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ORIGINAL PAPER

Composting the Invasive Toxic Seaweed *Rugulopteryx okamurae* Using Five Invertebrate Species, and a Mini-review on Composting Macroalgae

D. Patón[1] · J. C. García-Gómez[2] · J. Loring[2] · A. Torres[1]

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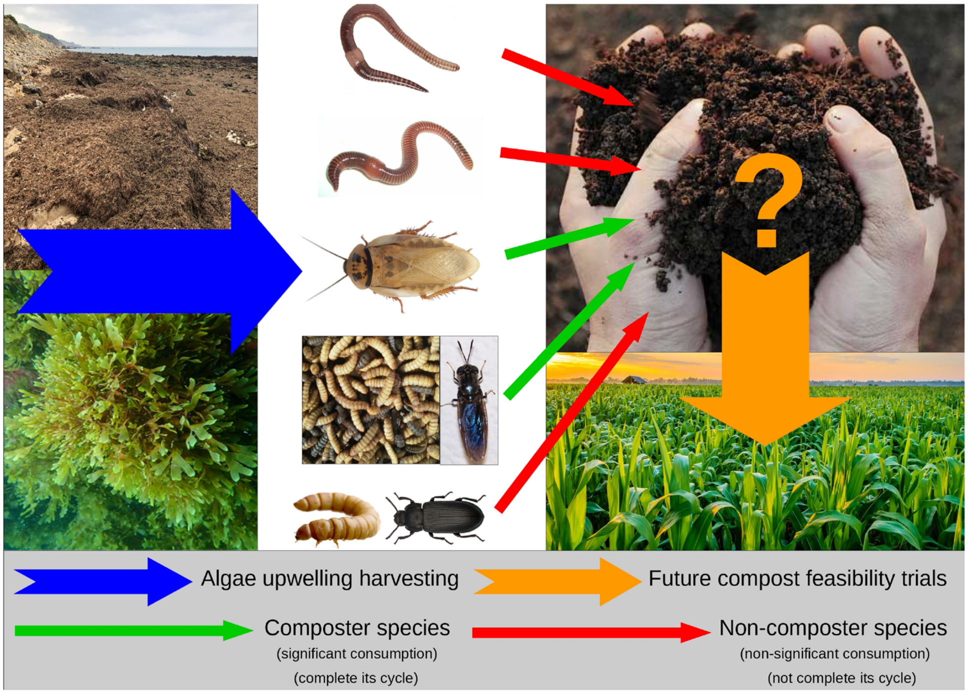
Abstract

Since 2015, the invasive alga *Rugulopteryx okamurae* has explosively burst into the waters of the Strait of Gibraltar with serious repercussions on marine biodiversity, tourism and the fishing industry. Its elimination entails an enormous cost for the municipalities in the area and vermicomposting is proposed as a solution, but the anti-food secondary metabolites of the algae make it unfeasible. This work analyzed for the first time the bioremediation of this toxic algae using vermicomposting (*Dendrobaena veneta* and *Eisenia fetida*), blatticomposting (*Eublaberus* spp. "Ivory"), mealworms (*Tenebrio molitor*) and black soldier fly larvae (BSFL, *Hermetia illucens*). Both BSFL composting and blatticomposting are viable alternatives, as the toxics in the algae do not affect the long-term survival, growth or reproduction of these invertebrates. All other tested species do not resist consumption of *R. okamurae*. In parallel, a synthesis of current knowledge on marine macroalgae composting has been carried out. The results of this work will allow the use of insect farms in the upwelling areas that will eliminate algae, providing fertilizers and animal proteins that will be an economic aid to the municipalities in the affected coasts of southern Mediterranean Spain.

Graphical Abstract



Extended author information available on the last page of the article

Keywords *Composting* · *Dendrobaena* · *Eisenia* · *Eublaberus* · *Hermetia* · *Rugulopteryx okamurae* · *Tenebrio*

Statement of Novelty

Tons of invasive algae of the genus *Rugulopteryx* reach the coasts of southern Spain every year. Their effect is catastrophic on marine ecosystems and the entire economy of the affected areas. Tourism plummets and fishing disappears. A solution to this problem is urgently needed. Traditional worm composting techniques do not work appropriately. In consequence, other alternatives of composting are necessary. In the present work, several invertebrate species were studied and at least two (soldier flies and tropical cockroaches) were found to consume algae at adequate rates and without loss of viability. Finally, the ivory cockroaches *Eublaberus* spp. have been chosen as the species that consumes the algae and is the easiest to maintain, thus allowing the creation of bioremediation plants on an industrial scale.

Introduction

Marine algal blooms in coastal areas are a growing biological phenomenon in many regions of the world [1]. To date, more than 400 species of invasive marine algae have been counted worldwide, of which 50 affect the Iberian Peninsula [2, 3]. In the short term, these invasions can become explosive and occupy a large part of the coastal seabed surface, generating tons of debris and causing severe environmental impact [4–6]. In the long term, some local seaweed species can be recovered and the native biota may eventually integrate the invasive species into the marine ecosystem [7]. These biological invasions are due, among other factors, to the increase in temperatures caused by the greenhouse effect [1].

In this sense, some ecosystems which are highly vulnerable to rising temperatures, such as coral reefs and estuaries, can be seriously damaged, producing a punctual void of native algae which is immediately exploited by invasive species [8]. