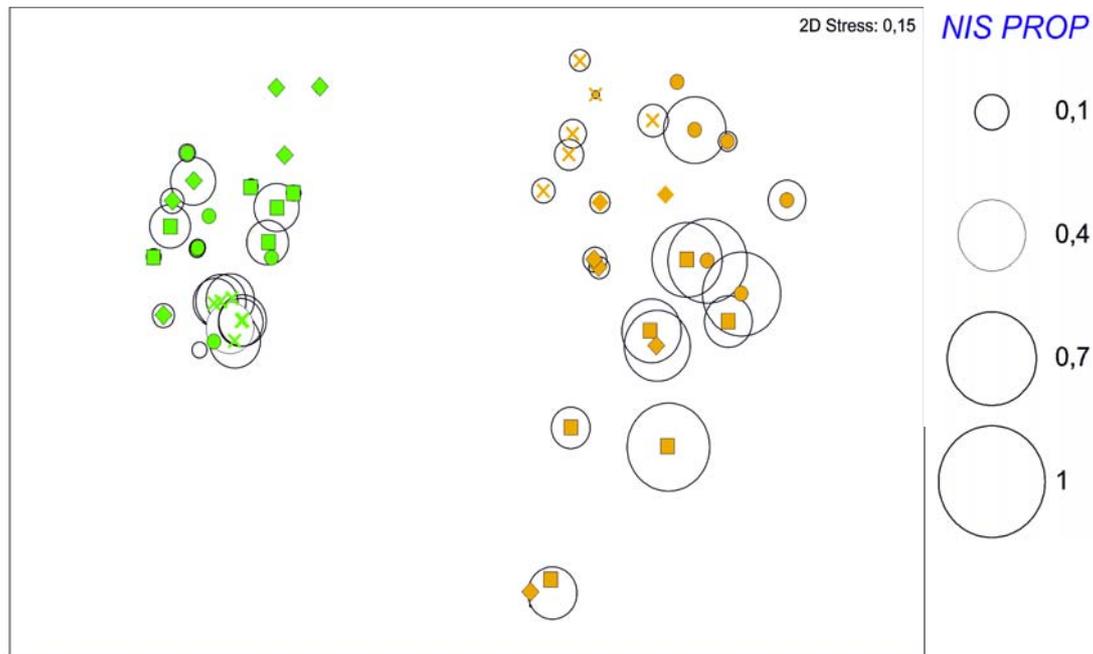


Fig. 7 Multidimensional scaling ordination of the fish assemblage structure in terms of biomass per habitat (*Posidonia oceanica* beds, ■; sandy bottoms, ■), and season (spring, ●; summer, ×; autumn, ■ and winter, ◆). The radius of each circle corresponds to the proportion of NIS (NIS PROP) per replicate.

The sampling method used in this study was a boat seine. This is an active gear, found to be an effective fishing method in catching a large variety of fish species, a large size range of fish, and sampling *Posidonia oceanica* meadows and sandy bottoms similar efficiency (Kalogirou et al. 2010). Sampling design of locations was considered appropriate due to support from a recent study in the area revealing lack significant west-east differences between locations within habitat (Kalogirou et al. 2010). The standard sampling area covered (0.04 km² per replica) was assumed to give reliable estimates of fish density, biomass and number of fish species. While records of NIS provides valuable information upon arrival of a species e.g. Papaconstantinou (1990), Corsini-Foka (2010), Corsini-Foka & Economides (2007), seasonal quantitative measurements and classification of fish species into feedings guilds allowed us to compare the abundance and biomass contribution of non-indigenous fish species in the fish assemblage between habitats. Density of fish species can seasonally vary due to migration of fish species between habitats, a common pattern found when studying fish assemblage structure of seagrass meadows. Several studies report that juveniles of many fish species are highly abundant over

seagrass meadows during spring and summer, a pattern attributed to the nursery and refuge function provided by the canopies of the seagrass (Bell & Harmelin-Vivien 1982, Francour 1997, Guidetti 2000, Moranta et al. 2006, Deudero et al. 2008). Since a main objective of this study was to investigate the position and contribution of non-indigenous species in the food web of the two under study habitats, we mainly based our analyses on biomass of fish to better estimate the impact of non-indigenous species in the food web. Assessing possible rearrangements in the food web, attributed to the introduction of non-indigenous fish species will be an important step for future research on the impact of NIS. We hereby provide a thorough quantitative study in order to reveal possible rearrangements attributed to the introduction of NIS in future studies.

The two dominating habitats investigated (*Posidonia oceanica* and sandy bottoms) within the coastal zone of Rhodes Island was found to harbour a highly diverse indigenous and non-indigenous fish fauna including at least 85 species, belonging to 32 families. Not surprisingly, all NIS recorded during this study were of Indo-Pacific origin, a fact that can be attributed to the presence of the man-made Suez Canal in the eastern Mediterranean. The fish fauna of the Mediterranean Sea, which developed after the Messinian salinity crisis, is characterized by a mixture of temperate and subtropical species revealing that westerly species have already colonized the eastern Mediterranean through natural migration. A species immigrating from the Red Sea to the Mediterranean must pass through substantial physical and ecological difficulties such as the shallowness and narrowness of the Suez Canal, its high salinity and its lack of rocky substrate (Golani 1998a, Golani 2010). When succeeded, species physiological demands must fall into similar abiotic conditions (temperature, salinity) to the source area. However, the high number of NIS in the eastern Mediterranean indicates that species which have succeeded to overcome the Suez Canal's barriers have a good chance of becoming established and to spread to other areas (Golani 2010). Success to establish will also depend on appropriate food resources in the recipient community as well as competitive abilities and level of competition in the food web within habitats.

