

Why the damselfish *Chromis chromis* is a key species in the Mediterranean rocky littoral – a quantitative perspective

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The damselfish *Chromis chromis* is typically the most abundant fish species in the rocky littoral environment of the Mediterranean Sea, where it feeds in huge shoals on incoming zooplankton and rests near the seabed each night. Research has shown that large populations of *C. chromis* play a fundamental role by transferring carbon, nitrogen and phosphorus directly from the pelagic system to the littoral in the form of solid and liquid wastes and therefore that this species acts as a vital conduit for nutrients. In addition, *C. chromis* represents a major prey item for predatory fish and seabirds, it has been shown to exert significant predation pressure on coastal zooplankton populations, but it is also a major consumer of fish eggs and hence may have a strong influence on the dynamics of other fish species. In this review paper the contention is that *C. chromis* represents a key species in the Mediterranean Sea rocky littoral. This view is supported by quantitative evidence that has been amassed over a number of years, but is collated here for the first time. *Chromis chromis* is of only minor importance to commercial fisheries (it is usually discarded), but trends in population abundance of this species can be indicative of levels of fishing pressure on other commercial species. It has been demonstrated that where predator numbers are able to recover from intensive fishing (e.g. in marine protected areas; MPAs), this is often mirrored by lower densities of *C. chromis*. Several papers have championed *C. chromis* as a possible indicator species for human disturbance. As well as being directly and indirectly affected by fishing, the species is also sensitive to a number of other anthropogenic pressures, most notably poor water quality and noise pollution.

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Key words: damselfish; indicator; Mediterranean Sea; nutrients; predator; zooplankton.

INTRODUCTION

Surface waters of the Mediterranean Sea are among the most oligotrophic anywhere in the world and this is particularly so in the eastern basin (Krom *et al.*, 2014). Despite this, Mediterranean coastal zones support highly diverse assemblages of both fish and invertebrates (Harmelin, 1990) with a high concentration of marine endemism. The aim of the present study was to investigate the role of plankton feeding-fishes and the Mediterranean Sea damselfish *Chromis chromis* (L. 1758) in particular. A diverse assemblage of planktivorous fishes exists in the Mediterranean rocky littoral but *C. chromis* is typically the most abundant species as determined by visual census throughout the region (Table I). Planktivorous fish may represent as much as 80–85% of the

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fish assemblage at some Mediterranean Sea sites (Harmelin, 1990), however, the roles played by these species in the overall functioning of the ecosystem have been little studied, despite being shown to be vitally important elsewhere in the World (Bray *et al.*, 1981; Hamner *et al.*, 1988).

In this review paper, particular attention is paid to observational and experimental work carried out at the Station de Recherches Sous-Marines et Océanographiques (STARESO) research station, situated in the Bay of Calvi, north-western Corsica (8° 45' E; 42° 35' N). The bay has a total area of c. 2200 ha and many aspects of ecology and biology (including seagrass *Posidonia oceanica* communities, benthic invertebrates, fish assemblages) have been studied over the past 50 or so years, largely by researchers from the University of Liège, Belgium (Spyker & van den Bergh, 1995; Goffart *et al.*, 2015). Between 1997 and 2000 the present author conducted research on planktivorous fishes at this research station, but there have subsequently been many developments elsewhere in the Mediterranean Sea that are reviewed here. Planktonic communities of the Bay of Calvi have been widely studied (Dauby, 1980; Dauby & Hecq, 1981; Brohee *et al.*, 1989) and these appear to be greatly influenced by the upwelling of nutrients in the spring (Goffart *et al.*, 2015). The contention promoted here is that *C. chromis* is a key fish in the Mediterranean rocky littoral, by virtue of its great abundance and the important role that planktivorous species play in channelling nutrients from the pelagic-zooplankton system to the rocky littoral as allochthonous detritus but also when they are themselves eaten by littoral predators. This view is supported by quantitative evidence that has been amassed over a number of years but for the most part is presented here for the first time.

C. chromis is a small (typically <15 cm total length, L_T) fish, that is found above rocky reefs, and seagrass (*Posidonia* sp.) meadows at depths ranging from 3 to 35 m. *Chromis chromis* is distributed throughout the entire Mediterranean Sea, in the Black Sea and Sea of Azov. It is comparatively rare off the Portuguese coast south of Lisbon, but it is found more frequently on the Algarve coast (Wood, 1977). Specimens described as *C. chromis* from various locations on the east African coast (Senegal to Pointe Noire), are suggested to have possessed features more characteristic of *Chromis limbatus* (Valenciennes, 1833) (Wood, 1977). Thus at the present time it is thought that the westerly and southerly limit of *C. chromis* distribution is around the Strait of Gibraltar.

During daylight *C. chromis* feed in large aggregations near the water surface on incoming plankton [Fig. 1(a)], but when night falls they gather over the rocky littoral (Harmelin, 1987) and settle into crevices among the rocks [Fig. 1(b)]. In the process, large amounts of plankton-derived material is picked up as food offshore and released as faecal pellets directly onto the substratum. Densities of resting planktivorous fish may reach 5–10 individuals m^{-2} at some localities (Harmelin, 1987) and so *C. chromis* act as an important vector for nutrients and nano-minerals (Pinnegar & Polunin, 2006).

Mapstone & Wood (1975) reported on the social organization and behaviour of *C. chromis*, whilst the reproductive cycle has been described by Contini & Donato (1973), Dulčić & Kraljević (1994) and Picciulin *et al.* (2004). In early June, male fish start to exhibit the first signs of display–courtship behaviour (Picciulin *et al.*, 2004). They synchronously establish territories, prepare nests and court females through vigorous visual and acoustic display (Picciulin *et al.*, 2001). Females lay demersal eggs that are guarded and fanned by males until hatching. When egg hatching has concluded, males abandon the nests and rejoin the feeding school. Males remain on their territory

TABLE I. Importance of *Chromis chromis* in Mediterranean rocky littoral ecosystems, based on visual census survey data

Geographical location	Habitat	Population density (m^{-2})	% of in the fish community (rank)	Reference
Cabo de Palos-Islas Hormigas (in–outside marine protected area, MPA), southern Spain	Rocky habitats	1.5	45.9% (1)	Prato <i>et al.</i> (2017)
Cabo de Palos, Murcia, southern Spain	Rocky reef	1.0	41.8% (1)	Garcia Charton & Perez Ruzafa (1998)
Galère, Port-Cros Island, France (spring)	Coralligenous hard bottom	0.6	55.2% (1)	Harmelin (1990)
Montrémian, Port-Cros Island, France (spring)	Coralligenous hard bottom	0.4	49.4% (1)	Harmelin (1990)
Banyuls-Celebere, France (MPA, deep)	Rocky reef	0.3	22.2% (2)	Bell (1983)
Banyuls-Celebere, France (outside MPA, deep)	Rocky reef	0.2	26.4% (2)	Bell (1983)
Galère, Port-Cros Island, France	Rocky infra-littoral	1.6	62.8% (1)	Harmelin (1987)
Montrémian, Port-Cros Island, France	Rocky infra-littoral	0.7	39.6% (1)	Harmelin (1987)
Bay of Calvi, Corsica	Rocky substratum	0.8	56.9% (1)	Spyker & van den Berghe (1995)
Scandola (in–outside MPA), Corsica	Rocky habitats	1.5	38.7% (1)	Prato <i>et al.</i> (2017)
Tavolara-Punta Coda Cavallo (in–outside MPA), Sardinia	Rocky habitats	1.1	46.7% (1)	Prato <i>et al.</i> (2017)
Malta (4–20 m depth)	Rocky reef	1.3	53.1% (1)	Azzurro <i>et al.</i> (2013b)
Lampedusa (4–20 m depth)	Rocky reef	1.2	64.7% (1)	Azzurro <i>et al.</i> (2013b)
Plemmirio (outside marine reserve), Sicily, 2009	Rocky substrata	1.2	59.4% (1)	Consoli <i>et al.</i> (2013)
Plemmirio (outside marine reserve), Sicily, 2010	Rocky substrata	0.9	59.4% (1)	Consoli <i>et al.</i> (2013)
Cape Milazzo (northern Sicily)	Boulder and pebbles	0.7	28.7% (1)	Consoli <i>et al.</i> (2008)
Cape Milazzo (northern Sicily)	Vermetid reef	0.5	18.1% (1)	Consoli <i>et al.</i> (2008)
Italian Adriatic Sea: off Otranto	Rocky – algal	3.4	50.7% (1)	Guidetti (2000)
Tremiti Islands, southern Adriatic Sea	Rocky slopes	0.5	56.4% (1)	Fasola <i>et al.</i> (1997)
Salento Peninsula, SE Italy, (outside shallow)	Rocky cliff	1.3	45.9% (1)	Bussotti & Guidetti (2009)
Salento Peninsula, SE Italy, (outside deep)	Rocky cliff	5.3	66.0% (1)	Bussotti & Guidetti (2009)
Santorini island, Aegean Sea, Greece	Infra-littoral rocky reef	0.4	47.8% (1)	Salomidi <i>et al.</i> (2016)
Dalyanköy, Aegean Sea, Turkey	Artificial rocky reef	~1.1	56.3% (1)	Lök <i>et al.</i> (2008)
Gümüldür-Ürkmez, Aegean Sea, Turkey	Artificial rocky reef	~0.9	78.1% (1)	Lök <i>et al.</i> (2008)
Ramkine, Lebanon	Littoral rocky reef	0.5	32.3% (1)	Harmelin-Vivien <i>et al.</i> (2005)
Anfeh, Lebanon	Littoral rocky reef	0.6	35.4% (1)	Harmelin-Vivien <i>et al.</i> (2005)
Selaata, Lebanon	Littoral rocky reef	0.6	25.6% (1)	Harmelin-Vivien <i>et al.</i> (2005)

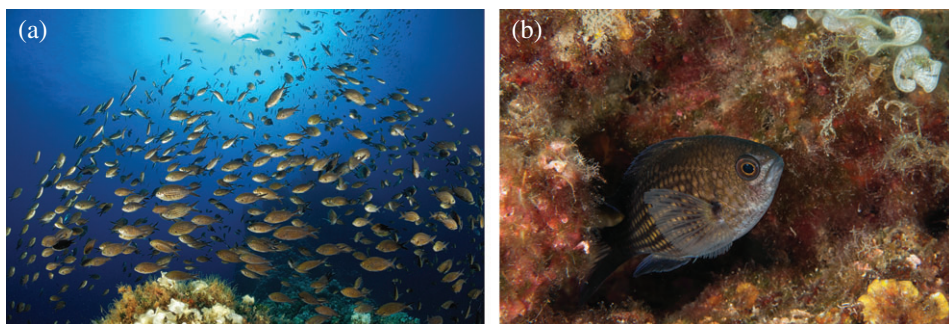


FIG. 1. (a) Large shoal of *Chromis chromis* feeding over the Mediterranean rocky littoral during the day. (b) *C. chromis* sheltering among the rocks at night (images reproduced under licence from Alamy Stock Photo, credit (a) WaterFrame, (b) Roberto Nistri).

for a total of about 10 days. *Chromis chromis* males have been reported to parasitically spawn in other males' nests (Picciulin *et al.*, 2004). The species produces sounds during both agonistic interactions but also during courtship (Picciulin *et al.*, 2001). Dulčić & Kraljević (1994) showed that *C. chromis* fecundity (the number of mature eggs) increased exponentially with fish age–length and that females become sexually mature at 6.8–7.3 cm L_T as they approached age 2 years. Age, growth and mortality of *C. chromis* were described by Dulčić & Kraljević (1995) and individual size, sex-ratio and body condition were all explored by Bracciali *et al.* (2014).

Chromis chromis has a long history of scientific investigation (Cooper & Santini, 2006), it is one of only two damselfish species (family Pomacentridae) included in Linnæus's *Systema Naturae* (1758), though referred to at the time as *Sparus chromis*. *Chromis chromis* had been previously described in Peter Artedi's *Philosophia Ichthyologica* (1738), which is often considered the foundational text for the discipline of ichthyology. Furthermore, 'Chromis' (*Χρอมις*) are mentioned in the first great biology text Aristotle's *History of Animals* (4th century B.C.). In book VIII, Aristotle noted, 'Some people maintain that fishes have better hearing capacities than any other animal - - -. The best hearing abilities are --- chromis and fishes of this order'.

CHROMIS CHROMIS AS THE MOST ABUNDANT FISH IN THE ECOSYSTEM

Most authors who have carried out visual-census surveys of rocky littoral fish assemblages throughout the Mediterranean Sea (from southern Spain, eastwards to Lebanon) have suggested that *C. chromis* is the most abundant fish species in the ecosystem, reaching densities of up to three individuals m^{-2} at some localities, with a mean density of 1.0 m^{-2} (Table I). Indeed, this species is always ranked either number 1 or 2 in terms of most abundant species and it can comprise more than 60% of all individual fish by number at some sites (Table I).

Many investigators have suggested that estimates of reef-fish abundance by visual census are to some extent biased (Harmelin-Vivien *et al.*, 1985), but this technique is still very widely applied (especially in the Mediterranean Sea), because it is usually assumed to be the best available non-destructive method of population assessment.

Typically, visual censuses miss the presence or underestimate abundance of cryptic fish species (e.g. *Parablennius* spp., *Tripterygion* spp. etc.). In addition, diurnally active species are reasonably well counted, but the most common are often underestimated and nocturnal species [e.g. *Apogon imberbis* (L. 1758)] are usually very poorly quantified. Thus, comparisons among fish communities based on visual-census data should be restricted to the diurnally exposed species only. De Raedemaeker *et al.* (2010) provided littoral fish abundance estimates for shallow-water sites around the island of Arki in Greece based on visual-census data. This study suggested that Atherinidae dominated the assemblage as a whole but that these fish, occurred only sporadically (but in large numbers) and hence they were excluded from the analyses. *Chromis chromis* and wrasses (Labridae) dominated during most diurnal visual censuses conducted by these authors.

Pinnegar (2000) demonstrated that although planktivorous fish represent only 11.1% of the total fish species richness in the Bay of Calvi, Corsica, altogether they comprise c. 31.7% of fish biomass and that this constituted a greater part of the total fish biomass, than any other group. Indeed, *C. chromis* alone represented 20.6% of total fish biomass (56.9% by number), more than any other individual species. McClanahan & Sala (1997), were previously unable to include planktivorous fish in their Mediterranean rocky-bottom ecosystem model 'because there is a generalised lack of data concerning planktophagous and detritivore dynamics in Mediterranean rocky bottoms'. Therefore, as far as is known, Pinnegar (2000) provided the first ever estimate of total planktivore biomass for any Mediterranean Sea site. Since the year 2000, however, several other food-web models have been published for the Mediterranean Sea (Coll & Libralato, 2012) that also provide estimates of planktivorous fish biomass. As a result of the ECOPATH food-web model constructed by Pinnegar (2000) and subsequently used by Pinnegar & Polunin (2004) and Pinnegar *et al.* (2014), it was possible to estimate the total throughput of material *via* planktivorous fish at $158.4 \text{ t km}^{-2} \text{ year}^{-1}$ in the Bay of Calvi, Corsica. This represented 39.81% of all fish throughput in the model, which was more than twice as high as that of any other fish group.

CHROMIS CHROMIS AS A PREDATOR ON ZOOPLANKTON

The main types of prey consumed by *C. chromis* have been described as calanoid copepods and larvaceans (Bell & Harmelin-Vivien, 1983; Duka & Shevenko, 1988; Fasola *et al.*, 1997). Duka & Shevenko (1988) in particular, reviewed the diet of male and female *C. chromis* in the Mediterranean Sea and suggested that they feed most heavily on copepods (male 27.9%, female 37.63%), Cladocera (11.03%, 12.9%), Appendicularia (13.6%, 10.75%), as well as decapod larvae, pelagic polychaetes, isopods and fish eggs (including those of *C. chromis*). Khoury (1987) again noted many fish eggs in the stomachs of *C. chromis* at Ile de Port-Cros, France, consequently, the species might play an important role in influencing the recruitment dynamics of other Mediterranean rocky littoral fishes.

Although there have been several studies in the Mediterranean rocky littoral that have estimated consumption rates for herbivorous fish and those that consume benthic invertebrates (Havelange *et al.*, 1997; McClanahan & Sala, 1997), prior to Pinnegar *et al.* (2007), no attempt had been made to determine feeding rates of planktivorous species

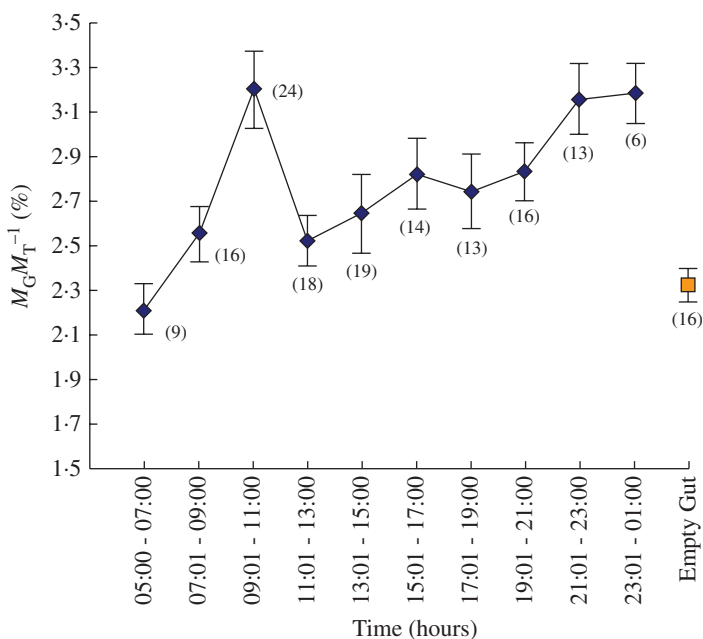


FIG. 2. Mean \pm S.E. gut fullness (\blacklozenge , gut mass (M_G) as % total mass (M_T), including gut] in *Chromis chromis* throughout a daily cycle (from Pinnegar *et al.*, 2007). \blacksquare , Empty guts. Sample sizes are shown in parentheses.

in the Mediterranean Sea region. Pinnegar *et al.* (2007) examined the mass of stomach contents at different times of day in order to obtain an estimate of daily ration (R_D) for *C. chromis*. This analysis revealed that *C. chromis* exhibits two periods of feeding activity, one in the morning commencing just after dawn and one in the afternoon–evening prior to dusk (Fig. 2). These peaks appeared to coincide with diurnal patterns of plankton abundance.

During the morning feeding period of each day, fish were purported to consume around 1.4% of their own body mass and 3.27% during the second feeding phase, thus daily ration was estimated to be around 4.7% of body mass day^{-1} or, for a fish of mean fresh mass 10.25 g, this equates to around 0.48 g of plankton day^{-1} . Assuming that the mean wet mass of an individual zooplankton (*e.g.* a single *Clausocalanus arcuicornis* in the Bay of Calvi) was around 0.058 mg, then this amounted to a total of 8000 individual prey items consumed day^{-1} , which is remarkable bearing in mind the low density of zooplankton in the surrounding water column (Dauby, 1980) and the fact that prey are picked individually from the water using a ram-jaw action (Frédérich *et al.*, 2014) at a rate of *c.* 2 prey every 5–10 s.

In the evening, prior to dusk, *C. chromis* form large gatherings over the substratum, but appeared to continue to feed, possibly consuming the abundant meroplankton, *e.g.* mysids, ostracods and caprellids, that rise from the substratum during this period (Fage, 1933), along with the vertically-migrating offshore copepods and cladocerans being advected shorewards. This bimodal pattern in the feeding of *C. chromis*, around or shortly after the crepuscular periods, may be common among planktivorous fishes and has been reported for other species (Woodhead, 1966).

The estimate for daily ration reported by Pinnegar *et al.* (2007) was based solely on fish caught during or shortly after the spring plankton bloom period, feeding rates at other times of the year may be lower when food is less abundant. Attempts were made by Pinnegar (2000) to calculate yearly consumption to biomass ($Q:B$) ratios, using the daily ration estimate obtained from gut masses and the complex integration procedure of Palomares & Pauly (1989). A $Q:B$ value (adjusted for temperature) of 5.43 times body mass year⁻¹ was obtained using this methodology. This corresponds to a 10.25 g fish consuming 55.7 g of plankton. An alternative value was obtained by Pinnegar (2000) through completely independent means, using calculated growth, temperature and morphometric data (see protocols in Christensen & Pauly, 1992). This value was higher than that obtained from daily ration and inferred that fish consume 10.27 times their own body mass in plankton year⁻¹, (equivalent to a 10.25 g fish, consuming 105.27 g of plankton annually). The weighted mean $Q:B$ for all planktivorous fish (weighted by relative biomass of each species) was estimated at 10.28 times biomass year⁻¹ in the Bay of Calvi (Pinnegar, 2000). Assuming a total biomass for planktivorous of 15.40 g m⁻² this equates to a total consumption rate of 158.4 g m⁻² year⁻¹.

