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Review

Invasive Crayfish Stepping as a Potential Threat for Coastal Waters

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Abstract: Species belonging to the crustacean infraorder Astacoidea represent taxa of particular interest from a conservation point of view, such as the threatened European crayfish (i.e., *Austropotamobius pallipes*), and at the same time include invasive taxa having highly negative impacts where they are introduced. Among the latter, some freshwater-dwelling species seem to show some abilities to tolerate high salinity levels, such as *Procambarus clarkii* Girard, 1852. By using metadata and field observation, this review will investigate whether the alien *P. clarkii* can threaten coastal waters. Specifically, we will shed light on *P. clarkii*'s (1) invasiveness, (2) its dispersal pattern, (3) its tolerance to salinity, and (4) its ecological plasticity as an invasive species in relation to estuaries. This new habitat colonization is also possible as *P. clarkii* has been observed to survive up to 20 ppt of water salinity and a maximum of 30–35 ppt with its lifetime drastically reduced. As a result, *P. clarkii* colonizes different ecosystems globally, reaching estuarine and coastal ecosystems due to active and passive transport by human and animal vectors. Due to recent discoveries of alien crayfish in estuarine and coastal waters, monitoring activities have become mandatory to preserve coastal habitats and all the aquatic resources (e.g., limicolous birds, endemic fish, fishery and aquaculture activities) inhabiting therein.

Keywords: transitional water; colonization; alien species; biodiversity conservation; ecosystem preservation

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1. Introduction

Astacoideans include species of particular concern from a conservation point of view as many crayfish are listed as threatened or endangered (see *Austropotamobius pallipes* in [1]), but also many taxa amongst the most threatening introduced worldwide [2–4] driving detrimental constraints to the native biodiversity shaping [5,6].

Indeed, once they became established in the new habitat, introduced crayfish began to receive great attention [4]. Here, they can pose several threats to the native biota due to their (i) tolerance to extreme environmental conditions, (ii) rapid spread, and (iii) parasite transmission [7,8], significantly altering the food web structure [9]. For these reasons, astacoideans are the largest and long-lived invertebrates in temperate areas, playing an important role in the community structure [10]. They are indeed keystone consumers, feeding on diverse living and non-living resources (e.g., [11,12]), and constitute a new resource for native taxa as well [13,14]. Additionally, alien crayfish are able to induce a decline in the species richness [15] and detrimental habitat changes also in industrial and agricultural areas [16–20].

In this context, the ecological plasticity of non-indigenous crayfish may represent a new unexpected threat to brackish and transitional aquatic ecosystems despite their habit of inhabiting freshwaters. This could also have an impact on fragile and ephemeral ecosystems, such as the Mediterranean temporary ponds (MTPs, hereafter). Particularly, Mediterranean coasts are characterized by these temporary habitats that are listed in the Habitat Directive according to the Natura 2000 network of the European Union (i.e., Natura code 3170* on MTPs, the 3120 habitats with *Isoeto-NanoJuncetea* and the 3130 containing *Littorelletea uniflorae* and/or *IsoetoNano-Juncetea*, Habitats Directive 92/43/EEC). The importance of those MTPs is widely recognized, being refugia and unique transitional habitats for biodiversity and protected species. Among the latter, many migratory bird and reptile species use MPTs as biological corridors (e.g., *Ardea* spp. and *Emys orbicularis* listed in the Habitat Directive and IUCN). MTPs also show several important ecosystem functions [14], such as being hotspots for cryptobiont species, unique organisms living in those habitats. Being a disappearing habitat, MTPs have great importance as they contain rare, endangered, and endemic species, which are going to disappear with the degradation of these ponds due to several threats, among these also alien species [14].

Among all alien crayfish species, this review investigates whether any crayfish species, with a focus on the most dangerous (i.e., *Procambarus clarkii* (Girard, 1852)), can threaten coastal waters. Specifically, we shed light on the adaptive features of crayfish as an invasive species of estuaries. In particular, the (1) invasiveness of *P. clarkii*, (2) its dispersal pattern, (3) its tolerance to salinity and (4) its ecological plasticity. Throughout the review, we will use metadata from the literature, and a particular field observation of *P. clarkii* in sea and coastal ecosystems.