Four out of six feeding guilds found within *Posidonia oceanica* meadows were matched by similar feeding guilds on sandy bottoms, although both the relative and absolute contribution in biomass differed between habitats. The *P. oceanica* fish assemblage had all feeding guilds previously described, while sandy substrata lacked herbivores and true zooplanktivores. The sandy bottom habitat was characterized mainly by infauna feeding fish, utilizing the various invertebrates found in this substratum. Macrovegetation is the main difference between the two habitats and the habitat forming *P. oceanica* meadows can be hypothesized to support a higher number of species and guilds than the sand habitat. Since the investigation included the contribution of ten versus five species in *P. oceanica* and sandy habitats, respectively, individual species will be conclusive. The contribution of true non-indigenous invertebrate feeders in *P. oceanica* meadows (1 %) was lower than that in sandy habitats (19 %). *Pteragogus pelycus* made up 0.7 % of true invertebrate feeders in *P. oceanica* indicating its ability in finding a suitable niche. On sandy habitats, *Upeneus pori* represented 10% of true invertebrate feeders and it is suggested that lack of competition over the available resources might be the driving force. The contribution of non-indigenous IF was found to be similar in the *P. oceanica* habitat (2 species; 63 %) and on sandy bottoms (2 species; 59 %). *Lagocephalus sceleratus* represented 62 % of IF on *P. oceanica* and 56 % on sandy bottoms. When comparing

size structure of *L. sceleratus* between habitats, this species was found to inhabit *P. oceanica* as an adult while spending its earlier life stages on sandy bottoms (Kalogirou, unpublished). This indicates that *L. sceleratus* success during early life stages on sandy bottoms might be attributed to low level of competition over the available resources while its presence only as an adult on *P. oceanica* during summer and autumn is attributed to improved feeding and competitive capabilities with increased size (Kalogirou, unpublished). *Lagocephalus suezensis* usually does not exceed 15 cm and since it was classified as an occasional visitor in *P. oceanica* habitats of the studied area we extend the knowledge of the preferred habitats of *L. suezensis* by showing that its higher contribution on sand indicates that size is a crucial component of invasion success and spread. The zooplanktivorous species, excluded from the analysis, mainly rely on pelagic food items brought in with water currents to both habitats, explaining the lack of difference in affinity between the habitats. The only ZP species included in the analysis was *Sardina pilchardus* found to spend its juvenile stages in the *P. oceanica* beds. The contributions of non-indigenous piscivorous species were similar in both habitats (22 % in seagrass; 26 % on sand) and consisted primarily of *Fistularia commersonii* and *Sphyraena chrysotaenia*. Native piscivores mainly rely on small-sized coastal zooplanktivorous species and species using the coastal habitats as a nursery ground, while also to a lesser extent on the juveniles of resident species (Golani 1993b). This pattern holds for the non-indigenous piscivorous species *F. commersonii* (Kalogirou et al. 2007). The high prevalence of the blue-spotted cornetfish, *F. commersonii*, among the piscivores within both habitats studied clearly suggests that this invasive species now has become established in the area. Several studies have emphasized the impact of the non-indigenous rabbitfishes among herbivorous species in different coastal areas of the eastern Mediterranean and report the competitive exclusion of the indigenous *S. salpa*. (Bariche et al. 2004, Harmelin-Vivien et al. 2005, Azzurro et al. 2007b). Accordingly, in the present study, the two non-indigenous rabbitfishes made up more than 99 % among the herbivores in the *P. oceanica* habitat while *S. salpa* contributed only a very small fraction to this guild.

The spread and establishment of NIS is a major concern from a conservation perspective (Galil 2007). Given the ecological, social and economical costs of species introductions, understanding the environmental driving forces has become a major goal for ecologists and managers. In marine systems the introduction of NIS can have major effects on the structure and function of ecosystems (Grosholz 2002). The relationship between indigenous species richness and non-indigenous species ability to colonize new habitats, i.e. the community “invasibility” (Stachowicz & Byrnes 2006) is of main interest (Francour et al. 2010). This concept implies that highly diverse systems are difficult to invade while species-poor communities, or stressed ecosystems are more prone to introductions, attributed to a lack of biotic resistance (Occhipinti-Ambrogi & Savini 2003). The underlying theory is that high diverse assemblage of plants or animals utilizes its resources more efficient than less diverse communities. Through this mechanism, increased competition intensity makes it more difficult for new species to establish (Francour et al. 2010). Even though it was impossible to directly test the biotic resistance hypothesis there is a good indication that this hypothesis might hold true. In another context, taxonomic affiliation of invader’s to the local fish fauna will make species rich communities more prone to introductions. According to our data, there is no support to postulate that this hypothesis might hold true since several families in the *Posidonia oceanica* habitat

include both indigenous and NIS. Even if NIS does not constitute a high proportion of the *Posidonia* fish assemblage, shelter is easier found in this habitat but the risk of becoming a pest might be controlled by other factors.

The significant higher proportion and invasion success of NIS over sandy bottoms might be attributed to lower level of competition for benthic food resources within this habitat. Size was found highly important and thus growth rate is considered as highly important when predicting potential invaders. The opposite might hold true during summer due to ontogenetic habitat shift of species since feeding and competitive abilities increase with increased size. Many species uses *Posidonia oceanica* meadows as a habitat to reproduce or feed, explaining the high proportions of NIS during summer. Additionally, non-indigenous species were represented in different amounts within the various feeding guilds and their feeding preferences could be represented in more than one feeding guild. For that reason, the impact on the local invertebrate and fish resources is higher than that described for each guild simply because invertebrates and fish are represented in more than one feeding guild.

In conclusions, since NIS made up a larger proportion of the fish assemblage biomass on sandy bottoms compared to *Posidonia* meadows, there is a potential support to the hypothesis that more diverse systems are less prone to invasions. No support could be found in postulating that taxonomic affiliation could predict invasion success. In addition, size was considered highly important due to habitat shift of species with increased size. Two of the aspects considered in this study, the chance of establishing vs. the chance of being very dominant will depend upon competitive abilities strongly coupled to size and grounds for habitat shift. The function of *Posidonia oceanica* meadows as a habitat for reproduction and feeding for many fish species explain the high proportions of NIS in this habitat. However, success of establishment will also depend on appropriate food resources in the recipient community as well as competitive abilities and level of competition in the food web within habitats.

The diet of the non-indigenous cornetfish *Fistularia commersonii*

The diet of the bluespotted cornetfish *Fistularia commersonii*, which recently invaded Rhodes Island, was found to comprise almost entirely of fish prey according to analysis of the stomach contents of specimens collected between September 2004 and March 2005. Among the 245 specimens examined, 38 had empty stomachs. Fish were the predominant prey both by number (96% of the prey items), and by weight (99.95% of total prey biomass). Of the identified fish 20.6% belonged to the Gobiidae, 7.0% to the Centracanthidae, and 5.1% to the Labridae. All *Coris julis* specimens were found to be females. Prey biomass was dominated by Sparidae and Centracanthidae, with 29.4% and 28.3% of the biomass, respectively, followed by Mullidae (15.6%). Among the last named families, the most abundant prey species for *F. commersonii* were *Spicara smaris*, *Boops boops*, and *Mullus barbatus*, species of economical importance in the area. The size of the prey was generally positively related to the size of *Fistularia commersonii*. This was true for benthic and supra-benthic prey, but not for pelagic prey. The size of the benthic prey fish ranged from 7.8 to 68 mm in SL, the supra-benthic from 10.6 to 108 mm, the pelagic prey fish from 29 to 73 mm, and the size of all prey fish ranged from 5 to 108 mm. The division of prey taxa according to habitat made it possible to distinguish a change in foraging behavior of *F. commersonii* related to its body size. All size classes fed on supra-benthic fishes. The smaller cornet-fish also fed on benthic fish species whereas

the larger cornet-fish extended their diet to include pelagic fish species. The results also indicated that the middle sized fish were able to catch prey fish from all three habitats, although supra-benthic prey dominated (Fig. 8).

