Spreading and Establishment of the Non Indigenous Species *Caprella scaura* (Amphipoda: Caprellidae) in the Central Region of the Aegean Sea (Eastern Mediterranean Sea)

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**Abstract:** *Caprella scaura* is an invasive amphipod, native to the Indian Ocean, which has already spread to several regions of the world, including the Mediterranean Sea. The present study reports the first occurrence of the species on fish farms cages in Greece, in the Pagasitikos Gulf. Specimens were collected from colonies of the bryozoan *Bugula neritina*. Basic aspects of the population dynamics of the species, such as the population structure, sex ratio, and size frequency were studied for 13 months and tested for differences between two depth levels (30 cm and 5 m). Population density was significantly different between the two sampled depths. All the demographic categories were present during the whole study period, indicating that the species follows a continuous reproduction pattern in the region. Males were typically larger than females, but females were more abundant in most samples. It seems that the species is well established in the region and is probably moving towards the northern parts of the Aegean Sea.

**Keywords:** population dynamics; biofouling; invasive species; biodiversity threats; integrated multitrophic aquaculture; Pagasitikos Gulf

**1. Introduction**

The spreading of marine non-indigenous species (NIS) is considered a great threat to the marine environment [1,2]. Their impact on the structure, function and biodiversity of native ecosystems and communities can be very strong, thus they are very often being referred to as a form of “biological pollution” [3,4]. The implications of marine NIS invasions to the environment are becoming a huge concern to scientists and legislators. This concern is reflected within the Marine Strategy Framework Directive (MSFD) and the EU Biodiversity Strategy, which specifically stress the need to assess the threats posed by the introduction and spread of marine NIS [1,2].

The successful introduction of a NIS to a new environment depends on many factors, and is usually a multi-step process [5]. First, the species need to be transported from their original area to a new location, in which case ballast water, fouling of the hull from commercial vessels and aquaculture are generally considered the main vectors responsible for NIS movement across the oceans [2,6–9]. The second step requires a potential recipient community where the transported species will settle and start their expansion in their new “home”, in which case recreational marinas, harbors and off-coast aquaculture facilities and equipment provide the adequate substrate for NIS to establish and thrive [10–15]. However, the most important factor that facilitates a successful invasion is the ability of NIS to actually survive, both during the transportation and after their relocation to the new area, which usually involves living through rather unfavorable conditions [5]. This adaptability to new and challenging environments is usually linked to certain life-cycle features such as high reproductive potential and dispersal ability, especially for marine species [6]. These features are included in the study of the population dynamics, along
with other aspects, such as abundance, seasonal variation, distribution, breeding, sex ratio and population structure. Knowledge of these characteristics from NIS is an important step in order to understand the invasion process and its impacts on the invaded ecosystems and, to an extent, in the developing of management policies and practices [16].

The subphylum Crustacea is probably among the most successful taxonomic groups of aquatic NIS, since they fulfill most of the requirements for a potential invader such as rapid growth, production of several generations per year, early maturity and high fecundity and, of course, their association with fouling communities [6,17,18]. Within the Crustacea, the family Caprellidae has a fair share of species characterized as NIS, with most of them being part of a long list of invaders in the Mediterranean [1,2,19].

Caprellids are common inhabitants in coastal and deep water marine environments, with a worldwide distribution [20–23]. Their populations can reach high densities under favorable conditions, but with potential variations on a spatiotemporal scale, mostly depending upon a range of biotic and abiotic factors, such as temperature, food supply, depth and predation [10,24–26]. Additionally, seasonal patterns of caprellid populations have been correlated positively with the respective seasonal cycles of the natural substrate they inhabit [16,22,27]. They seem to play an important role in trophic cascades, as the connecting link between primary producers and higher trophic levels, while the discovery of high concentrations of polyunsaturated fatty acids in certain species has recently made them a promising aquaculture resource [15,25,28]. Their ability to swim is rather limited, due to their reduced pleopods, which hinders their active dispersal, thus making them good candidate species to carry out population and ecological studies [29]. On the other hand, their unique morphological features favor the clinging on both natural (e.g., macroalgae, hydroids, bryozoans) and artificial substrate (e.g., ship hulls, buoys, marine litter) [30,31]. This facilitates their passive dispersal, which is a crucial factor in the case of successful invasive species such as *Caprella scaura* [32,33].