2. Crayfish Invasiveness

European freshwaters are inhabited by several self-sustaining populations of diverse introduced species [15,21]. Regarding the Italian peninsula, the species actually found refer to the following: the narrow-clawed crayfish *Astacus leptodactylus* (Eschscholtz, 1823), the yabby *Cherax destructor* (Clark, 1936), the redclaw *C. quadricarinatus* (von Martens, 1868) (observed in rearing systems) [22], the spiny-cheek crayfish *Faxonius limosus* (Rafinesque, 1817), the signal crayfish *Pacifastacus leniusculus* (Dana, 1852), the red-swamp crayfish *Procambarus clarkii* (Girard, 1852), and a free-living population of marmorkrebs (marbled crayfish) *P. virginalis* Lyko, 2017 [23–25]. In central Italian freshwaters, five non-native crayfish occur: *A. leptodactylus*, *C. destructor*, *F. limosus*, *P. clarkii*, and *P. virginalis* [23,26,27].

Concerning *P. clarkii*, the red swamp crayfish is a pan-global taxon, found on every continent except Australia and Antarctica [28]. Its invasiveness is mainly due to the properties of an r-selected species facilitating the extensive colonization of diversified environments [29–31]. A long list of studies has demonstrated its detrimental effects (reviewed in [32]). Moreover, its habit of burrowing aids in holding out against dehydration [20], but at the same time may cause bank collapse and increased water turbidity as well [14]. Then, its aggressiveness and predatory ability allow it to threaten native flora and fauna [33,34], including endangered European indigenous crayfish [35]. These mechanisms add to the dangers posed by *P. clarkii* as a vector of *Aphanomyces astaci* Schikora 1922, responsible for outbreaks of the so-called crayfish plague (see [36]).

3. Dispersal Pattern of *Procambarus clarkii*

Regarding the pattern of introduction and dispersal, the spread of *P. clarkii* may happen with several transport mechanisms. *P. clarkii* can be transported by active and passive processes by both human and animal vectors, facilitated by its ability to survive outside the water [32]. For example, Anatidae ducks play an important role as vectors of crayfish passive dispersal [37]. In addition, *P. clarkii* may survive long-distance transportation, being carried by moving vehicles or by waterbird passive dispersal [37,38]. Recently, fishways and fish lifts have been highlighted as new dispersal ways used by *P. clarkii* [39]. Thus, crayfish can be successfully dispersed in new habitats, transported by several mechanisms, potentially posing a risk also for new areas (e.g., transitional and marine ecosystems).

Concerning its distribution pattern, *P. clarkii* is dispersed in Italy as well as in the rest of Europe with similar rates according to studies in the literature [32,40,41]. In general, *P. clarkii* follows the same pattern as other crayfish, such as faster movement at night due to high water temperature, followed by an intense wide-spreading period, alternating to stasis phases during colder periods [32,40]. This active dispersal pattern allows *P. clarkii* to cover a long-distance range, also exploiting its ability to move over land up to a 1 km distance [40,42–45].

4. Tolerance to Water Salinity in Captivity

Although the ancestor of Astacoidea colonized inland waters in the Triassic Period [46], some recent species retain the ability to tolerate high salinity levels [47]. This stimulated many studies in captivity on this topic, since they have many implications from diverse viewpoints in the fields of evolution, biology conservation and applied ecology [48–55]. Regarding the latter, farming and aquaculture activities provided insights on tolerance to water salinity [56–59]. For instance, Casellato and Masiero [58] conducted laboratory tests and in situ farming to assess *P. clarkii* adaptation to gradually increasing salinity on the Northeastern Adriatic Coast [58].

In this regard, Loyacano [56] discovered that freshly hatched *P. clarkii* directly exposed to 15 ppt of salinity died in less than one week, whereas adults survived at concentrations of 20 and 30 ppt. Interestingly, Sharfstein and Charfin [57] found that adults exposed to a gradual salt application could effectively survive and grow at 12 ppt. Additionally, Casellato and Masiero [58] pointed out that, when directly transferred into saltwater, individuals survived well up to 20 ppt, but at 30–33 ppt, their lifetime was drastically reduced. Finally, Bissattini et al. [59] discovered that crayfish had a decreased mortality rate at 35 ppt water salinity due to gradual acclimation in salt water rather than shock occurrence of specimens in water with high salt concentrations.