Identified prey fish belonged to eleven teleost families commonly found in trawl catches in the area (Corsini & Economidis 1999). The variety of prey families corresponded to the results of Takeuchi *et al.* (2002) recognizing ten fish families in the diet of a conspecific population of cornetfish in shallow reef waters of South Japan. Four prey-fish families (Gobiidae, Labridae, Mullidae and Scaridae) were also present among the prey reef fish of *Fistularia commersonii* in Japanese reef habitats (Takeuchi *et al.* 2002), confirming that many colonizers of Mediterranean coastal waters retain their basic feeding habits (Golani 1993b), at least in the early stage of their expansion into a new habitat.

This was the first study to focus quantitatively on the feeding ecology of *Fistularia commersonii* in the Mediterranean Sea and the detailed diet described here confirms the classification of this species among the top predators of coastal habitats in the Hellenic seas (Stergiou & Karpouzi 2005). The westward records of *F. commersonii* show its rapid establishment in new areas and its potential to become an important species of the Mediterranean Sea, thus indicating a need for further studies of its life history, and other aspects of its ecology not covered in this study.

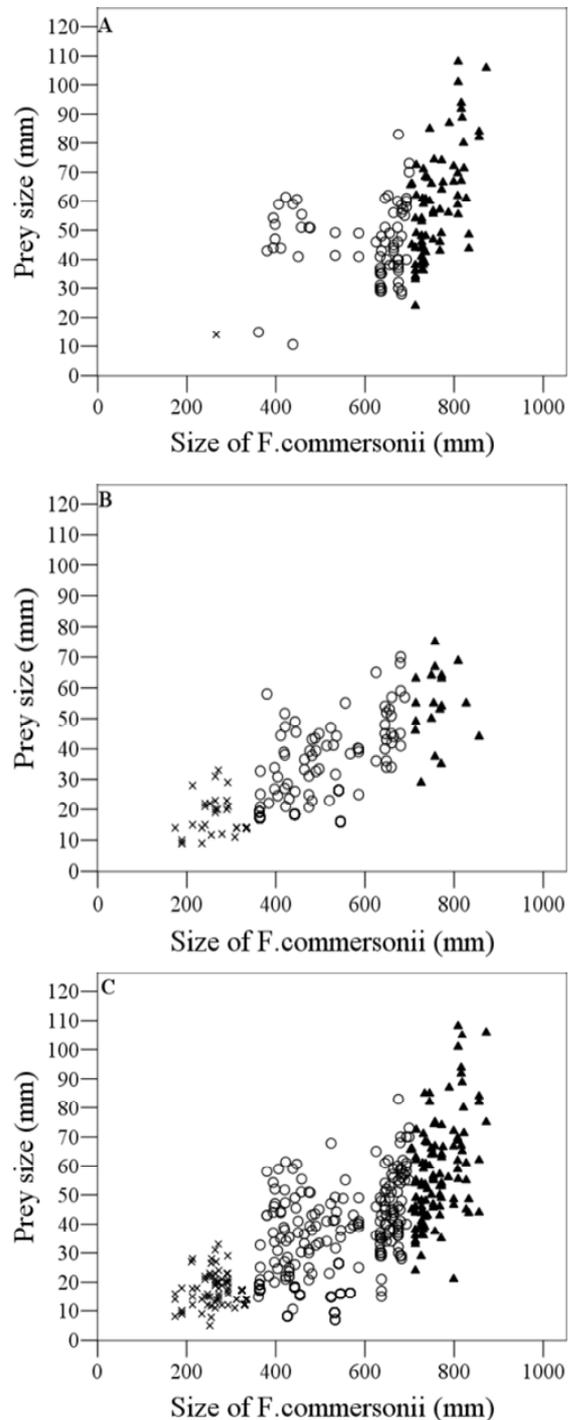


Fig. 8 Relationships between *F. commersonii* sizes (×: class 1, O: class 2, ▲: class 3) and prey sizes, according to prey habitat (A: benthic, B: pelagic) and for all preys (C).

Feeding ecology of indigenous and non-indigenous fish species within the family Sphyraenidae

This study was designed to investigate the feeding ecology of the most abundant sphyraenid species found in coastal ecosystems of the eastern Mediterranean. The results revealed that the sphyraenid species found in the study area are high-order specialized piscivores, displaying a narrow food spectrum and feed, to more than 90% on the three most abundant school-forming pelagic fish species found in the area (*Atherina hepsetus*, *Spicara smaris*, *Boops boops*; Fig. 10) (Kalogirou et al. 2010). For all three species examined, the highest prey selectivity was found to be towards *Atherina hepsetus*. With increased body size the three predators extended their diet to larger prey and to include a wider food spectrum, but there was no evidence of a clear ontogenetic diet shift. Highest prey richness and diet breadth was found for the indigenous *Sphyraena viridensis*, indicating its abilities to extend its foraging habits towards several prey items. In general, inter-specific diet overlap was shown to be biologically significant, according to significance levels given by Wallace (1981), both between indigenous species but also between indigenous and NIS. With increased body size the degree of diet overlap decreased while diet breadth and prey species richness increased, indicating that a potential coexistence between indigenous and NIS of the family Sphyraenidae is possible.

The diet of the indigenous and non-indigenous sphyraenid species comprised almost entirely of fish (>91 % by number and >92 % by weight). Identified prey fish belonged to 8 teleost families commonly found in boat seine catches in the area (Kalogirou et al. 2010). For all species examined, more than 70 % of the diet by weight was made up by three indigenous species of economical value – *S. smaris*, *B. boops* and *A. hepsetus* (Vidalis & Tsimenidis 1996, Stergiou & Karpouzi 2002). This indicates that *Spicara smaris*, *Boops boops* and *Atherina hepsetus* are the most important prey items in terms of the predator's energy budget. These three indigenous pelagic prey species also contributed to more than 70 % of the number of prey items taken. *Spicara smaris* and *B. boops* are abundant and exceed 70 % of the total fish catch weight on *Posidonia oceanica* habitats in the area (Kalogirou et al. 2010) indicating lack of food limitation for each of the predators.