Both Bray (1981) and Hamner *et al.* (1988) have demonstrated that zooplankton biomasses may be greatly depleted after passing through an assemblage of planktivorous damselfishes [*Chromis punctipinnis* (Cooper, 1863) and *Chromis atripectoralis* Welanders & Schultz, 1951]. In the food-web modelling work of Pinnegar (2000), mixed-trophic-impact analysis (MTI) suggested that an increase in planktivore biomass might result in a slight negative effect on zooplankton and macroplankton above the Mediterranean rocky littoral. Leitner & Nguyen (2016) found *C. chromis* schools consistently aggregated over the interface between the *P. oceanica* meadows and the rocky slope in the Bay of Calvi, Corsica. This may be due to food availability as well as proximity to shelter. Copepod densities were significantly higher within schools than outside of schools. This could be due to entrapment and retention mechanisms of plankton in this region, mediated by physical processes. Bracciali *et al.* (2016) suggested that local hydrodynamics might affect morphological traits of *C. chromis* with repercussions at the population level. Specimens showed higher body condition at localities with higher current speeds *c.* 20 cm s⁻¹, where conditions offered greater amounts of food and which were able to support larger individuals. Individuals smaller than 60 mm were typically more abundant at localities with lower current speeds *c.* 10 cm s⁻¹. Morphometric analysis revealed that high-hydrodynamics were favoured by fish with a more fusiform body shape and body traits developed for propellant swimming.

Contrary to the observational data presented by Pinnegar *et al.* (2007) suggesting two feeding periods in *C. chromis* (dawn and dusk) based on stomach fullness, Bracciali *et al.* (2012) suggested that feeding activity in planktivorous species is a function of light polarization (Mussi *et al.*, 2005) and that foraging rates peak at midday when the greatest amount of light is available (Thetmeyer & Kils, 1995). Bracciali *et al.* (2012) did not themselves collect data on *C. chromis* in the Mediterranean Sea; rather they reported on studies elsewhere, although including work on other *Chromis* spp.

Frangoulis *et al.* (2011) used the data from Pinnegar (2000) to demonstrate that in the Bay of Calvi, planktivorous fishes are the predominant source of predatory mortality on mesozooplankton, since other microzooplankton predators (*e.g.* chaetognaths) are scarce or appear only sporadically (cnidarians, ctenophores; Dauby, 1985). The mean predatory mortality rate on mesozooplankton is estimated to be close to 0.2 day⁻¹, using the present depth-integrated spring mean values of mesozooplankton biomass

and assuming a density of 1 *C. chromis* m⁻² (Table I; Spyker & van den Berghe, 1995). Over the coastal rocky littoral, predatory mortality rate could be much higher as densities of planktonic fish may reach 4–6 individuals m⁻² in some places (Table I).

CHROMIS CHROMIS AS A CONDUIT FOR NITROGEN AND PHOSPHORUS

Elsewhere in the world, planktivorous fish have been shown to generate substantial quantities of plankton-derived detritus (Bray *et al.*, 1981) and dissolved wastes (Bray *et al.*, 1986) and these are very important in the functioning of nutrient-deprived ecosystems. Pinnegar *et al.* (2007) estimated that *C. chromis* egests approximately 41.3% of the total material it ingests in the form of faeces and thus a fish of 10.25 g would excrete c. 43.48 g year⁻¹ faecal material. *C. chromis* faecal pellets were shown to be particularly rich sources of nitrogen and phosphorus and of the material originally consumed by *C. chromis* 13.8% of the nitrogen and 33.1% of the phosphorus was egested into the environment. However, only a limited proportion of the faecal material released by *C. chromis* is actually deposited into the rocky littoral system. Assuming a minimum night-time density of *C. chromis* at 1 individual m⁻² (values can be as high as 5–10 individuals m⁻²; Harmelin, 1987) and a mean fish mass of 10.25 g, only 15.2 mg m⁻² or 7.7% of the total (0.198 g m⁻²) is actually deposited during the night, the remainder is released during the day and Verlaque (1985) noted that the faeces of planktivorous fish are sometimes consumed by the herbivorous fish *Sarpa salpa* (L. 1758). This being said, c. 1.23 mg of nitrogen and 0.10 mg of phosphorus may be deposited m⁻² of rocky littoral substratum each night and for phosphorus in particular this represents a very significant input, almost equalling the daily net incorporation of phosphorus by macroalgae (0.12 mg P m⁻² day⁻¹).

Pinnegar & Polunin (2006) established that many benthic organisms (particularly crustaceans and molluscs) are attracted to the faeces of *C. chromis* and that when faeces were left uncovered they were rapidly (within 1 h) removed by mobile species such as shrimps and hermit crabs (*Lysmata* spp. and *Pagurus* spp.). *Chromis chromis* faeces were identified within the gut contents of the shrimp *Lysmata seticaudata* and the types of coprophagous organisms observed by Pinnegar & Polunin (2006) were very similar (even in the same genus) to those described for sites elsewhere in the world (Rothans & Millar, 1991). Faeces released by fish into the water column were demonstrated to sink rapidly to the substratum and to travel only short distances horizontally from the place where they were egested. Coprophagy by several species of fish [notably *Coris julis* (L. 1758) and *S. salpa*] was observed and confirmed the suggestion of Robertson (1982) that fishes will readily eat the faeces of other fishes if these faeces are of greater nutritional quality than the consumer's normal diet. Stable-isotope analysis (Pinnegar & Polunin, 2000) confirmed that *L. seticaudata* receive substantial quantities of originally planktonic material in their diets, whilst also suggesting that the nitrogen consumed by *S. salpa* derives from an animal source rather than the macroalgae used as a source of carbon. Mediterranean macroalgae are particularly poor sources of dietary nitrogen and phosphorus (Atkinson & Smith, 1983) and consequently it has been suggested that many littoral species may need to supplement their diet with a readily available, nutritious food source such as the faeces of planktivorous fish.

Excretion rates of dissolved wastes have been estimated for many planktivorous fish species (Durbin & Durbin, 1981; Bray *et al.*, 1986), but nothing was known prior to Pinnegar *et al.* (2007) concerning excretion patterns among planktivorous fish species in the Mediterranean rocky littoral. It was estimated that 53.7% of all phosphorus ingested by *C. chromis* is excreted as dissolved wastes (chiefly molybdate-reactive P); 45.5% of ingested nitrogen was also suggested to be excreted, mainly in the form of ammonia and 45% of all carbon ingested by *C. chromis* was excreted to the environment (not including the 19.6% lost as CO₂ *via* respiration). The nature of this excretory material remains uncertain, but it was suggested that some of this may consist of mucus exudates from the gills and skin. The excretion of dissolved nutrients by fish and invertebrates has been linked with enhanced growth of macroalgae, corals and anemones (Meyer & Schultz, 1985; Bray *et al.*, 1986) and this topic demands further attention in the Mediterranean Sea.

CHROMIS CHROMIS AS A PREY RESOURCE FOR PISCIVOROUS PREDATORS

Gut-content analysis has shown that many predatory seabirds and fish feed upon *C. chromis* in the Mediterranean Sea (Table II), but there have been few attempts to quantify the absolute magnitude of this predation pressure. Pinnegar (2000) estimated total fishing and natural mortalities for planktivorous fish species and *C. chromis* in particular, using the method of Pauly (1980). The most useful manner of expressing the decay (decrease) of an age group of fishes through time, is by means of exponential population decay curve:

$$N_t = N_0 e^{-Zt} \quad (1)$$

where N_0 is the initial number of fish at time zero, N_t is the number of remaining fishes at the end of time t and Z is the instantaneous rate of total mortality. Using the food-web model derived by Pinnegar (2000), total mortality (Z) for planktivorous species was estimated at 0.94 year⁻¹, of which 2.4% consisted of fishing mortality, 14.5% was predation mortality and 83.1% was other mortality. When this value for Z was inserted into equation 1, it was possible to estimate that only 39.2% of all fish survive to reach one year old and only 15.3% reach 2 years old. This great mortality during the early years of life is almost certainly attributable to largely undetected predation on eggs and larvae; Khoury (1987) reported that in the winter, juvenile fish (and particularly *C. chromis*) may represent 37% of the total mass of prey ingested by the fish assemblage. Of the 37 fish species and two seabirds included in the food-web model of Pinnegar (2000), 12 were reported to consume planktivorous fish and total predation pressure on this group amounted to 2.1 g m⁻² year⁻¹ in the Bay of Calvi, Corsica. Fluxes of planktivorous fish to seabirds, piscivorous fish and macro-carnivorous fish amounted to 0.084, 0.770 and 1.074 g m⁻² year⁻¹, respectively. MTI analysis suggested that increases in the biomass of piscivorous and macro-carnivorous fish species would result in a negative effect on planktivorous fish (subsequently explored further by Pinnegar & Polunin, 2004) and conversely that an increase in the biomass of planktivorous fish would have a positive effect on seabirds.

Stable-isotope analysis by Pinnegar & Polunin (2000) suggested, that most littoral predators [*e.g.* the Roman eel *Muraena helena* L. 1758 conger eel *Conger conger*

(L. 1758) common *dentex* *Dentex dentex* (L. 1758) black scorpionfish *Scorpaena porcus* L. 1758 and painted comber *Serranus scriba* (L. 1758)] actually subsist primarily on benthic prey, rather than planktivorous fish, although the seabird *Phalacrocorax aristotelis* clearly fed on planktivorous prey.

CHROMIS CHROMIS AS A TARGET FOR FISHERIES

Due to its small size *C. chromis* plays only a minor role as a target species for commercial fishing in the Mediterranean Sea. It is sometimes used as a baitfish (in traps or on rod and line) for larger species such as *C. conger* and *D. dentex* that naturally prey on damselfish schools. In addition, large quantities of *C. chromis* are caught throughout the Mediterranean Sea in small-scale artisanal fisheries using beach seines (Cetinić *et al.*, 2011; Riutort 1989). Unlike other littoral species, a high percentage (as much as 100%) of *C. chromis* caught are typically discarded, even though the species may dominate catches in terms of numbers at some localities (*e.g.* the eastern Adriatic; Cetinić *et al.*, 2011).

Dulčić & Kraljević (1995) report that in the coastal fishery of Dalmatia (especially on islands in the eastern middle Adriatic; Šolta, Lastovo, Korčula and Hvar) *C. chromis* form a small but significant component of the coastal beach-seine and gill-net catch and are very much appreciated as food among local inhabitants. Grubšić (1982) reported that the annual catch of *C. chromis* in this region of Dalmatia (Croatia) is around 30 t year⁻¹, which Dulčić & Kraljević (1995) suggested results in an estimated fishing mortality (*F*) of 0.35 year⁻¹. Pinnegar (2000) suggested that fishing pressure on *C. chromis* is much lower in Corsica, although some are still caught as by-catch. Pinnegar (2000) estimated fishing mortality of *C. chromis* in the Bay of Calvi at 0.10 year⁻¹, based on catch statistics (Riutort 1989), that list *C. chromis* among the species that are caught (and mostly discarded) in this particular region. Similarly, M. J. Culioli (unpubl. data) noted small numbers of *C. chromis* among the commercial catches of the Iles Lavezzi in southern Corsica.