Information on the tolerance to salt water by some crayfish has recently been collected by Dobrzycka-Krahel and Fidalgo [60], who reported a long list of articles highlighting the great overall plasticity of *P. clarkii*, which, however, requires further field studies to understand the real threats for natural environments (Table 1).

Table 1. Studies reporting captive or field observations reporting salinity (‰ or PSU or "not reported") by habitat (coastal, sea). Bibliographic references are available in Dobrzycka-Krahel and Fidalgo [60].

Reference	Observation (Indoor or Field)	Habitat Type	Salinity Tolerance
Scalici et al., 2010 [61]	Field	Coastal ecosystem	16.2–29.6‰
Casellato and Masiero 2011 [58]	Indoor	-	5–33‰
Bissattini et al., 2015 [59]	Indoor	-	5–35‰
Dorr et al., 2020 [53]	Indoor	-	2.5–35.3‰
Nota et al., 2024 [62]	Field	Marine ecosystem	Not reported
Scalici and Gallitelli (This study)	Field	Marine ecosystem	14–21‰

5. *Procambarus clarkii* in Transitional Waters and Coastal Habitats

The ecological features of *P. clarkii* allow it to colonize a wide range of habitats including coastal brackish waters in the Iberian Peninsula [63,64], Italy [61,62,65,66], and France [67] (Figure 1). This has aroused great interest among many conservation biologists since the salt tolerance of *P. clarkii* was observed in captivity studies for many years but was neglected in research in situ (Table 1).

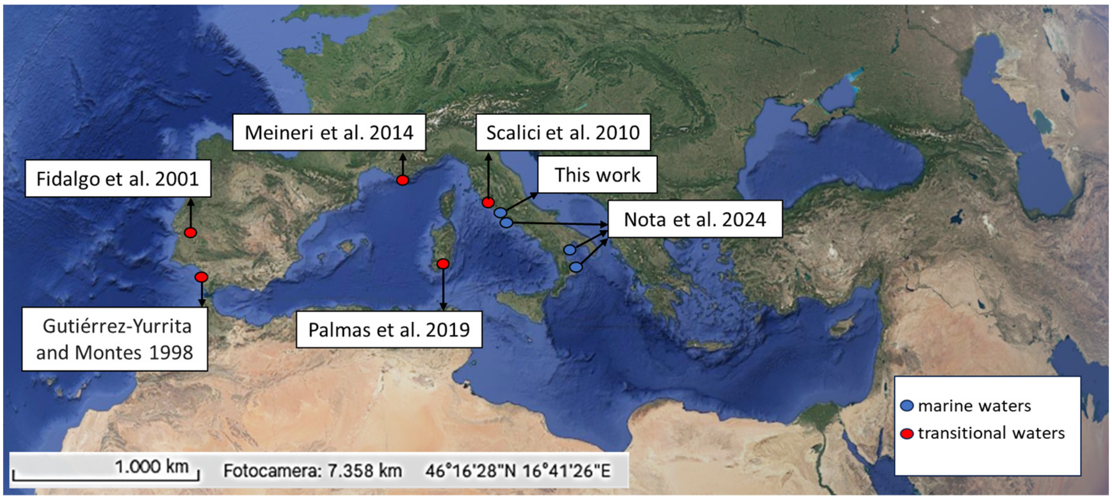

Figure 1. Sites with *Procambarus clarkii* present in European coastal habitats. The blue and red dots indicate marine and transitional waters, respectively. The image was obtained by Google Earth and Copernicus. Data on the presence of *P. clarkii* were obtained by studies like Gutiérrez-Yurrita and Montes (1998) [41], Fidalgo et al. (2001) [63], Scalici et al. (2010) [61], Meineri et al. (2014) [67], Palmas et al. (2019) [66], Nota et al. (2024) [62], and Scalici and Gallitelli (2025, this work).