To our knowledge, no other quantitative studies on the diet of either sphyraenid species exist from Mediterranean waters and their diet is only generally described as feeding mainly on school-forming species and supplementing their diet with cephalopods (Golani et al. 2006). The feeding habits of *Sphyraena viridensis* has, however, been described from the Azores and it has been shown that *S. viridensis* preys on pelagic school-forming species (Barreiros et al. 2002). The study by Barreiros *et al.* (2002) focused on predatory behaviour and demonstrated that predation was most effective when several individuals formed schools and attacked school-forming prey. Nevertheless, the variety of prey families found in the stomachs of the predators examined in our study corresponds to the results of Kalogirou *et al.* (2007) who identified 11 fish families in the diet of another piscivorous NIS, recently established in the area (*Fistularia commersonii*). Six prey families (Atherinidae, Centracanthidae, Mullidae, Pomacentridae, Sparidae, and Scaridae) were also present among the prey fish of the invasive piscivorous fish *Fistularia commersonii* in the coastal area studied (Kalogirou et al. 2007) and in a conspecific population in Japan (Takeuchi 2009). In contrast, *F. commersonii* was shown to feed on a larger variety of species within families, as compared to the three sphyraenid species examined.

All predators were highly selective towards *Atherina hepsetus*, a prey that was found to be the most preferred. The high selectivity values for this prey species was caused both by its high abundance in the diet and by its low abundances in the fish community. Another prey species, *Diplodus annularis* was also found to be selected by the indigenous species *Sphyraena viridensis*. Indigenous sphyraenid species develop into larger predators and showed an ability to extend foraging to other prey species.

All three barracuda species were generally found to possess a narrow food spectrum dominated by fish.

The NIS *Sphyraena chrysotaenia* had the most narrow food spectrum, limited only to pelagic fish species (Fig. 9), whereas indigenous species extended their feeding to supra-benthic species (e.g. *Boops boops*) (Fig. 9). This difference in food spectrum was mainly attributed to the larger maximum body size of the indigenous species, where the larger individuals include new prey types in their diet.

The significant confamilial diet overlap found between the indigenous and the NIS of the Sphyraenidae family clearly indicates a similarity in feeding preferences that could give rise to feeding competition. In general, competition is evident when two or more species share the same resources. However, high fishing intensity might have reduced abundances of the sphyraenid species enough to eliminate competition for prey fish populations and fishing may thus be the regulating factor for a potential coexistence between indigenous and NIS (Pauly et al. 1998). In fact, the three sphyraenid species examined have a high commercial value in the study area being fished with handlines, and longlines as well as with boat seines and gillnets. With increased body size, diet overlap decreases indicating lower levels of competition. This might not be true since the predators widen their feeding preferences with increased body size. Nevertheless, biologically significant inter-

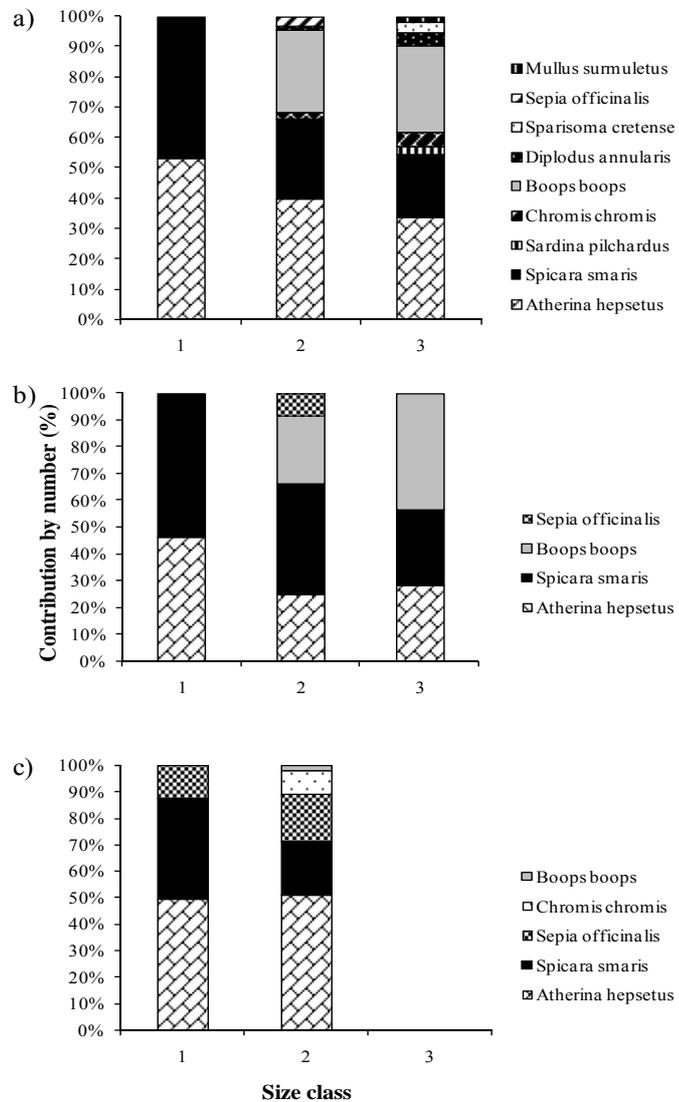


Fig. 9 Percentage numerical contribution of prey species for each predator (a, *Sphyraena viridensis*; b, *Sphyraena sphyraena*; c, *Sphyraena chrysotaenia*) and size class (1, 2 and 3).

specific diet similarities found for each size class clearly indicate an impact on prey populations. Lack of quantitative studies, prior to the establishment of NIS, limits the strength of inference that can be made about competition although a potential coexistence between indigenous and NIS is evident. Whether indigenous and NIS may utilize similar niches are of major importance for understanding the impact of NIS on local indigenous species and local prey resources but one of the most central difficulties in assessing the impact of NIS on indigenous species communities is lack of information on ecological aspects of native species (feeding, time of spawning, habitat preferences, migration patterns etc.) prior to the introduction of a NIS as is the case in the area under study.