Dulčić & Kraljević (1995) noted that the exploitation ratio $E (FZ^{-1})$, where *F* is the instantaneous fishing mortality rate) was significantly less than 0.50; but it ranged between 0.30 and 0.34 depending on sex in the central Adriatic and was generally slightly higher for females than males (0.34 compared with 0.30). The low values of *E* obtained, indicated that the fishing pressure exerted on *Chromis* spp. was rather light in this area (*i.e.* indicative of an underfished stock).

Chromis chromis may represent only a small proportion of retained fish catches in the Mediterranean rocky littoral (landings are dominated by *Scorpaena* spp., *D. dentex*, *Diplodus* spp., other Sparidae, *Mullus surmuletus* L. 1758 and *Serranus* spp.), but changes in fishing pressure overall can have a dramatic effect on this species, through indirect means (Kruschel *et al.*, 2012). Modelling studies have shown that a cessation or intensification of fishing pressure on predatory species such as those listed above can theoretically affect populations of planktivorous fishes (Pinnegar & Polunin, 2004) and this has been demonstrated within and outside Mediterranean Sea MPAs or at sites with differing fishing intensities where higher predator numbers have often coincided with lower densities of *C. chromis* (Kruschel *et al.*, 2012; Zubak *et al.*, 2017) and other prey organisms.

CHROMIS CHROMIS AS AN INDICATOR SPECIES FOR HUMAN PRESSURES

Several papers (Bracciali *et al.*, 2012, 2014) have championed *C. chromis* as a possible indicator species for human disturbance in the western Mediterranean Sea. As well as being directly and indirectly affected by fishing, the species is also sensitive to a number of other anthropogenic pressures, most notably poor water quality and noise pollution that may exert an influence in isolation or may act synergistically.

In recent decades, proliferation of human activities in the seas and oceans has increased the exposure of organisms to noise pollution, thus evoking great interest in potential biological effects. The hearing sensitivity of *Chromis chromis* is more enhanced in the frequency range between 200 and 600 Hz (Wysocki *et al.*, 2009), which falls well within the spectral range of the noise generated by boats. Specifically, Picciulin *et al.* (2010) demonstrated that a frequency of *c.* 400 Hz could have a detrimental effect on *C. chromis* behaviour, masking sounds emitted by males during courtship (*e.g.* pops) with consequences for reproductive fitness. Bracciali *et al.* (2012) showed that low frequency noise (*viz.* 100 and 1000 Hz), such as that generated by boats, elicited behavioural modification in damselfish and suppression of natural feeding rates. Given that these factors in turn affect overall fitness and growth rates, anthropogenic noise could have long-term consequences for population dynamics in *C. chromis* making it a useful and ubiquitous indicator species for human disturbance.

Bracciali *et al.* (2012) measured nautical traffic noise during the summer of 2007 in a southern Mediterranean Sea MPA and simultaneously monitored the feeding behaviour of *C. chromis*. Feeding frequencies, escape reaction and school density were all analysed. Greater traffic volume corresponded with lower feeding frequencies. The escape reaction was longer in duration (>1 min) when a boat passed nearby, while moored boats did not induce an escape response. Vazzana *et al.* (2017) set out to investigate the biochemical markers of stress in the blood plasma of *C. chromis* following *in vivo* exposure to noise levels of 200 and 300 Hz. Results suggested that fish exposed to noise had significantly increased levels of stress biomarkers such as glucose, lactate and total proteins in blood plasma, as well as a rise in the expression of heat shock protein 70 (Hsp70).

Several studies have suggested a strong response in Mediterranean *C. chromis* to inputs of sewage contamination. Azzurro *et al.* (2010) examined the effects of sewage outfalls on subtidal fish assemblages in Malta by means of underwater visual census. Fish assemblage structures were different between controls and sites contaminated by sewage, where total abundance of fish was higher. Azzurro *et al.* (2007) suggested that at moderate levels, nutrient enrichment can influence the fish assemblage by attracting gregarious and planktivorous fishes, with a small but significant increase in the abundances of *C. chromis* and *Oblada melanura* (L. 1758). However, the most striking responses related to a decline in species richness which usually reflects a severe negative effect on the fish community.

An increased density of planktivorous fishes was also observed by Bell & Harmelin-Vivien (1982), who studied the influence of a sewage outfall on the fish fauna within *P. oceanica* beds near Marseille, France. Guidetti *et al.* (2003) examined assemblage structure and temporal trends in shallow subtidal rocky-reef fish populations affected by sewage contamination in southern Apulia (south-east Italy). Planktivorous fishes (including *C. chromis*) were more abundant at the contaminated

location and contributed most to dissimilarities in assemblage structures between the outfall and controls. Furthermore, the outfall significantly affected total fish abundance (which was consistently about five-fold greater at the outfall site than at the controls).

A further human pressure that has significantly affected littoral fish communities in the Mediterranean Sea is the introduction of non-native and invasive species. *Caulerpa taxifolia* is a species of seaweed native to the Indian Ocean. After its accidental introduction to the Mediterranean Sea (in Monaco) in 1984, *C. taxifolia* spread rapidly along the coast of the Alpes-Maritimes invading various biotopes (rock, sand and *P. oceanica* beds) with dramatic consequences for fish communities. Several authors (Francour *et al.*, 1995; Relini *et al.*, 2000) have noted an effect on *C. chromis* populations. Francour *et al.* (1995) suggested that overall, fish density and biomass were slightly lower in colonized sites, but that *C. chromis* remained the dominant fish species at both invaded and non-invaded localities. Similarly Relini *et al.* (2000) showed that planktivorous species, including *C. chromis*, remained dominant in both *P. oceanica* and *C. taxifolia* meadows although *C. chromis* were significantly more abundant on the former in the Ligurian Sea.

The Mediterranean Sea is a region that has witnessed major changes in fish communities as a consequence of non-native species introductions, both from the North Atlantic Ocean and especially through the Suez Canal. The opening of the Suez Canal in 1869 allowed entry of Indo-Pacific and Red Sea fishes for the first time and these so-called Lessepsian migrants now dominate the community at some eastern Mediterranean Sea localities. Recent records of Lessepsian fish species as far west as Spain (Sanchez-Tocino *et al.*, 2007) show that alien species are now present throughout the whole Mediterranean Sea basin. The blue cornetfish *Fistularia commersonii* Rüppell 1838 was first recorded in January 2000 by a fisherman on the coast of Israel (Golani, 2000). *Fistularia commersonii* is considered the fastest and farthest spreading Lessepsian fish migrant and has now reached the north-eastern part of Corsica (Golani *et al.*, 2007; Miniconi, 2010). Multiple authors have recorded *F. commersonii* feeding on *C. chromis* throughout the Mediterranean Sea (Kalogirou *et al.*, 2007; Pais *et al.*, 2007; Bariche *et al.*, 2009). Pinnegar *et al.* (2014) attempted to model the indirect food-web consequences of expanding *F. commersonii* populations in the Bay of Calvi and suggested that invasion of this predator could have dramatic consequences for planktivorous fish populations including *C. chromis*. Similarly, Kalogirou *et al.* (2012) has demonstrated that *C. chromis* represent an important component in the diet of the introduced barracuda *Sphyraena pinguis* Günther 1874 off Rhodes in Greece.

DISCUSSION

While there are undoubtedly other fish species in the Mediterranean Sea that can be viewed as being most important (compared with *C. chromis*) in terms of overall fisheries catches or abundance, these fish [e.g. sardine *Sardina pilchardus* (Walbaum 1792), anchovy *Engraulis encrasicolus* (L. 1758) and European hake *Merluccius merluccius* (L. 1758)] typically exist offshore and do not interact significantly with littoral systems. *Chromis chromis* are probably the species encountered most often by coastal residents and tourists visiting the Mediterranean Sea and yet surprisingly little has been written about this species. *Chromis chromis* is the most abundant coastal species over the vast majority of its distribution range from Murcia in southern Spain to Lebanon in the east (Table I).

C. chromis have been shown to represent a key prey resource for many important fish and seabird predators (Table II). Itself, *C. chromis* can have an influence on plankton dynamics and therefore on throughputs of energy. *Chromis chromis* are consumers of fish eggs and hence have the potential to influence populations of many other fish species and *C. chromis* populations can provide an indicator of anthropogenic stressors, most notably overfishing, but also noise pollution, nutrient inputs and the effects of non-indigenous species. The species is ubiquitous and relatively easy to monitor using visual census techniques.

For the past 0.93–3.26 M years *C. chromis* has existed as the sole representative of the Pomacentridae in the Mediterranean Sea (Domingues *et al.*, 2005). *Chromis limbata* (Valenciennes 1833), the most likely sister species of *C. chromis*, is restricted to the Macaronesian Islands (Azores, Madeira and Canaries) and the western coast of north Africa (between Senegal and Congo). Eastern and central Atlantic Ocean *Chromis* species also include *Chromis lubbocki* Edwards 1986 (Cape Verde Islands), *Chromis sanctaehelenae* Edwards 1987 (Saint Helena Island), *Chromis cadenati* Whitley 1951 (Senegal to Ghana) and *Chromis multilineata* (Guichenot 1853) (from western Africa to the western Atlantic Ocean), but no other damselfish had penetrated the Mediterranean Sea until relatively recently (Domingues *et al.*, 2005).

Introduced Pomacentridae species of the genus *Abudefduf* Forsskål 1775 have been reported in the Mediterranean Sea since 1957 starting from the Gulf of Naples in Italy (Tardent, 1959). According to Deidun & Castriota (2014), two *Abudefduf* species have been regularly observed, the Atlantic Sergeant major *Abudefduf saxatilis* (L. 1758), recorded in Tarragona, Spain (Azzurro *et al.*, 2013a) and Valletta, Malta; as well as the Indo-Pacific sergeant *Abudefduf vaigiensis* (Quoy & Gaimard 1825), recorded from three localities: the Gulf of Naples in the lower Tyrrhenian Sea, the north coast of Israel and the Gulf of Genoa in the Ligurian Sea. On 4th January 2014 a specimen of the east African species *Abudefduf hoefleri* (Steindachner 1881) was caught in shallow coastal waters close to Delimara, Malta (Vella *et al.*, 2016) and identified using mitochondrial DNA barcoding. *Chrysiptera cyanea* (Quoy & Gaimard 1825) was collected from the Gulf of Trieste, north Adriatic Sea (Lipej *et al.*, 2014) and *Stegastes variabilis* (Castelnau 1855), a herbivorous damselfish, was caught on Senglea waterfront, Malta (Vella *et al.*, 2015), on 15 September 2013. Whether this recent influx of non-native pomacentrids (some of which are also planktivorous) represents a competitive threat to *C. chromis* remains unclear. No additional members of the genus *Chromis* Cuvier 1814 have yet been identified in the Mediterranean Sea, despite more than 127 exotic fish species having become successfully established since the beginning of the 20th century, including 65 fish Lessepsian migrant species (Ben Rais Lasram & Mouillot, 2009).