*Caprella scaura* was originally described from Mauritius and later reported from several regions of the world [32]. Its native region is the Western Indian Ocean, while its first occurrence in the Mediterranean Sea was recorded in Venice (Italy), in 1994 [34]. Subsequently, it has been reported in locations along the coastlines of several Mediterranean countries [14,15,32,33,35–39]. Even though the geographical distribution of *C. scaura* is well documented, especially for the Western part of the Mediterranean, there are still areas that remain unexplored and, as a result, the total extent of its expansion in the Mediterranean remains unknown. Furthermore, population dynamics studies of the species are very scarce and only focused in the Western Mediterranean [8,16], contrary to the Eastern Mediterranean where no such study exists.

The aim of this study was, first of all, to report a new occurrence of *C. scaura* for Greece and describe the temporal variation of basic aspects of its population and set the baseline in the effort to assess and explain the successful adaptation of the species in the region.

2. Materials and Methods

2.1. Sampling Design

A preliminary study of the biofouling communities from the two fish farms in the Pagasitikos Gulf, in search for caprellids to analyze their nutritional content for potential use in aquaculture applications [40–42], led to an unexpected finding. Based on previous studies in the region [43] we were expecting to find common native caprellids such as *Caprella acanthifera* or *Phtisica marina*, instead we found an exclusive abundance of *C. scaura*. Since it was a new record of a NIS for the region, we decided to investigate the seasonal population dynamics of the alien species. Furthermore, since there might be a potential interest in using *C. scaura* as a candidate species in Integrated Multi-trophic Aquaculture (IMTA) systems [28], we thought it would be useful to have some information regarding the potential effects of depth on the population dynamics of the species, since this would affect the optimal deployment of their culturing system in the future. The initial planning for the study included both fish farms, but because of a major reconstruction and relocation
of the fish cages from one of the farms, we were unable to continue the samplings there, so all data analyzed and presented in the paper are from one fish farm (Figure 1).

For the collection of the samples, we adopted the design proposed by Boos (2009) [26]. We used plastic meshes (40 cm × 25 cm, mesh size 2 mm) as a substrate for biofouling and colonization by C. scaura. In order to test for potential differences in the population structure of the species in a depth gradient, the meshes were attached to ropes and submerged in two different depth levels: The first level was about 30 cm below surface (referred to as “surface”, hereafter) and the second level at 5 m depth (hereafter referred to as “deep”). Five replicates were used for each depth level and they were deployed in two groups. The first group (5 surface and 5 deep meshes) was deployed in May 2018 and the second group (another 5 surface and 5 deep meshes) was deployed 4 weeks later, in June 2018. After the initial deployment, the meshes of each group were collected and replaced as “deep”).

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2.2. Laboratory Processing

Immediately after collection, the meshes were placed in separate labeled containers, fixed in a 4% formalin solution and transferred to the laboratory. Each sample was then repeatedly rinsed with tap water and sieved through a 250 µm mesh in order to retain mobile organisms. *Caprella scabra* male and female individuals were identified by the distinctive external characteristics described in several studies [32,33,44], sorted out from the rest of the fauna and fixed in 85% ethanol. Small individuals without visible signs of sex and/or maturity were classified as juveniles [15]. The total number of individuals (N) was counted from each sample, and population density (D) was expressed as the number of individuals per m².

Due to the large number of individuals, a representative subsample for each sampling was created by randomly selecting 50 males, 50 females and 15 juveniles in order to perform a balanced statistical design for length comparisons (i.e., between sexes, depth level and among samplings) as well as to construct the length-frequency distribution (LFD) of the population from each sampling [8]. Digital photos of specimens were taken using an Olympus SZX-9 stereomicroscope, and each individual was measured from the anterior margin of the head to the posterior margin of the telson to the nearest 0.1 mm [16], using the image processing and analysis software ImageJ (v. 1.53e National Institute of Mental Health, Bethesda, MD, USA) [45].

Females were further classified as non-breeding (when no eggs were visible in the brood pouch) and breeding (visible eggs in the brooding pouch), in which case the total number of eggs was counted. Sex ratio (SR) of the population was calculated for each sample, as the proportion of females in the whole sample (SR = F/F + M) and tested for significant difference from the expected sex ratio (SR = 0.5, i.e., equal proportion of two sexes) using the chi-squared test [16,46].