The two indigenous fish species were found to maintain a relative stable condition throughout the year, except for *Sphyraena sphyraena* exhibiting slightly lower values in summer. This indicates that the indigenous sphyraenid species are in good condition and that the condition has not been affected to any larger extent by the establishment of a NIS barracuda. In contrast, the NIS *Sphyraena chrysotaenia*'s lower condition in winter indicates that temperature minimums may be a limiting factor for growth through reduced feeding. Seasonal variations in the condition of *S. sphyraena* and *S. chrysotaenia* have been investigated from the Egyptian waters of Mediterranean (Allam et al. 2004a) but differences in size distribution did not allow for a comparison. Allam *et al.* (2004a) showed that *S. chrysotaenia* is in a better condition than the indigenous *S. sphyraena*. *Sphyraena chrysotaenia* was also found to reproduce at smaller size than the indigenous species indicating abilities which could favour its successful establishment (Allam et al. 2004b). The relative condition factor used during this study is believed to be a good indicator of the physiological state of a fish species since it is related to its fitness. The relative condition factor is, however, also influenced by other factors such as reproductive period and fat storage.

Even though the area under study has a high diversity of NIS of Indo-Pacific origin (Corsini-Foka & Economidis 2007, Corsini-Foka 2010) few are abundant and have an economical value (Kalogirou et al. 2010). The NIS *Sphyraena chrysotaenia* is already a commercially important species in the area (Corsini-Foka 2010) and is generally not distinguished from confamilial indigenous species on the fish market. All sphyraenid species preyed on indigenous and economically important species, and the low prevalence of other non-indigenous fish species in their diet may just be related to the absence of small-sized school-forming pelagic NIS in the area. It should be mentioned that another NIS, *Sphyraena flavicauda*, is also found in the area, although this species is much less abundant (Kalogirou et al. 2010).

Food availability is considered an important component for the establishment of a NIS. Colonizers from Red Sea have been shown to retain their basic feeding habits when establishing populations in the Mediterranean Sea (Golani 1993b, Kalogirou et al. 2007, Bariche et al. 2009). The high level of diet overlap between the three sphyraenids does not necessarily indicate a high level of competition. All these three predators are economically important. Fishery, through top-down effects, might control their populations to a level that prey densities rarely become a limiting resource. Competition for food resources would occur when prey availability is limited. *S. chrysotaenia* has been recorded in the Mediterranean Sea since the 1930's (Spicer 1931) and would therefore be expected to be well established. It has been shown that the longer the time elapsed since the first introduction of a NIS the higher the probability for a species to have established abundant populations (Golani 1998b). However, the non-indigenous species *S. chrysotaenia* exhibited a low condition factor

in winter, indicating that temperature minimums in the area could be an important limiting factor for elevated population growth.

The distribution and impact of NIS is a major issue for conservation (Galil 2007). In marine systems the introduction of NIS can have major effects on the structure and function of ecosystems (Groszholz 2002, Goren & Galil 2005). The success and impact of a non-indigenous fish species may, however, be hard to predict given the high complexity of marine food-webs and multi-habitat use. In fresh-water systems, in which the impacts of introduced species have been more extensively studied, some “empirical rules” have been proposed as an aid to understand biological invasions (Moyle & Light 1996). Fresh water systems generally have a simpler food-web structure and are easier to study compared to marine systems. Among the empirical rules mentioned for fresh-water systems, the ability of piscivorous invaders to alter fish assemblages with cascading effects through the ecosystem is particularly well documented (Carpenter et al. 1985, Goldschmidt et al. 1993). Marine coastal ecosystems are however open, complex, and species may use different habitats during their life cycle, which makes it even harder to link changes in ecosystem structure attributed to the appearance of a specific species. This highlights the importance of conducting quantitative studies on the abundance and biomass proportions of indigenous and NIS, found in different coastal habitats for successful conservation (Kalogirou et al. 2010) and also serves help identify potential ecosystem changes due to the arrival of NIS. Studies of the interactions between large and highly mobile predators and prey are rarely amenable to field experiments which highlight the value of diet descriptions as an important and feasible first step in evaluating the potential impact of a newly introduced piscivorous species. Another important ecological aspect is energy acquisition, which has been an important aspect in predicting the survival as well as the fitness of a species. It is affected by prey density and behaviour as well as foraging abilities of a predator (detect, capture and consume). Evolution of foraging abilities will influence the structure and function of ecological communities by changing predator-prey dynamics (Svanbäck & Bolnick 2008). Moreover, con-familial diet overlap is an important aspect in understanding the impact and role of a NIS in a system, since most con-generic species maintains similar feeding habits may provide insights of feeding competition between indigenous and non-indigenous species. By that one would also have the opportunity to test whether Darwin’s naturalization hypothesis for non-indigenous plant species holds for fish species (Ricciardi & Mottiar 2006). Darwin (1859) proposed that introduced species tend not to invade areas containing native con-generic plant species because introduced species would compete with their close-related natives and encounter pathogens (Ricciardi & Mottiar 2006). In this study we found that taxonomic affiliation was not an important predictor for invasion success of the non-indigenous barracuda, which is in agreement with the results of Ricciardi and Mottiar (2006).

Food availability in combination with appropriate abiotic conditions was therefore considered as two important factors for the invasion success in the area. With this study we provide new information on the feeding habits of the most abundant high-order piscivores in the coastal study area. This is the first study to contrast the feeding habits of indigenous and NIS Sphyraenidae species in the Mediterranean Sea.

The non-indigenous invasive and pest pufferfish *Lagocephalus sceleratus* in an area of the eastern Mediterranean

In this study I investigated the status of establishment of the most invasive fish species, *Lagocephalus sceleratus*, five years after it was first reported from the studied area. Quantitative sampling allowed measurements on population size-structure of *L. sceleratus* in two important coastal habitats. Together with information on size at maturity and feeding habits I provide important life-cycle characteristics of this species in its new environment.

In sandy habitats, *Lagocephalus sceleratus* were present throughout the year and most of the specimens did not exceed size class 2 (30 cm) (Fig. 10). Larger fish (size classes 3 to 6) were mainly found to inhabit *Posidonia oceanica* meadows (Fig. 10). This reveals that with increasing body size, *L. sceleratus* shift habitat. According to the results of this study, habitat shift from sand to seagrass meadows is related to shift in feeding preferences with increased body size. In the Gulf of Suez, Sabrah *et al.* (2006) showed that *L. sceleratus* reach maturity during the third year of life at a size of 42-43 cm (size class 4). In this study, size at which 50% of *L. sceleratus* individuals reach maturity was 36 cm, indicating that size at maturity and habitat shift are also correlated (Fig. 10). Higher densities of *L. sceleratus* were generally found in sandy habitats (168 individuals) compared to *Posidonia oceanica* meadows (122 individuals) due to high concentrations of small-sized individuals in this habitat during summer. Size range of *L. sceleratus*