The Mediterranean Sea is currently becoming warmer, in a manner similar to the rest of the world. The Mediterranean Sea, however, is a semi-enclosed sea and so there is limited opportunity for native species to shift their distributions to accommodate any long-term changes in seawater temperature. Ben Rais Lasram & Mouillot (2009) asked whether the recent influx of thermophilic exotic species from the Red Sea might be a reflection of changes in temperature in the Mediterranean Sea region and hence whether we might expect a further acceleration in the rate of introduction of Lessepsian species and a rebalancing between exotic and endemic species richness in the future. Francour *et al.* (1994) noted increases in the abundance of thermophilic fish and invertebrate species that were previously very scarce in the western basin of the Mediterranean Sea and this was confirmed by Bianchi & Mori (2000).

TABLE II. Documented predators of *Chromis chromis* based on stomach content analysis

Predator species	Category	Common name	Locality	Reference
<i>Phalacrocorax aristotelis</i>	Bird	Shag	Corsica, France	Guyot (1990)
<i>Phalacrocorax aristotelis</i>	Bird	Shag	Marseilles, France	Morat <i>et al.</i> (2014)
<i>Phalacrocorax aristotelis</i>	Bird	Shag	Slovenian coast	Lipej <i>et al.</i> (2017)
<i>Phalacrocorax aristotelis</i>	Bird	Shag	Libyan Sea (South Crete)	Xirouchakis <i>et al.</i> (2017)
<i>Phalacrocorax aristotelis</i>	Bird	Shag	Southern Mallorca	Al-Ismail <i>et al.</i> (2013)
<i>Fistularia commersonii</i>	Fish	Blue cornetfish	Arbatax (Sardinia, Italy)	Pais <i>et al.</i> (2007)
<i>Fistularia commersonii</i>	Fish	Blue cornetfish	Lebanese coast	Bariche <i>et al.</i> (2009)
<i>Fistularia commersonii</i>	Fish	Blue cornetfish	South-east Aegean Sea	Kalogirou <i>et al.</i> (2007)
<i>Sphyræna viridens</i>	Fish	Yellow-mouth barracuda	Rhodes Island, Greece	Kalogirou <i>et al.</i> (2012)
<i>Sphyræna sphyræna</i>	Fish	European barracuda	Rhodes Island, Greece	Kalogirou <i>et al.</i> (2012)
<i>Sphyræna chrysotaenia</i>	Fish	Yellowstripe barracuda	Rhodes Island, Greece	Kalogirou <i>et al.</i> (2012)
<i>Scorpaena porcus</i>	Fish	Black scorpionfish	Eastern Adriatic Sea	Pallaoro & Jardas (1990)
<i>Scorpaena scrofa</i>	Fish	Red scorpionfish	Central Adriatic Sea	Šantić <i>et al.</i> (2011)
<i>Dentex dentex</i>	Fish	Common dentex	Balearic Islands	Morales-Nin & Moranta (1997)
<i>Oblada melanura</i>	Fish	Saddled seabream	Adriatic Sea, Croatia	Pallaoro <i>et al.</i> (2003)
<i>Sarda sarda</i>	Fish	Atlantic bonito	North-east Aegean Sea	Fletcher <i>et al.</i> (2013)
<i>Phycis phycis</i>	Fish	Forkbeard	Kastellorizo, Greece	Papaconstantinou & Caragitsou (1989)
<i>Epinephelus marginatus</i>	Fish	Dusky grouper	Balearic Islands	Renoies <i>et al.</i> (2002)
<i>Epinephelus marginatus</i>	Fish	Dusky grouper	Balearic Islands	Linde <i>et al.</i> (2004)
<i>Epinephelus marginatus</i>	Fish	Dusky grouper	Spanish coast and Balearic Islands	Gracia López & Castelló i Orvay (2005)
<i>Epinephelus marginatus</i>	Fish	Dusky grouper	Algerian east coast	Derbal & Kara (1996)
<i>Muraena helena</i>	Fish	Mediterranean moray eel	Southern Adriatic Sea	Matić-Skoko <i>et al.</i> (2014)
<i>Raja miraletus</i>	Fish	Brown ray	Eastern central Adriatic Sea	Šantić <i>et al.</i> (2013)

Albouy *et al.* (2013) attempted to forecast the potential effects of climate change on the species richness and mean body size of coastal fish assemblages in the Mediterranean Sea. Using an ensemble forecasting approach, these authors used species distribution modelling to project the potential distribution of 288 coastal fishes (including *C. chromis*) by the middle and end of the 21st century based on the IPCC A2 scenario (www.ipcc.ch/ipccreports/sres/emission/index.php?idp=94). A mean rise of 1.4°C was projected for the Mediterranean Sea by the middle of the 21st century and 2.8°C by the end of the 21st century. Projections for the end of the century suggest that: 54 species are expected to lose their climatically suitable habitat; species richness is predicted to decrease across 70.4% of the continental shelf area, especially in the western Mediterranean Sea and several parts of the Aegean Sea; mean fish body size will increase over 74.8% of the continental shelf area. Small-bodied species that are not currently targeted by either commercial or recreational fleets presented the highest predicted decreases in geographic range size. For *C. chromis* (Appendix S3 in Albouy *et al.*, 2013) future range modifications and centroid shift were determined and these amounted to a slight but insignificant expansion in range (2491 model cells compared with 2516 cells in 2080–2099) in a south-westerly direction. By contrast, model projections for perturbations to the zooplankton community suggest that strengthening of thermal stratification as a result of climate change, will exacerbate nutrient limitation in the Mediterranean Sea (Durrieu de Madron *et al.*, 2011), resulting in a decline in zooplankton density in the future and this may well have serious deleterious consequences for the number of planktivorous fish that can be supported in the future.

Chromis chromis has been shown to perform a vital function in the Mediterranean Sea, in transferring scarce nutrients (nitrogen and phosphorus) from the pelagic-planktonic system into the nutrient-limited coastal littoral, thus any long-term decline in *C. chromis* in the future should be viewed as being particularly worrisome. Bracciali *et al.* (2012) has stated that *C. chromis* should be considered as a key species for the ecosystem, where ‘key species’ means a ‘functional taxon without redundancy’ the loss or density changes of which could result in significant modifications to community structure.

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References

- Albouy, C., Guilhaumon, F., Leprieur, F., Ben Rais Lasram, F., Somot, S., Aznar, R., Velaz, L., Le Loc'h, F. & Mouillot, D. (2013). Projected climate change and the changing biogeography of coastal Mediterranean fishes. *Journal of Biogeography* **40**, 534–547. <https://doi.org/10.1111/jbi.12013>
- Al-Ismail, S., McMinn, M., Tuset, V. M., Lombarte, A. & Alcover, J. A. (2013). Summer diet of European Shags *Phalacrocorax aristotelis desmarestii* in southern Mallorca. *Seabird* **26**, 8–23.
- Atkinson, M. J. & Smith, S. V. (1983). C:N:P ratios of benthic marine plants. *Limnology and Oceanography* **28**, 568–574. <https://doi.org/10.4319/lo.1983.28.3.0568>

- Azzurro, E., Matiddi, M., Fanelli, E., Camilleri, J., Giordano, P., Scarpato, A. & Axiak, V. (2007). Effects of sewage discharges on coastal fish assemblages in Malta, Strait of Sicily, Mediterranean Sea. *Rapport Commission Internationale pour la Mer Méditerranée* **38**, 424.
- Azzurro, E., Matiddi, M., Fanelli, E., Guidetti, P., La Mesa, G., Scarpato, A. & Axiak, V. (2010). Sewage pollution impact on Mediterranean rocky-reef fish assemblages. *Marine Environmental Research* **69**, 390–397. <https://doi.org/10.1016/j.marenvres.2010.01.006>
- Azzurro, E., Broglio, E., Maynou, F. & Bariche, M. (2013a). Citizen science detects the undetected: the case of *Abudefduf saxatilis* from the Mediterranean Sea. *Management of Biological Invasions* **4**, 167–170. <https://doi.org/10.3391/mbi.2013.4.2.10>
- Azzurro, E., La Messa, G. & Fanelli, E. (2013b). The rocky-reef fish assemblages of Malta and Lampedusa islands (Strait of Sicily, Mediterranean Sea): a visual census study in a changing biogeographical sector. *Journal of the Marine Biological Association of the United Kingdom* **93**, 2015–2026. <https://doi.org/10.1017/S0025315413000799>
- Bariche, M., Alwan, N., El-Assi, H. & Zurayk, R. (2009). Diet composition of the Lessepsian bluespotted cornetfish *Fistularia commersonii* in the eastern Mediterranean. *Journal of Applied Ichthyology* **25**, 460–465. <https://doi.org/10.1111/j.1439-0426.2008.01202.x>
- Bell, J. D. (1983). Effects of depth and marine reserve fishing restrictions on the structure of a rocky reef fish assemblage in the north-western Mediterranean Sea. *Journal of Applied Ecology* **20**, 357–369.
- Bell, J. D. & Harmelin-Vivien, M. L. (1982). Fish fauna of French Mediterranean *Posidonia oceanica* seagrass meadows I: community structure. *Tethys* **10**, 337–347.
- Bell, J. D. & Harmelin-Vivien, M. L. (1983). Fish fauna of French Mediterranean *Posidonia oceanica* seagrass meadows: 2. Feeding habits. *Tethys* **11**, 1–14.
- Ben Rais Lasram, F. & Mouillot, D. (2009). Increasing southern invasion enhances congruence between endemic and exotic Mediterranean fish fauna. *Biological Invasions* **11**, 697–711. <https://doi.org/10.1007/s10530-008-9284-4>
- Bianchi, C. N. & Mori, C. (2000). Marine biodiversity of the Mediterranean Sea: situation, problems and prospects for future research. *Marine Pollution Bulletin* **40**, 367–376. [https://doi.org/10.1016/S0025-326X\(00\)00027-8](https://doi.org/10.1016/S0025-326X(00)00027-8)
- Bracciali, C., Campobello, D., Giacoma, C. & Sarà, G. (2012). Effects of nautical traffic and noise on foraging patterns of Mediterranean damselfish (*Chromis chromis*). *PLoS ONE* **7**, e40582. <https://doi.org/10.1371/journal.pone.0040582>
- Bracciali, C., Piovano, S., Sarà, G. & Giacoma, C. (2014). Seasonal changes in size, sex-ratio and body condition of the damselfish *Chromis chromis* in the central Mediterranean Sea. *Journal of the Marine Biological Association of the United Kingdom* **95**, 1053–1061. <https://doi.org/10.1017/S0025315414000459>
- Bracciali, C., Guzzo, G., Giacoma, C., Dean, J. M. & Sarà, G. (2016). Fish functional traits are affected by hydrodynamics at small spatial scale. *Marine Environmental Research* **113**, 116–123. <https://doi.org/10.1016/j.marenvres.2015.12.002>
- Bray, R. N. (1981). Influence of water current and zooplankton densities on daily foraging movements of blacksmith, *Chromis punctipinnis*, a planktivorous reef fish. *Fishery Bulletin* **78**, 829–841.
- Bray, R. N., Miller, A. C. & Geesey, G. G. (1981). The fish connection: a trophic link between planktonic and rocky reef communities. *Science* **214**, 204–205. <https://doi.org/10.1126/science.214.4517.204>
- Bray, R. N., Purcell, L. J. & Miller, A. C. (1986). Ammonia excretion in a temperate-reef community by a planktivorous fish, *Chromis punctipinnis* (Pomacentridae) and potential uptake by young Giant Kelp, *Macrocystis pyrifera* (Laminales). *Marine Biology* **90**, 327–334. <https://doi.org/10.1007/BF00428556>
- Brohee, M., Goffart, A., Frankignoulle, M., Henri, V., Mouchet, A. & Hecq, J. H. (1989). Variations printanières des communautés planctoniques en baie de Calvi (Corse) en relation avec les contraintes physiques locales. *Cahiers de Biologie Marine* **30**, 321–328.
- Bussotti, S. & Guidetti, P. (2009). Do Mediterranean fish assemblages associated with marine caves and rocky cliffs differ? *Estuarine, Coastal and Shelf Science* **81**, 65–73. <https://doi.org/10.1016/j.ecss.2008.09.023>
- Cetinić, P., Škeljo, F. & Ferri, J. (2011). Discards of the commercial boat seine fisheries on *Posidonia oceanica* beds in the eastern Adriatic Sea. *Scientia Marina* **75**, 289–300.