Although a recent review on decapods highlighted that *P. clarkii* could potentially be found in the sea [60], to date, only one (to be verified) reference on *P. clarkii* occurrence in the sea is reported (see below). The species currently appears to be limited to European transitional areas in Portugal, Spain, and France ([41,61–66], Figure 1), even if it was recently more and more frequently observed in Tyrrhenian central Italian coasts. Indeed, during a sampling session of a monitoring project on native and non-native crayfish populations' health evaluation, we observed 544 individuals (from 29 in Marina di Pescia, the northernmost locality, to 177 in Sabaudia, the southernmost locality) of the red swamp crayfish. They were caught using baited traps on eight coastal water localities with salinity values ranging from 14 to 21‰. In detail, the traps were baited using cat food and set for 2–5 nights at a height of 1.5–2 m above sea level, positioned 10–25 m from the shoreline. The eight study sites were characterized by a sandy littoral, typical of the central Italian coast. Along the sea–land gradient, the sites were characterized by a backdune landscape surrounded by agricultural areas with irrigation ditches and canals. At only one site, we observed two individuals of *P. clarkii* emerging from the sea near the locality Passoscuro, Prov. Rome (Figure 2). Here, in Mediterranean marine ecosystems, water salinity may reach 35‰ (near the locality studied by Scalici et al. [61]). However, salinity was not measured here. Considering that the river mouth is a transitional area with fluctuating salinity, we tend to consider the water salinity in our study area to be characteristic of marine habitats, based on previous studies outlined in Table 1.

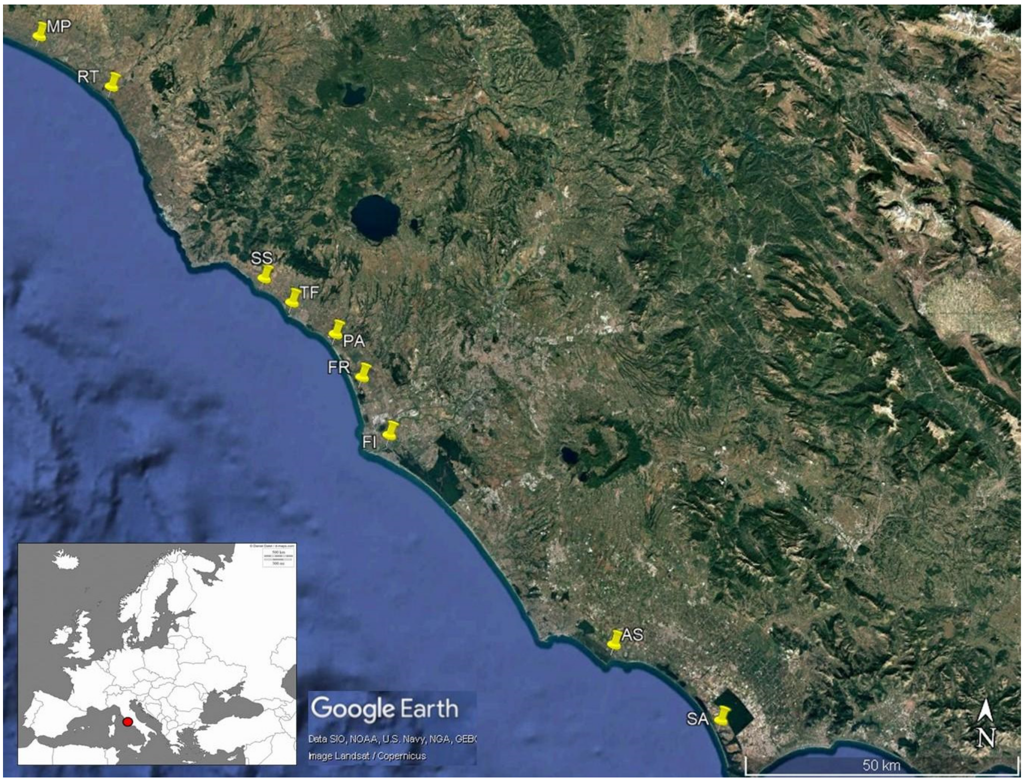

Figure 2. Records of the red swamp crayfish *Procambarus clarkii* in transitional and marine waters of Tyrrhenian central Italian coasts. The red dot indicates the study area in central Italy, while the yellow points indicate the specific locations. Specifically, Marina di Pescia, Santa Severa, and Astura are brackish temporary ponds; Riva dei Tarquini and Fiumicino are estuarine zones; Torre Flavia and Sabaudia are brackish wetlands; and Passoscuro is the marine locality where *P. clarkii* was found. The image was obtained from Google Earth and Copernicus. MP = Marina di Pescia, RT = Riva dei Tarquini, SS = Santa Severa, TF = Torre Flavia, PA = Passoscuro, FR = Fregene, FI = Fiumicino, AS = Astura, and SA = Sabaudia.