Temporal differences in population densities and total body were tested with one-way ANOVA, whereas Student’s t-test was used to detect differences between the two depth levels. The number of eggs found in the pouch of breeding females was tested for correlation with total body length using Spearman’s rank correlation, and the Student’s t-test was used to detect potential differences between the two depth levels. Significant pair-wise comparisons by the Fisher’s LSD procedure were performed post hoc, to identify the potential individual group differences.

All statistical analyses were performed by the “Statgraphics Centurion” software package (v.18.1 Statgraphics Technologies, Inc., The Plains, VA, USA) and values of \( p < 0.05 \) were considered significant.

3. Results

All abiotic factors measured during the study fluctuated between seasons, following a typical temporal pattern, as expected in the Mediterranean region (Figure 3). Water temperature had the strongest variation in recorded values, ranging between 27.9 °C in August 2018 and 12.3 °C in February 2019. Salinity values were within the typical seawater range, with a small variation between 36.3‰ and 38.1‰. Dissolved oxygen concentration values ranged between 6.90 mg L⁻¹ in December 2018 and 5.13 mg L⁻¹ in August 2018.

The biofouling on the sampling meshes included several taxa, which are common in these communities in the Mediterranean, such as hydroids (*Eudendrium* spp) or algae (*Gellidium* spp., *Jania* spp. and *Polysiphonia* spp.), but the dominant species throughout the whole study period was the bryozoan *Bugula neritina*. In regard to the motile epifauna, apart from the obvious dominance of *C. scabra*, *Jassa* spp. and *Elasmopus* spp. were the next species with the strongest presence. It is worth noting that another caprellid, *Caprella equilibra* was also identified, but its presence was quite scarce (0–10 individuals per sampling, mostly males).
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Figure 3. Temporal variation of abiotic parameters measured (A) temperature, (B) salinity and (C) dissolved oxygen, during the study period. Bars indicate standard deviation.

Student’s t-test revealed that population densities had significant differences between the two depth levels ($p < 0.05$), with higher values found on the surface populations. Average density for the surface populations was estimated 1,292.8 ± 550.1 ind m$^{-2}$, with a minimum of 500 and maximum of 2,930 ind m$^{-2}$, whereas deep population density ranged between 400–2,370 and had an average of 1,092.9 ± 476.6 ind m$^{-2}$. One-way ANOVA on population densities among months revealed significant differences for both Surface ($F_{12,64} = 42.75, p < 0.05$) and Deep ($F_{12,64} = 21.86, p < 0.05$) populations. Fisher’s LSD procedure identified June, October and March as the months with the highest values for both depth levels, whereas January, February, May and August were the months with the lowest values (Figure 4).
Population structure was consistent during the study period, with all the demographic categories (i.e., males, breeding / non-breeding females, juveniles) present in all samplings (Figure 5). The total number of individuals, from both depths, was 18,090 out of which 7,731 (42.7%) were males, 3,416 (18.9%) breeding females, 5,199 (28.7%) non-breeding females and 1,744 (9.6%) juveniles. Number of breeding females peaked in August, November and during February–April, whereas juveniles had increased numbers during November–December and March–April. Sex ratio followed a different pattern between depths. Although in most of the samplings female individuals were more than males (in absolute numbers), sex ratio was not significantly different from 1:1 for the surface population, except from the last sampling in July 2019. On the contrary, sex ratio of the deep population was significantly different from the expected equilibrium and always in favor of the females in most samplings, except from November–February (Figure 6).

![Figure 4](image1.png)

**Figure 4.** Temporal variation of the surface and deep population density of *Caprella scaura* from a fish farm in the Pagasitikos Gulf. Bars indicate standard deviation.

![Figure 5](image2.png)

**Figure 5.** Temporal variation of all demographic categories of *Caprella scaura* from a fish farm in the Pagasitikos Gulf.
Figure 6. Temporal variation of Sex ratio of the surface and deep population of *Caprella scaura* from a fish farm in the Pagasitikos Gulf. Red asterisks (*) indicate deviation from 1:1. Values over the dashed line indicate female dominance, whereas values below the dashed line indicate male dominance.