- Christensen, V. & Pauly, D. (1992). ECOPATH II – a software for balancing steady-state ecosystem models and calculating network characteristics. *Ecological Modelling* **61**, 169–185. [https://doi.org/10.1016/0304-3800\(92\)90016-8](https://doi.org/10.1016/0304-3800(92)90016-8)
- Coll, M. & Libralato, S. (2012). Contributions of food web modelling to the ecosystem approach to marine resource management in the Mediterranean Sea. *Fish and Fisheries* **13**, 60–88. <https://doi.org/10.1111/j.1467-2979.2011.00420.x>
- Consoli, P., Romeo, T., Fiongrandi, U. & Andaloro, F. (2008). Differences among fish assemblages associated with a nearshore vermetid reef and two other rocky habitats along the shores of Cape Milazzo (northern Sicily, central Mediterranean Sea). *Journal of the Marine Biological Association of the United Kingdom* **88**, 401–410. <https://doi.org/10.1017/S0025315408000489>
- Consoli, P., Sarà, G., Mazza, G., Battaglia, P., Romeo, T., Incontro, V. & Andaloro, F. (2013). The effects of protection measures on fish assemblage in the Plemmirio marine reserve (central Mediterranean Sea, Italy): a first assessment 5 years after its establishment. *Journal of Sea Research* **79**, 20–26. <https://doi.org/10.1016/j.seares.2013.01.004>
- Contini, A. & Donato, A. (1973). The reproductive cycle of the teleost *Chromis chromis*. *Memorie di Biologia Marina e di Oceanografia* **3**, 173–184.
- Cooper, W. J. & Santini, F. (2006). A revised damselfish taxonomy with a description of the tribe Microspathodontini (Gian Damselfishes). In *Biology of the Damselfishes* (Parmentier, E. & Frédérick, B., eds), pp. 13–30. Boca Raton, FL: Taylor and Francis.
- Dauby, P. (1980). Cycle annuel du zooplancton de surface de la baie de Calvi (Corse). Biomasse totale et plancton copépodien. *Oceanologica Acta* **3**, 403–407.
- Dauby, P. (1985). Le macrozooplancton gélatineux, une source considérable d'enrichissement en matière organique des substrats benthiques infralittoraux. *Rapport Commission Internationale pour la Mer Méditerranée* **29**, 321–322.
- Dauby, P. & Hecq, J. H. (1981). Le zooplancton de surface de la baie de Calvi. Synthèse de l'étude d'un cycle annuel (1978–1979). *Rapports Commission Internationale pour la Mer Méditerranée* **27**, 123–124.
- Deidun, A. & Castriota, L. (2014). First record of *Abudefduf cfr saxatilis* Linnaeus 1758 (Perciformes: Pomacentridae) from the Maltese Islands (central Mediterranean). *BioInvasions Records* **3**, 53–56. <https://doi.org/10.3391/bir.2014.3.1.10>
- De Raedemaeker, F., Miliou, A. & Perkins, R. (2010). Fish community structure on littoral rocky shores in the eastern Aegean Sea: effects of exposure and substratum. *Estuarine Coastal and Shelf Science* **90**, 35–44. <https://doi.org/10.1016/j.ecss.2010.08.007>
- Derbal, F. & Kara, M. (1996). Alimentation estivale du Merou *Epinephelus marginatus* (Serranidae) des côtes est Algériennes. *Cybiu* **20**, 295–301.
- Domingues, V. S., Bucciarelli, G., Almada, V. C. & Bernardi, G. (2005). Historical colonization and demography of the Mediterranean damselfish, *Chromis chromis*. *Molecular Ecology* **14**, 4051–4063. <https://doi.org/10.1111/j.1365-294X.2005.02723.x>
- Duka, L. A. & Shevenko, N. F. (1988). Morphology and nutrition of *Chromis chromis* (Linné) in the Mediterranean and Black Seas. *Ehkol Morya* **3**, 26–33.
- Dulčić, J. & Kraljević, M. (1994). The fecundity of damselfish (*Chromis chromis*) in the eastern middle Adriatic. *Acta Adriatica* **35**, 53–57.
- Dulčić, J. & Kraljević, M. (1995). Age, growth and mortality of damselfish (*Chromis chromis* L.) in the eastern middle Adriatic. *Fisheries Research* **22**, 255–265. [https://doi.org/10.1016/0165-7836\(94\)00318-Q](https://doi.org/10.1016/0165-7836(94)00318-Q)
- Durbin, E. G. & Durbin, A. G. (1981). Assimilation efficiency and nitrogen excretion of a filter-feeding planktivore, the Atlantic menhaden, *Brevoortia tyrannus* (Pisces: Clupeidae). *Fishery Bulletin* **79**, 601–616.
- Durrieu de Madron, X., Guieu, C., Sempéré, R., Conan, P., Cossa, D., D'Ortenzio, F., Estournel, C., Gazeau, F., Rabouille, C., Stemmann, L., Bonnet, S., Diaz, D., Koubbi, P., Radakovitch, O., Babin, M., Baklouti, M., Bancon-Montigny, C., Belviso, S., Bensoussan, N., Bonsang, B., Bouloubassi, I., Brunet, C., Cadiou, J.-F., Carlotti, F., Chami, M., Charmasson, S., Charrière, B., Dachs, J., Doxaran, D., Dutay, J.-C., Elbaz-Poulichet, F., Eléaume, M., Eyrolles, F., Fernandez, C., Fowler, S., Francour, P., Gaertner, J.-C., Galzin, R., Gasparini, S., Ghiglione, J.-F., Gonzalez, J.-L., Goyet, C., Guidi, L., Guizien, K., Heimbürger, L.-E., Jacquet, S. H. M., Jeffrey, W. H., Joux, F., Leblanc, K., Lefèvre, D., Lejeusne, C., Lemé, R., Lojze-Pilot, M.-D., Mallet, M., Méjanelle, L., Mélin, F.,