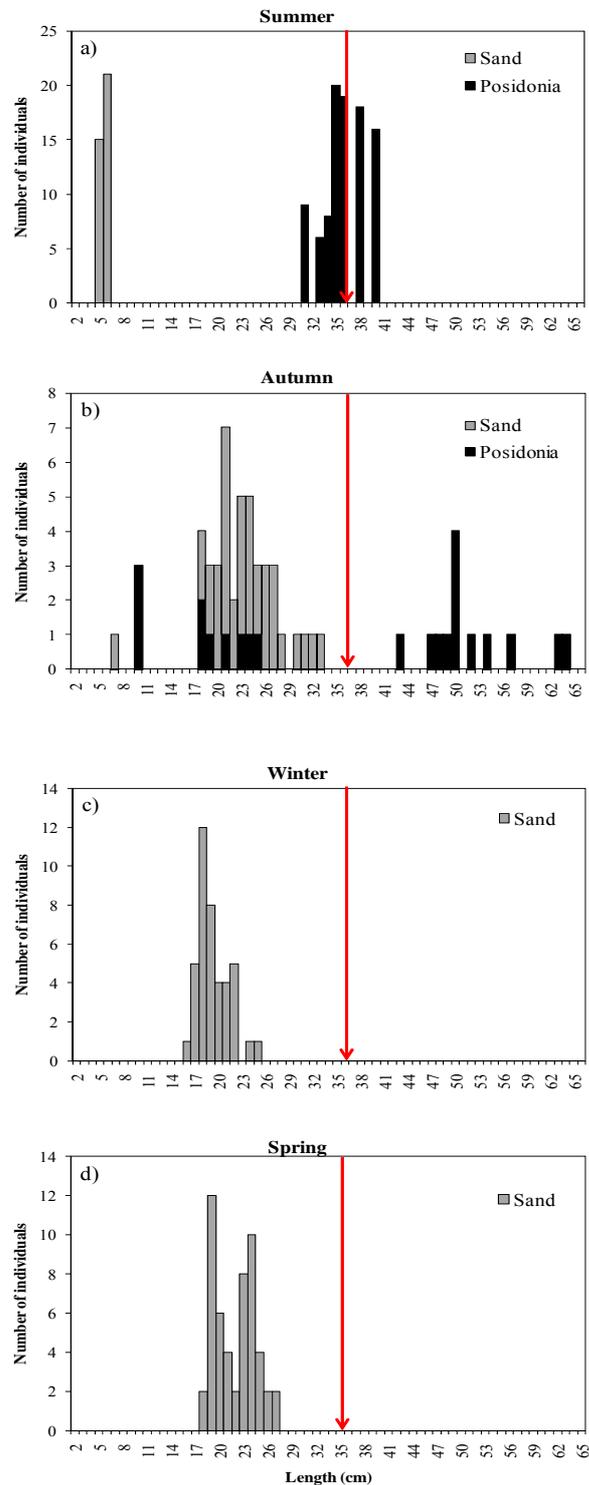


Fig. 10 Length and number of *Lagocephalus sceleratus* individuals found over *Posidonia oceanica* and sandy habitats in summer (a), autumn (b), winter (c) and spring (d). Red arrows indicate the minimum length of mature individual.

individuals during summer on sandy bottoms were predominantly five to six cm in length, suggesting that the fish recruit into this habitat. During summer, larger individuals (30 to 40 cm) were caught in *P. oceanica* meadows. Summer has been shown to be the main reproductive season for *L. sceleratus* in the Gulf of Suez (Sabrah et al. 2006). In the autumn, density of fish increased on sandy bottoms and fish size varied between 5 and 32 cm. In this habitat, only few species were close to 32 cm and the average size of fish was 22 cm explaining that small sized species inhabits sandy bottoms. The few small-sized specimens (9 to 26 cm) caught during the same season in *P. oceanica* meadows were likely attributed to its patchy habitat interrupted by sand. At this time, adult *L. sceleratus* individuals (42 to 62 cm) were present in the seagrass habitat. Later in the season, during winter and spring, *L. sceleratus* were only found on sandy bottoms and fish size ranged from 15 to 27 cm signifying the importance of this habitat for the early life stages of *L. sceleratus*. Additionally, *L. sceleratus* was previously classified as a seagrass resident with intermediate affinity to *Posidonia oceanica* habitats of the studied area (Kalogirou et al. 2010). This study extends the knowledge of habitats used during the life cycle, revealing a habitat shift from sand to *P. oceanica* habitats with increased size. Habitat shift was shown to occur when *L. sceleratus* reach approximately 27-32 cm.

All the above underline that *Lagocephalus sceleratus* is well established in the area, but the lack of larger (> 65 cm) individuals from the data could be attributed to the recent establishment of *L. sceleratus* in the area (only for 5 years) or to further habitat shift. Long-line fishery indicates that larger individuals reaching 78 cm in length are caught over rocky bottoms (pers. obs.).

Even though several authors have mentioned that *Lagocephalus sceleratus* feeds on benthic invertebrates (Golani et al. 2006) this study extends the knowledge on feeding preferences by revealing it as an invertebrate and fish feeder. This study suggests a diet shift with increased body size (to a molluscivore feeding), possibly explaining habitat shift due to changed prey availability or preferences. It is commonly believed that *L. sceleratus* rapid expansion might have affected commercial squid and octopus populations negatively. It is, however, difficult to quantify the predation impact by puffer fish due to the lack of quantitative studies on local invertebrate communities and extended state of digestion of prey items.

Lagocephalus sceleratus was for the first time reported in the Mediterranean Sea in 2003 off Akayka, Gökova Bay in Turkey (Akyol et al. 2005). It has since then showed a rapid expansion throughout the eastern Mediterranean Sea reaching the northern most parts of the Aegean Sea, but has to date not been observed in the western Mediterranean and has not reached Italy (Fig. 11) (Golani 2010). Nevertheless, the rapid expansion indicates that the species is well adapted in its new environment. *Lagocephalus sceleratus* was generally found to be in a good condition in the area under study with low seasonal fluctuations. Even though the condition factor used during this study is believed to be a good indicator of the physiological state of the species, it is to be mentioned that condition is also related to other factors such as reproductive period and fat storage. The α (0.0164) and β (2.8932) values given from the length-weight relationship during this study corresponds to values given by Sabrah (2006) from a con-specific population in Attaka fishing harbour of the Suez Canal revealing similar growth rates.