The total length (TL) of the 2,990 measured individuals (1,300 males, 1,300 females and 390 juveniles), from both depths, ranged between 2.6 – 21.1 mm. TL values ranged between 5.4 – 21.1 mm for males, 5.0 – 10.3 mm for females and between 2.6 – 4.9 mm for juveniles (Table 1). Student’s t-test revealed that TL values had significant differences between the two depth levels (\(p < 0.05\)). One-way ANOVA, on the other hand, did not detect any differences in TL among the sampling months, either for surface (\(F_{12,1494} = 0.67, p = 0.782\)) or for deep (\(F_{12,1494} = 1.30, p = 0.212\)) populations. Fisher’s LSD procedure identified that male size was significantly different between depths, contrary to female and juvenile size. The length–frequency distribution (LFD) differed between sexes, with males exhibiting a wider size range than females. Females were more abundant in smaller TL size classes, but their numbers decreased significantly with the increase in size and no females larger than 11 mm were found (Figure 7). In fact, the larger female (10.3 mm) was smaller in size than the average size of all males (10.7 mm from Deep and Surface pooled data, data not shown).

Table 1. Minimum, maximum and mean (± SD) total length values (mm) of the different demographic categories from the surface and deep population of *Caprella scaura* from the Pagasitikos Gulf.

| TL (mm) | Males | Breeding Females | Non-Breeding Females | Juveniles |
|---------|-------|------------------|----------------------|-----------|
|         | Surface |                  |                      |           |
| Minimum | 5.8   | 5.6              | 5.1                  | 2.6       |
| Maximum | 21.1  | 10.1             | 10.2                 | 4.9       |
| Mean ± SD | 11.1 ± 3.0 | 8.3 ± 1.2 | 7.3 ± 1.1            | 3.8 ± 0.5 |
|         | Deep   |                  |                      |           |
| Minimum | 5.4   | 5.3              | 5.0                  | 2.8       |
| Maximum | 19.0  | 10.2             | 10.3                 | 4.9       |
| Mean (SD) | 10.4 ± 2.6 | 8.3 ± 1.2 | 7.3 ± 1.3            | 3.9 ± 0.6 |
4. Discussion

Number of eggs found in the pouch of breeding females was not significantly different between depths (t-test, $p < 0.05$) and it was positively correlated with female TL size (Spearman’s $r = 0.720$, $p < 0.05$). Brood size ranged between 11–53 eggs, with an average value ($\pm SD$) of 30.3 ($\pm 9.2$) eggs per brood.

Figure 7. Length–frequency distributions of (A). Male and (B). Female individuals from the Surface and Deep populations of *Caprella scaura*, from a fish farm in the Pagasitikos Gulf.

In the present paper, a new occurrence of *Caprella scaura* is reported for Greece, raising the total number of country records to three. Contrary to the previous two reports [32,47], where *C. scaura* was found in marinas, this is the first occurrence of the species on fish farm cages and the first in the northern part of the Aegean Sea, thus expanding the northernmost distribution range of the species in the region. Additionally, this is the first occurrence of the species on a cage from a sea bream/sea bass farm, since to the previous record occurrence was from tuna farms [14]. The fact that there are over 20,000 floating fish cages along the Mediterranean coastline and almost half of them are located in Greece [48] highlights the key role of fish farms as potential vectors and facilitating factor for the establishment and spreading of NIS in the whole Mediterranean basin.

*Caprella scaura* was present in throughout the whole study period and, even though it was not possible to collect relevant data from the other fish farm in the region, our initial results from that area were quite similar so it would be safe to assume that the species is successfully established in the Pagasitikos Gulf. The presence of the species did not seem to be affected directly by the fluctuations of the measured abiotic factors (i.e., temperature, salinity, dissolved oxygen), which indicates a relative tolerance to environmental variability.

Ovigerous females were present during the whole study, indicating that the species follows the common pattern of continuous reproduction throughout the year, which most caprellids share [30]. A positive correlation between body and brood size was found, which is also to be expected, not only in caprellids, but in amphipods in general [30]. Most breeding females were recorded in summer and autumn, which probably marks the peak of the reproduction of the species for the Mediterranean, since similar findings were reported...
in other studies [8,16]. Males were typically larger than females, which is considered an evolutionary trait associated with the reproductive process, either because females invest more energy in the production of eggs or because the aggressive behavior among males reduces the number of smaller-sized individuals [49]. Body size of males and females in our study are within the size range of other studies [8,16,32,33,50], with small differences between values, which can be attributed to the apparent ecophenotypic adaptation of the species to the different biotic and abiotic factors of each sampling location.