- Mellon, C., Mérigot, B., Merle, P.-L., Migon, C., Miller, W. L., Mortier, L., Mostajir, B., Mousseau, L., Moutin, T., Para, J., Pérez, T., Petrenko, A., Poggiale, J.-C., Prieur, L., Pujo-Pay, M., Pulido-Villena, E., Raimbault, P., Rees, A. P., Ridame, C., Rontani, J.-F., Ruiz Pino, D., Sicre, M. A., Taillandier, V., Tamburini, C., Tanaka, T., Taupier-Letage, I., Tedetti, M., Testor, P., Thébault, H., Thouvenin, B., Touratier, F., Tronczynski, J., Ulses, C., Van Wambeke, F., Vantrepotte, V., Vaz, S. & Verney, R. (2011). Marine ecosystems' responses to climatic and anthropogenic forcings in the Mediterranean. *Progress in Oceanography* **91**, 97–166. <https://doi.org/10.1016/j.pocean.2011.02.003>
- Fage, L. (1933). Pêches planctoniques à la lumière effectuées à Banyuls-sur-Mer et à Concarneau: III Crustacés. *Archives de Zoologie Expérimentale et Générale* **76**, 105–248.
- Fasola, M., Canova, L., Foschi, F., Novelli, O. & Bressan, M. (1997). Resource use by a Mediterranean rocky slope fish assemblage. *PSZN Marine Ecology* **18**, 51–66. <https://doi.org/10.1111/j.1439-0485.1997.tb00426.x>
- Fletcher, N., Batjakas, I. E. & Pierce, G. J. (2013). Diet of the Atlantic bonito *Sarda sarda* (Bloch, 1793) in the northeast Aegean Sea. *Journal of Applied Ichthyology* **29**, 1030–1035. <https://doi.org/10.1111/jai.12164>
- Francour, P., Boudouresque, C. F., Harmelin, J. G., Harmelin-Vivien, M. L. & Quignard, J. P. (1994). Are the Mediterranean waters becoming warmer? Information from biological indicators. *Marine Pollution Bulletin* **28**, 523–526. [https://doi.org/10.1016/0025-326X\(94\)90071-X](https://doi.org/10.1016/0025-326X(94)90071-X)
- Francour, P., Harmelin-Vivien, M., Harmelin, J. G. & Duclerc, J. (1995). Impact of *Caulerpa taxifolia* colonization on the littoral ichthyofauna of north-western Mediterranean Sea: preliminary results. *Hydrobiologia* **300/301**, 345–353. <https://doi.org/10.1007/BF00024475>
- Frangoulis, C., Skliris, N., Lepoint, G., ElKalay, K., Goffart, A., Pinnegar, J. K. & Hecq, J. H. (2011). Importance of copepod carcasses versus faecal pellets in the upper water column of an oligotrophic area. *Estuarine Coastal and Shelf Science* **92**, 456–463. <https://doi.org/10.1016/j.ecss.2011.02.005>
- Frédérich, B., Olivier, D., Litsios, G., Alfaro, M. E. & Parmentier, E. (2014). Trait decoupling promotes evolutionary diversification of the trophic and acoustic system of damselfishes. *Proceedings of the Royal Society B* **281**, 20141047. <https://doi.org/10.1098/rspb.2014.1047>
- Garcia Charton, J. A. & Perez Ruzafa, A. (1998). Correlation between habitat structure and a rocky reef fish assemblage in the southwest Mediterranean. *PSZNI Marine Ecology* **19**, 111–128. <https://doi.org/10.1111/j.1439-0485.1998.tb00457.x>
- Goffart, A., Hecq, J. H. & Legendre, L. (2015). Drivers of the winter-spring phytoplankton bloom in a pristine NW Mediterranean site, the Bay of Calvi (Corsica): a long-term study (1979–2011). *Progress in Oceanography* **137**, 121–139. <https://doi.org/10.1016/j.pocean.2015.05.027>
- Golani, D. (2000). First record of the bluespotted cornetfish from the Mediterranean Sea. *Journal of Fish Biology* **56**, 1545–1547. <https://doi.org/10.1111/j.1095-8649.2000.tb02163.x>
- Golani, D., Azzurro, E., Corsini-Foka, M., Andaloro, F. & Bernardi, G. (2007). Genetic bottlenecks and successful biological invasions: the case of a recent Lessepsian migrant. *Biology Letters* **3**, 541–545. <https://doi.org/10.1098/rsbl.2007.0308>
- Gracia López, V. & Castelló i Orvay, F. (2005). Food habits of groupers *Epinephelus marginatus* (Lowe, 1834) and *Epinephelus costae* (Steindachner, 1878) in the Mediterranean Coast of Spain. *Hidrobiológica* **15**, 27–34.
- Grubišić, F. (1982). *Ribe, rakovi i školjke Jadrana*. Zagreb: ITRO Naprijed.
- Guidetti, P. (2000). Differences among fish assemblages associated with nearshore *Posidonia oceanica* seagrass beds, rocky-algal reefs and unvegetated sand habitats in the Adriatic Sea. *Estuarine Coastal and Shelf Science* **50**, 515–529. <https://doi.org/10.1006/ecss.1999.0584>
- Guidetti, P., Terlizzi, A., Fraschetti, S. & Boero, F. (2003). Changes in Mediterranean rocky-reef fish assemblages exposed to sewage pollution. *Marine Ecology Progress Series* **253**, 269–278.
- Guyot, I. (1990). Le Cormoran Huppé en Corse: biologie et interactions avec la pêche professionnelle. *Travaux Scientifiques Parc Nat Régional et National de Corse* **28**, 1–40.

- Hamner, W. M., Jones, M. S., Carleton, J. H., Hauri, I. R. & Williams, D. M. (1988). Zooplankton, planktivorous fish and water currents on a windward reef face, Great Barrier Reef, Australia. *Bulletin of Marine Science* **42**, 459–479.
- Harmelin, J. G. (1987). Structure et variabilité de l'ichtyofaune d'une zone rocheuse protégée en Méditerranée (Parc national de Port-Cros, France). *PSZNI Marine Ecology* **8**, 263–284. <https://doi.org/10.1111/j.1439-0485.1987.tb00188.x>
- Harmelin, J. G. (1990). Ichtyofaune des fonds rocheux de Méditerranée: structure du peuplement du coralligène de l'île de Port-Cros (Parc National, France). *Mesogée* **50**, 23–30.
- Harmelin-Vivien, M. L., Harmelin, J.-G., Chauvet, C., Duval, C., Galzin, R., Lejeune, P., Barnabé, G., Blanc, F., Chevalier, R., Duclerc, J. & Lasserre, G. (1985). Evaluation des peuplements et populations de poissons. Méthodes et problèmes. *Revue Ecologie (Terre Vie)* **40**, 467–539.
- Harmelin-Vivien, M. L., Bitar, G., Harmelin, J. G. & Monestiez, P. (2005). The littoral fish community of the Lebanese rocky coast (eastern Mediterranean Sea) with emphasis on Red Sea immigrants. *Biological Invasions* **7**, 625–637. <https://doi.org/10.1007/s10530-004-5852-4>
- Havelange, S., Lepoint, G., Dauby, P. & Bouqueneau, J. M. (1997). Feeding of the sparid fish *Sarpa salpa* in a seagrass ecosystem: diet and carbon flux. *PSZNI Marine Ecology* **18**, 289–297. <https://doi.org/10.1111/j.1439-0485.1997.tb00443.x>
- Kalogirou, S., Corsini, M., Kondilatos, G. & Wennhage, H. (2007). Diet of the invasive piscivorous fish *Fistularia commersonii* in a recently colonized area of the eastern Mediterranean. *Biological Invasions* **9**, 887–896. <https://doi.org/10.1007/s10530-006-9088-3>
- Kalogirou, S., Mittermayer, F., Pihl, L. & Wennhage, H. (2012). Feeding ecology of indigenous and non-indigenous fish species within the family Sphyraenidae. *Journal of Fish Biology* **80**, 2528–2548. <https://doi.org/10.1111/j.1095-8649.2012.03306.x>
- Khoury, C. (1987). Ichtyofaune des herbiers de Posidonies du parc national de Port-Cros: composition, éthologie alimentaire et rôle dans le réseau trophique. PhD Thesis, Université Aix-Marseille II, France.
- Krom, M., Kress, N., Berman-Frank, I. & Rahav, E. (2014). Past, present and future patterns in the nutrient chemistry of the eastern Mediterranean. In *The Mediterranean Sea* (Goffredo, S. & Dubinsky, Z., eds), pp. 49–68. Dordrecht: Springer. https://doi.org/10.1007/978-94-007-6704-1_4
- Kruschel, C., Schultz, S. T., Bakran-Petricioli, T. & Petricioli, D. (2012). Comparing predator abundance and fish diversity in MPA sites (Kornati NP, Croatia) and adjacent sites exploited by fisheries. *Croatian Journal of Fisheries* **70**(Suppl. 1), S65–S78.
- Leitner, A. & Nguyen, S. (2016). Investigation into the Patchy Coastal Distribution of *Chromis chromis* in Revellata Bay, Corsica. *Marine Ecology Field Quarter* (BIOE 159), University of California, Santa Cruz. Available at www.courses.pbsci.ucsc.edu/eeb/bioe159/wp-content/uploads/2016/09/2012_Astrid_Chromis.pdf (accessed 08/08/2017).
- Linde, M., Grau, A. M., Riera, F. & Massutí-Pascual, E. (2004). Analysis of trophic ontogeny in *Epinephelus marginatus* (Serranidae). *Cybium* **28**, 27–35.
- Lipej, L., Mavri, B. & Dulcic, J. (2014). First record of *Chrysiptera cyanea* (Quoy and Gaimard, 1825) (Perciformes: Pomacentridae) in the Mediterranean Sea. *Journal of Applied Ichthyology* **30**, 1–3. <https://doi.org/10.1111/jai.12472>
- Lipej, L., Mavrič, B., Odorico, R. & Koce, U. (2017). The diet of the Mediterranean shag *Phalacrocorax aristotelis desmarestii* roosting along the Slovenian coast. *Acrocephalus* **37**, 51–158. <https://doi.org/10.1515/acro-2016-0008>
- Lök, A., Gül, B., Ulaş, A., Düzbastılar, F. O. & Metin, C. (2008). Diel variations on the fish assemblages at artificial reefs in two different environments of the Aegean Sea (western coast of Turkey). *Turkish Journal of Fisheries and Aquatic Sciences* **8**, 79–85.
- Mapstone, G. M. & Wood, E. M. (1975). The ethology of *Abudefduf luridus* and *Chromis chromis* (Pisces: Pomacentridae) from the Azores. *Journal of Zoology* **175**, 179–199. <https://doi.org/10.1111/j.1469-7998.1975.tb01395.x>
- Matić-Skoko, S., Tutman, P., Varezić, D. B., Skaramuca, D., Đikić, D., Lisičić, D. & Skaramuca, B. (2014). Food preferences of the Mediterranean moray eel, *Muraena helena* (Pisces: Muraenidae), in the southern Adriatic Sea. *Marine Biology Research* **10**, 807–815. <https://doi.org/10.1080/17451000.2013.863351>