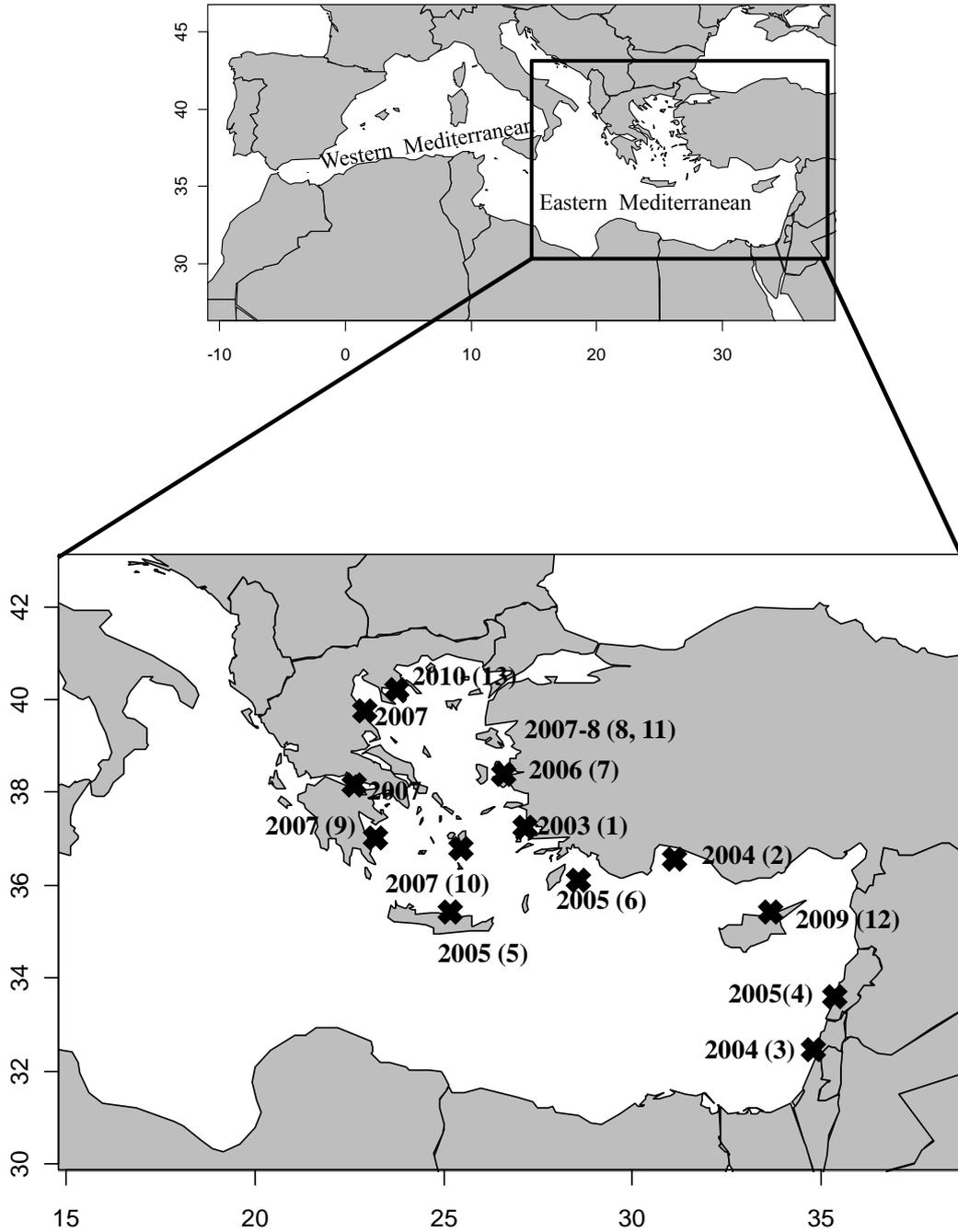


Fig. 11 Spatial and temporal distribution of *Lagocephalus sceleratus* in the eastern Mediterranean Sea with numbers (1-12) representing the order of reports: 1, (Akyol et al. 2005); 2, (Bilecenoglu et al. 2006); 3, (Golani & Levy 2005); 4, (Carpentieri et al. 2009); 5, (Kasapidis et al. 2007); 6, (Corsini et al. 2006); 7, (Bilecenoglu et al. 2006); 8, (Peristeraki et al. 2006); 9, (Peristeraki et al. 2006); 10, (Kasapidis et al. 2007), 11; (Türker-Çakır et al. 2009); 12, (Katsanvakis et al. 2009) and 13, (Minos et al. 2010).

Lagocephalus sceleratus possess one of the strongest paralytic toxin known today, tetrodotoxin (Sabrah et al. 2006) and has been regarded as one of the "worst alien fish" of the Mediterranean Sea (Streftaris & Zenetos 2006); harmful to human health, fishing gears (Katsanevakis et al. 2009) and biodiversity (Bilecenoglu 2010). European legislation (Regulation 854/2004/EC) declares that poisonous fish of the family Tetraodontidae are prohibited from European markets. In Turkey, *L. sceleratus* is considered the most common pufferfish in terms of biomass (Bilecenoglu et al. 2006) while in south-eastern Aegean Sea, Rhodes, *L. sceleratus* was found to rank among the 10 most dominant fish species in terms of biomass in *Posidonia oceanica* habitats (Kalogirou et al. 2010). This undoubtedly shows its vast abilities in rapidly colonizing and establishing populations in new areas. Its large size was considered the main reason for this species to be marketed in some fishing ports and there are several cases of poisonings (Bentur et al. 2008, Bilecenoglu 2010, Golani 2010). Both Turkish (Bilecenoglu 2010), Greek and Cypriot (EastMed 2010) ministries of Agriculture has recently banned fishing and marketing of *L. sceleratus*. Complains of local fishermen in newspapers has been mentioned from Turkey (Bilecenoglu 2010), Cyprus, and Greece (Kalogirou, pers. obs.). Complains of fishermen included destruction of gill nets due to entangling or predation on already captured fish, reduction of local commercial catches of *Sepia officinalis*, cut-off of long-line hooks and worrying of fish consumers due to alert by national authorities in difficulties of separating small-sized individuals of *L. sceleratus* with other commercial important fishes of the same size (*Spicara smaris*, *Atherina hepsetus* and *Boops boops*) (Katikou et al. 2009). As an indication of the economical impact from Fethiye Bay of Turkey, five minutes of recreational fishing resulted in 3 broken fishing lines, ten missing hooks and a capture of one *L. sceleratus* weighing 1 kg (Bilecenoglu 2010). Bilecenoglu's observations correspond to the results of this study where 52 long-line hooks were found in 33 stomachs thus confirming its pest status for commercial long-line fishermen. In economical terms, the time consumed to clean the gear from discarded fish is also considered as negative even though this measurement was not considered in this study. Adaption of long- and handline fisheries, included fishing on deeper grounds (>60 m) where *L. sceleratus* was considered to be absent and the reconstruction of fishing lines empowered with steel lines prohibiting removal of hooks.