These findings do not represent the unique report of the red swamp crayfish in the sea. In the literature, Nota et al. [62] recently published findings of *P. clarkii* in Italian coastal habitats in three different regions (Figure 1), exploiting information noted on social media. Particularly, the authors reported red swamp crayfish caught by professional fishermen in marine habitats at depths up to 20 m, suggesting that this species may disperse into marine environments for extended periods [62]. Reaching a depth of –20 m implies a significant distance from the shoreline, indicating that individuals must be able to survive in marine conditions for some time before being captured by nets at such depths. Although the precise duration of survival remains uncertain, previous studies [47–50,62] suggest that red swamp crayfish may survive in marine environments for approximately 2–3 days.

Although some detrimental effects on *P. clarkii* emerged after the colonization of transitional habitats, such as the growth rate and the expected longevity [61], it is likely that crayfish may initially benefit from colonizing transitional waters, probably due to the absence of ecological resistance (natural competitors/predators), which has a pivotal role in alien crayfish establishment and surviving. Its physiological plasticity may facilitate transitional habitat colonization because the energetic costs of maintaining salt and water balance are reduced since less than 10% of the total metabolism is sufficient for osmoregulatory purposes [68,69].

As *P. clarkii* is able to invade ephemeral waterbodies, as observed by Gherardi et al. [33] and Aquiloni et al. [40], we expected that crayfish might move from a river to another watercourse using ephemeral temporary habitats (i.e., MTPs) and canals as steppingstones.

Survival in unfavorable aquatic habitats may depend on the anatomical and physiological responses facilitating certain forms of character displacement in colonized habitats. Particularly, the salinity increase affects the antennal gland organization in the red swamp crayfish, driving the acclimation to detrimental osmotic and hydric conditions [58]. Such structural alterations make the crayfish antennal glands similar to those of marine decapods, which have no nephridial tubule and produce urine iso-osmotic with the hemolymph [70], although mechanisms of ultrafiltration, secretion, and reabsorption involved in salt water colonization need to be clarified [71].

Given these findings, new research is needed to assess the effects of invasive crayfish on temporary aquatic habitats, as studies have so far mainly focused on the spread of *P. clarkii* among rivers or in the same river. Considering the fragile habitats listed in the Habitat Directive (3120, 3130, and 3170*), conservation efforts should be provided through specific monitoring in the coming years to preserve these habitats, with the possibility to control and eventually eradicate alien species.

6. Potential Threats to Coastal and Transition Habitats Due to Crayfish Stepping

Since some crayfish are able to survive high salinities, this adaptative process ought to be better investigated in order to understand (i) whether crayfish select transitional waters as a new elective habitat or merely use them as a biological corridor (given that salt tolerance, combined with their dispersal ability, may facilitate such movement—see Aquiloni et al. [40]) (Figure 3), and (ii) which driving environmental and evolutionary forces may facilitate the colonization of transitional waters within the area of introduction (such as the absence of natural competitors and/or predators and/or parasites). Beyond the adaptive aspects, this represents an issue of concern in the habitat conservation field, particularly with regard to (1) the massive introduction of non-indigenous crayfish in many European countries [23,26,27,72]; (2) the control of alien threats in coastal habitats (see [61,63,64,67]); and (3) their increasingly frequent presence in transitional waters.