- McClanahan, T. R. & Sala, E. (1997). A Mediterranean rocky-bottom ecosystem fisheries model. *Ecological Modelling* **104**, 145–164. [https://doi.org/10.1016/S0304-3800\(97\)00121-X](https://doi.org/10.1016/S0304-3800(97)00121-X)
- Meyer, J. L. & Schultz, E. T. (1985). Tissue condition and growth rate of corals associated with schooling fish. *Limnology and Oceanography* **30**, 157–166. <https://doi.org/10.4319/lo.1985.30.1.0157>
- Miniconi, R. (2010). Inventaire des poissons de Corse (3e^e complement). *Stantari* **21**, 67–68.
- Morales-Nin, B. & Moranta, J. (1997). Life history and fishery of the common dentex (*Dentex dentex*) in Mallorca (Balearic Islands, western Mediterranean). *Fisheries Research* **30**, 67–76. [https://doi.org/10.1016/S0165-7836\(96\)00560-7](https://doi.org/10.1016/S0165-7836(96)00560-7)
- Morat, F., Mante, A., Drunat, E., Dabat, J., Bonhomme, P., Harmelin-Vivien, M. & Letourneur, Y. (2014). Diet of Mediterranean European shag, *Phalacrocorax aristotelis desmarestii* in a northwestern Mediterranean area: a competitor for local fisheries? *Scientific Reports of Port-Cros National Park* **28**, 113–132.
- Mussi, M., Haimberger, T. J. & Hawryshyn, C. W. (2005). Behavioural discrimination of polarized light in the damselfish *Chromis viridis* (family Pomacentridae). *Journal of Experimental Biology* **208**, 3037–3046. <https://doi.org/10.1242/jeb.01750>
- Pais, A., Merella, P., Follesa, M. C. & Garippa, G. (2007). Westward range expansion of the Lessepsian migrant *Fistularia commersonii* (Fistulariidae) in the Mediterranean Sea, with notes on its parasites. *Journal of Fish Biology* **70**, 269–277. <https://doi.org/10.1111/j.1095-8649.2006.01302.x>
- Pallaoro, A. & Jardas, I. (1990). Food and feeding habits of black scorpionfish (*Scorpaena porcus* L., 1758) (Pisces, Scorpaenidae) along the Adriatic Coast. *Acta Adriatica* **32**, 885–898.
- Pallaoro, A., Šantić, M. & Jardas, I. (2003). Feeding habits of the saddled bream, *Oblada melanura* (Sparidae), in the Adriatic Sea. *Cybiu* **27**, 261–268.
- Palomares, M. L. & Pauly, D. (1989). A multiple regression model for predicting the food consumption of marine fish populations. *Australian Journal of Marine & Freshwater Research* **40**, 259–273.
- Papaconstantinou, C. & Caragitsou, E. (1989). Feeding interaction between two sympatric species *Pagrus pagrus* and *Phycis phycis* around Kastellorizo Island (Dodecanese, Greece). *Fisheries Research* **7**, 329–342. [https://doi.org/10.1016/0165-7836\(89\)90065-9](https://doi.org/10.1016/0165-7836(89)90065-9)
- Pauly, D. (1980). On the interrelationships between natural mortality, growth parameters and mean environmental temperature in 175 fish stocks. *Journal du Conseil International pour l'Exploration de la Mer* **39**, 175–192. <https://doi.org/10.1093/icesjms/39.2.175>
- Picciulin, M., Costantini, M., Hawkins, A. D. & Ferrero, E. A. (2001). Sound emission of the Mediterranean damselfish *Chromis chromis* (Pomacentridae). *Bioacoustics* **12**, 236–237. <https://doi.org/10.1080/09524622.2002.9753707>
- Picciulin, M., Verginella, L., Spoto, M. & Ferrero, E. A. (2004). Colonial nesting and the importance of the brood size in male parasitic reproduction of the Mediterranean damselfish *Chromis chromis* (Pisces: Pomacentridae). *Environmental Biology of Fishes* **70**, 23–30. <https://doi.org/10.1023/B:EBFI.0000022851.49302.df>
- Picciulin, M., Sebastianutto, L., Codarin, A., Farina, A. & Ferrero, E. A. (2010). *In situ* behavioural responses to boat noise exposure of *Gobius cruentatus* (Gmelin 1789; fam. Gobiidae) and *Chromis chromis* (Linnaeus, 1758; fam. Pomacentridae) living in a marine protected area. *Journal of Experimental Marine Biology and Ecology* **386**, 125–132. <https://doi.org/10.1016/j.jembe.2010.02.012>
- Pinnegar, J. K. (2000). Planktivorous fishes: links between the Mediterranean littoral and pelagic. PhD Thesis, Newcastle University, Newcastle upon Tyne, U.K.
- Pinnegar, J. K. & Polunin, N. V. C. (2000). Contributions of stable-isotope data to elucidating food webs of Mediterranean rocky littoral fishes. *Oecologia* **122**, 399–409. <https://doi.org/10.1007/s004420050046>
- Pinnegar, J. K. & Polunin, N. V. C. (2004). The use of ECOSIM dynamic modelling to predict trophic cascades resulting from intensive fishing in the Mediterranean rocky littoral. *Ecological Modelling* **172**, 249–267. <https://doi.org/10.1016/j.ecolmodel.2003.09.010>
- Pinnegar, J. K. & Polunin, N. V. C. (2006). Planktivorous damselfish support significant nitrogen and phosphorus fluxes to Mediterranean reefs. *Marine Biology* **148**, 1089–1099. <https://doi.org/10.1007/s00227-005-0141-z>

- Pinnegar, J. K., Polunin, N. V. C. & Videler, J. K. (2007). Daily carbon, nitrogen and phosphorus budgets, for the Mediterranean planktivorous damselfish *Chromis chromis*. *Journal of Experimental Marine Biology & Ecology* **352**, 328–391. <https://doi.org/10.1016/j.jembe.2007.08.016>
- Pinnegar, J. K., Tomczak, M. T. & Link, J. S. (2014). How to determine the likely indirect food-web consequences of a newly introduced non-native species: a worked example. *Ecological Modelling* **272**, 379–387. <https://doi.org/10.1016/j.ecolmodel.2013.09.027>
- Prato, G., Thiriet, P., Di Franco, A. & Francour, P. (2017). Enhancing fish underwater visual census to move forward assessment of fish assemblages: an application in three Mediterranean marine protected areas. *PLoS ONE* **12**, e0178511. <https://doi.org/10.1371/journal.pone.0178511>
- Relini, G., Relini, M. & Torchia, G. (2000). Fish population changes following the invasion of the allochthonous alga *Caulerpa taxifolia* in the Ligurian Sea (N-W Mediterranean). *ICES CM 2000/U:17*. Available at <http://www.ices.dk/sites/pub/CM%20Documents/2000/U/U1700.pdf/>
- Renoñes, O., Polunin, N. V. C. & Goni, R. (2002). Size related dietary shifts of *Epinephelus marginatus* in a western Mediterranean littoral ecosystem: an isotope and stomach content analysis. *Journal of Fish Biology* **61**, 122–137. <https://doi.org/10.1111/j.1095-8649.2002.tb01741.x>
- Riutort, J. J. (1989). Première estimation des captures et de l'effort de pêche déployé par les 'petits métiers' sur le littoral nord-ouest de la Corse. *Report – Station de Recherches Sous-Marines et Oceanographiques (STARESO) Calvi*.
- Robertson, D. R. (1982). Fish faeces as fish food on a Pacific coral reef. *Marine Ecology-Progress Series* **7**, 253–265.
- Rothans, T. C. & Millar, A. C. (1991). A link between biologically imported particulate organic nutrients and the detritus food web in reef communities. *Marine Biology* **110**, 145–150. <https://doi.org/10.1007/BF01313101>
- Salomidi, M., Giakoumi, S., Gerakaris, V., Issaris, Y., Sini, M. & Tsiamis, K. (2016). Setting an ecological baseline prior to the bottom-up establishment of a marine protected area in Santorini island, Aegean Sea. *Mediterranean Marine Science* **17**, 720–737.
- Sanchez-Tocino, L., Hidalgo Puertas, F. & Pontes, M. (2007). Primera cita de *Fistularia commersonii* Rüppell 1838 (Osteichthyes: Fistulariidae) en aguas mediterráneas de la Península Ibérica. *Zoologica Baetica* **18**, 79–84.
- Šantić, M., Pallaoro, A., Staglicic, N. & Markov-Podvinski, M. (2011). Feeding habits of the red scorpionfish, *Scorpaena scrofa* (Osteichthyes: Scorpaenidae) from the eastern central Adriatic Sea. *Cahiers de Biologie Marine* **52**, 217–226.
- Šantić, M., Rađa, B. & Pallaoro, A. (2013). Feeding habits of brown ray (*Raja miraletus* Linnaeus 1758) from the eastern central Adriatic Sea. *Marine Biology Research* **9**, 301–308. <https://doi.org/10.1080/17451000.2012.739698>
- Spyker, K. A. & van den Berghe, E. P. (1995). Diurnal abundance patterns of Mediterranean fishes assessed on fixed transects by scuba divers. *Transactions of the American Fisheries Society* **124**, 216–224. [https://doi.org/10.1577/1548-8659\(1995\)124<0216:DAPOMF>2.3.CO;2](https://doi.org/10.1577/1548-8659(1995)124<0216:DAPOMF>2.3.CO;2)
- Tardent, P. (1959). Capture d'un *Abudefduf saxatilis vaigiensis* Q. und G. (Pisces, Pomacentridae) dans le Golfe de Naples. *Revue Suisse de Zoologie* **66**, 347–351.
- Thetmeyer, H. & Kils, U. (1995). To see and not be seen: the visibility of predator and prey with respect to feeding behaviour. *Marine Ecology-Progress Series* **126**, 1–8. <https://doi.org/10.3354/meps126001>
- Vazzana, M., Celi, M., Arizza, V., Calandra, G., Buscaino, G., Ferrantelli, V., Bracciali, C. & Sarà, G. (2017). Noise elicits hematological stress parameters in Mediterranean damselfish (*Chromis chromis*, Perciformes): a mesocosm study. *Fish and Shellfish Immunology* **62**, 147–152. <https://doi.org/10.1016/j.fsi.2017.01.022>
- Vella, A., Agius Darmanin, S. & Vella, N. (2015). Morphological and genetic barcoding study confirming the first *Stegastes variabilis* (Castelnau 1855) report in the Mediterranean Sea. *Mediterranean Marine Science* **16**, 609–612. <https://doi.org/10.12681/mms.1391>
- Vella, A., Vella, N. & Agius Darmanin, S. (2016). The first record of the African sergeant, *Abudefduf hoefleri* (Perciformes: Pomacentridae), in the Mediterranean Sea. *Marine Biodiversity Records* **9**, 15. <https://doi.org/10.1186/s41200-016-0008-7>

- Verlaque, M. (1985). Note préliminaire sur le comportement alimentaire de *Sarpa salpa* (Sparidae) en Méditerranée. *Rapport Commission Internationale pour la Mer Mediterranee* **29**, 193–196.
- Wood, E. M. (1977). A review of damselfishes (Pisces: Pomacentridae) of the genus *Chromis* from the central and eastern Atlantic and the Mediterranean. *Journal of Fish Biology* **10**, 331–345. <https://doi.org/10.1111/j.1095-8649.1977.tb04067.x>
- Woodhead, P. M. J. (1966). The behaviour of fish in relation to light in the sea. *Oceanography and Marine Biology: An Annual Review* **4**, 337–403.
- Wysocki, L. E., Codarin, A., Ladich, F. & Picciulin, M. (2009). Sound pressure and particle acceleration audiograms in three marine fish species from the Adriatic Sea. *Journal of the Acoustic Society of America* **126**, 2100–2107. <https://doi.org/10.1121/1.3203562>
- Xirouchakis, S., Kasapidis, P., Christidis, A., Andreou, G., Kontogeorgos, I. & Lymberakis, P. (2017). Status and diet of the European shag (Mediterranean subspecies) *Phalacrocorax aristotelis desmarestii* in the Libyan Sea (south Crete) during the breeding season. *Marine Ornithology* **45**, 1–9.
- Zubak, I., Kruschel, C. & Schiltz, S. T. (2017). Predators structure fish communities in *Posidonia oceanica* meadows: meta-analysis of available data across the Mediterranean basin. *Marine Ecology-Progress Series* **566**, 145–157. <https://doi.org/10.3354/meps12038>