The potential effects following the introduction of the NIS *Lagocephalus sceleratus* are hard predict, but fundamental knowledge on life-cycle characteristics are important to understand environmental responses. An invading species might sometimes reach a peak in density and then decline, a development often referred to as "boom and bust" (Reise et al. 2006). This dynamic leads to the significant reduction of the invading species population. When a NIS becomes established in an area where its preferred food is under-utilized by indigenous species the resulting population explosion can later be brought into equilibrium with available resources (Wellcome 1988). Competition, despite strong support (Moulton 1993), seems the less important factor for most of the examples (Reise et al. 2006). Decline and extinction from a build-up of enemies (predators and pathogens) and lack of sufficient resources to sustain population looks more likely explanations of failure of invading animals to establish permanent populations (Reise et al. 2006). The invasive NIS *Fistularia commersonii* (Kalogirou et al. 2007) clearly followed this boom and bust development in the studied according to personal observations. An obvious example of competitive exclusion/displacement of indigenous species was the introduction of

two herbivores. *Siganus rivulatus* Forsskål and *Siganus luridus* Rüppell out-competed the native herbivorous species *Sarpa salpa* (L.) and significantly reduced its abundance (Harmelin-Vivien et al. 2005, Azzurro et al. 2007a). Several non-indigenous fish species may have the ability to change the trophic food web by being highly dominant at a habitat or competing for food resources with indigenous inhabitants. This is due to that some species becoming highly abundant or even pests, thereby altering the community structure and reducing biodiversity (Boudouresque & Verlaque 2002). The impact of NIS on biodiversity is sometimes referred as positive due to the increased species richness, however others argues the opposite effect may result when NIS can become ecosystem engineers and significantly modify the habitat they invade (Wallentinus & Nyberg 2007, Rilov & Galil 2009). There is no doubt that biodiversity in the Mediterranean Sea is changing but to what extent warm-water species of tomorrow will affect the trophic web and the functioning of marine ecosystems needs continuous monitoring (Bianchi 2007, Kalogirou et al. 2010). Future investigations will reveal whether *Lagocephalus sceleratus* will be an ecosystem engineer and indicate how this species will affect the food web.

Conclusions and Future Perspectives

How will the future appear with respect to non-indigenous species (NIS) establishing self-sustaining populations in various coastal habitats of the eastern Mediterranean Sea?

During the last decades, coastal habitats of the eastern Mediterranean Sea have been extensively subjected to the establishment of non-indigenous fish species, mostly of Indo-Pacific and Red Sea origin. For four years, I have studied the associated fish fauna of two important coastal habitats, *Posidonia oceanica* meadows and sandy habitats. NIS are becoming important components of the fish fauna in both habitats, being represented by a number of species from different feeding guilds. An impact on the local fish fauna was most clearly indicated when the NIS were found to be dominant (*Lagocephalus sceleratus*) or act as piscivores (*Fistularia commersonii* and *Spyrhaena chrysotaenia*). By completion of my PhD-thesis, I am convinced that the introduction and spread of non-indigenous fish species in the eastern Mediterranean Sea cannot be fully barred. Once a NIS is established in a large ecosystem such as the Mediterranean Sea, it is almost impossible to eradicate. The opening of the Suez Canal has created a corridor for ‘naturally’ immigrating species by active or passive larval or adult movements (Galil et al. 2007). Temporal succession of NIS (‘stepping stones’) from the Red Sea, the Suez Canal, and along the Levantine coasts confirms this (Galil 2007). We live in an alarming and yet fascinating time of shift in biota of coastal ecosystems, and until today, impacts are only scarcely described.

On a European level it is considered that there is sufficient information regarding the rate of arrivals and vectors of introductions, but there are serious gaps in knowledge on monitoring methodology and on traits of introduced species. There is also a lack of risk assessments and information on impacts of NIS on good environmental status (GES) as well as control and management procedures (Olenin et al. 2010). From my studies it was obvious that there is an ongoing rearrangement in the food-web of coastal habitats, attributed to the introduction and establishment of NIS, but lack of earlier studies describing community structure prior to the

introduction of NIS limits the conclusions that can be drawn. Hence, the information provided by this thesis also provides a good starting point for future investigations relating to the re-composition of fish assemblage structure due to the establishment of NIS. In addition, very little information is available concerning the impact of NIS on ecosystem functioning (Olenin et al. 2010) and such studies should be set as priorities. Following the establishment of NIS and given the ecological, social and economical costs, understanding the environmental driving forces is now becoming a major goal for ecologists and managers. The physiological abilities in combination with different life history traits and ecological interactions in the recipient community (e.g. competition for resources, settlement habitats, spawning grounds, grazers or predators, potential trophic cascades, or even, the existence of empty niches) will determine the introduced species ability to succeed in the ecosystems that it arrives in.

Several factors may enhance the spread and establishment of NIS. I am convinced that global warming will have an increasing influence on the establishment and distribution of colonizers in the area studied. Rising sea-water temperatures will enable the potentially temperature-limited species in expanding their present distributions in the Mediterranean Sea, but also enhance the colonization process from the Red Sea into the Mediterranean Sea. While the opening of the Suez Canal (human mediated introduction) is the 'key' reason for the spread of NIS in the Mediterranean Sea, climate change (global warming) may determine much of the success and geographical expansion of NIS from the Red Sea in the future. Simple physiological (temperature) tolerances experiments of NIS in combination with predictive modeling could be one way of showing the potential impacts of climate change.

Where single NIS repeatedly and independently invade different ecosystem, which is quite common in freshwater, the success and impact of the NIS can be indicated by the history of its introduction in earlier invaded ecosystems. In the unique settings of this study, with the Suez Canal opening the barrier between two Oceans, there is however almost no historical information to conclude from. This point to the necessity of understanding the local ecosystem structures and processes in order to reveal possible rearrangements in the composition of fish assemblages, which could lead to loss of native biodiversity as well as in predicting economical and social costs. Identifying habitats that seem essential for NIS to complete their life-cycle may give insights into how different areas could be affected as well as the integration processes between indigenous and NIS. More extensive studies on the role of NIS should be set as priorities not only on local (Rhodes) but also on a larger spatial scale.

Research needs concerning impact of NIS includes studying the effect of NIS on ecosystem services (Wallentinus & Nyberg 2007), but also to develop methods for assessing changes in resilience and function of marine ecosystems. However, without monitoring and a fundamental understanding of the ecosystems monitored there is no rational basis for providing adequate advice for management (Olenin et al. 2010).

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