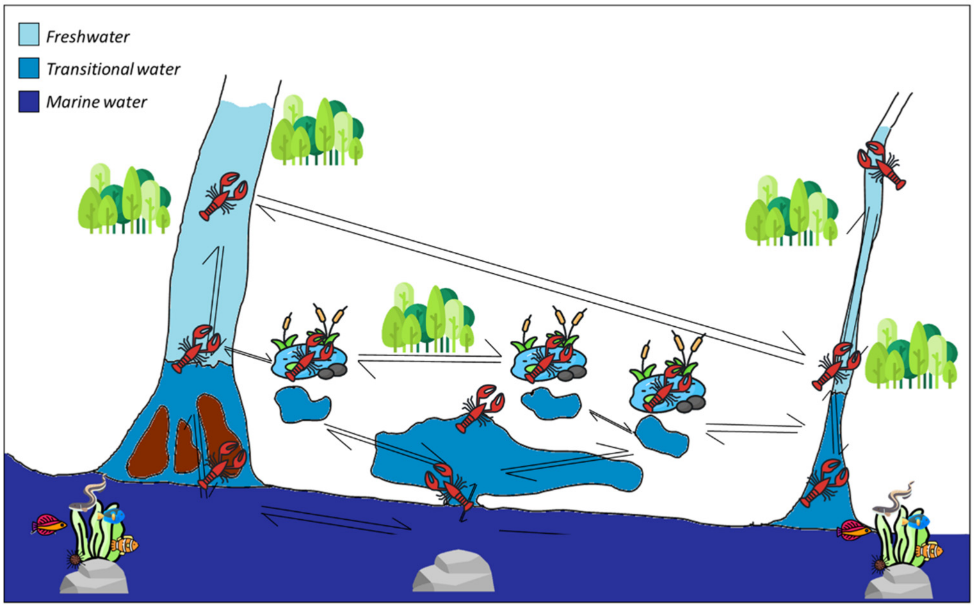

Figure 3. The potential theoretical dispersion routes of the red swamp crayfish *Procambarus clarkii*, exploiting and potentially impacting three aquatic habitat types: freshwater, transitional, and marine waters. The image was freely obtained from flaticon.com.

The potential dispersal routes of *P. clarkii* presented in Figure 3 are possible scenarios since it can act as a native decapod competitor, macroinvertebrate predator, pathogen vector, habitat and biodiversity shaper, native vertebrate diet supporter, ecosystem services injurer, and native food web influencer [8,11,32]. In light of this, crayfish represent a dangerous threat to the biodiversity of transition zones, wetlands, estuarine and temporary waters, and are likely to damage human livelihoods through their impact on fishing and aquaculture. However, although the threats posed by *P. clarkii* on freshwater habitats are well-known globally, their impact on the local fauna and flora in transitional waters is not yet evident. Considering the damage that invasive crayfish can cause in various regions worldwide where they have been introduced [15,18,19], the possibility of this species to impact fragile ecosystems such as coastal waters seems certain. This could be since transitional and coastal habitats offer important refuge zones for limicolous birds and endemic fishes confined to this type of transition area [58,61].

Regarding the threats posed by crayfish entering marine habitats, they can be several and of different ecological values. In a first remote scenario, the potential threat may not even occur since *P. clarkii* would use the sea as a biological corridor to go elsewhere (e.g., ponds, coastal lakes, river mouths, etc.; see Figure 3). In the second scenario, *P. clarkii* could threaten marine ecosystems through direct impacts (e.g., acting as opportunistic omnivores in the food web, consuming remaining *Posidonia* banquettes) or indirect impacts (e.g., reducing several ecosystem services by reducing biodiversity, carbon storage, and oxygen production by eating *Posidonia*, or by eating juvenile fish, which could impact fisheries). These impacts could be the same impacts posed by *P. clarkii* in freshwaters but translated to transitional, coastal, and marine habitats. *P. clarkii* could also become a food resource of invasive and native predators in marine habitats, which could regulate crayfish populations.

Taking the previously described experiments of acclimatization to salinity increasing values into account, the colonization of brackish waters by *P. clarkii* could represent a pre-adaptation to the use of sea waters as a possible subsequent biological corridor (see [73,74]), as evidenced by the discovery of several individuals on the beach that came out of the sea in the locality Passoscuro. This is why the tolerance of crayfish to salt waters should be further investigated in situ as a fundamental management activity for the conservation of transitional and marine habitats.

Finally, regarding the diffusion of the species, particular attention should be given to parasites that could be carried by *P. clarkii* [75–79]—in particular, *Aphanomyces astaci*, mycoflora, and fungus pathogens (e.g., *Phoma gomerata*, [73]). Consequently, the high ecological plasticity of *P. clarkii* indicates the need to intervene before the species and its parasites [73–77] spread further in transitional waters, in order to conserve Mediterranean coastal habitats—particularly to protect *Posidonia oceanica* seagrass beds, a priority marine habitat under the 1120* *sensu* Habitats Directive 92/43 EEC.

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