The population density exhibited a periodic pattern for both depths, with peaks in June, October and March and the lowest values in January and February, but deeper populations had significantly lower densities. This small difference could be attributed to higher predation from fish. Fish farms are known to attract large aggregations of wild fish in mid waters around fish cages, as well as fish that escaped from within the cages [51], which may lead to an increase in predation since fish tend to select caprellids because of their clinging behavior, large size and visual contrast with their substrate [24,25]. Population density values from our study were similar to those recorded in the Ionian Sea [16], but lower than the high densities recorded in the Iberian Peninsula [8,33]. This variability could be attributed to the apparent differences in abiotic and biotic factors between the locations, as well as differences in the sampling methods. In any case, the results from all studies support the claim that C. scaura is a strong invader and is well established in the Mediterranean.

The sex ratio was followed different patterns between depths. The shallow populations exhibited small monthly fluctuations with more females in one sampling and more males in another, but the ratio almost never deviated statistically from 1:1, except from the last sampling. On the contrary, the deeper populations displayed a strong female-biased sex ratio during the whole study and with most cases being statistically different from the 1:1 equilibrium. Usually, fluctuations in sex ratio can be attributed to different rates in growth, mortality or lifespan between sexes [30]. Female dominance could be explained again by the presence of more fish in deeper waters and males, because of their larger size are more visible and more susceptible to predation. This is probably why, apart from the difference in the sex ratio, larger males were also more scarce in deeper populations compared to the shallow population of our study.

According to Fernandez-Gonzalez and Sanchez-Jerez [14], the different conditions in a sea bream/sea bass farm comparing to a tuna farm, especially high predation from fish, were preventing factors for the establishment of C. scaura on farm structures. Our finding shows that, even though predation could be a regulating factor, which could affect the growth of the population, it is possible for C. scaura to adapt and establish its presence even in sea bream farms.

Most caprellid amphipods do not exhibit specific substrate preference [27,52], whereas C. scaura, although it has been reported from several habitats, seems to have a strong association with the bryozoan Bugula neritina [8,11,33,50,53]. The results from our study appear to support this association, since B. neritina was the dominant representative of the biofouling community during the whole sampling period and C. scaura was present throughout the whole study period. This affinity could be attributed to the cryptic adaptation of C. scaura to the bryozoan, since both species have similar coloration and external morphology. A similar association between a caprellid and B. neritina was reported for Caprella californica, a very close species to C. scaura, which seems to have the ability to undergo physical color changes in order to adapt to its substrate, contrary to C. equilibra, which was unable to adapt completely to dark substrates, such as B. neritina [54]. This is probably why C. equilibra was scarcely found during our study. Recent studies [8,11,14,55] seem to indicate that C. scaura is displacing C. equilibra from locations where it has been established, since they both compete for substrate use and C. scaura seems to perform better in terms of successful adaptation.

Furthermore, since B. neritina is also considered as a NIS for the Mediterranean [56] and, apparently, it acts as a favorable substrate for the establishment of C. scaura, then
this positive interaction could be assumed to be a typical case of “invasional meltdown”, where an introduced species facilitates the establishment of another NIS [57]. Of course, further research is needed to confirm this interaction, but the high population densities, the potential displacement of other species and the high adaptation ability of C. scaura strongly support this assumption. Even though this could pose a threat to local biodiversity, there are some potential benefits, which are probably worth looking into. First of all, B. neritina is a source of a natural anti-cancer agent called “bryostatin”, so there is an increasing interest in studying the species and exploring its exploitation [58–60]. On the other hand, caprellids have been found to be a potential alternative source of protein and lipids in fish feed production [25,40,41] and recently, C. scaura has been considered as a candidate species for use in Integrated Multi-Trophic Aquaculture (IMTA) Systems [28]. Therefore, this correlation between B. neritina and C. scaura could prove to be a valuable asset in the sustainable management of marine ecosystems, which might mitigate their impact as biodiversity threats. Our study showed that it is possible to “cultivate” both of these NIS on artificial substrate around fish-farm cages, but further studies and field experimentations are required in this direction, with the challenge being the establishment of safe and stable systems with an economically feasible output [28].

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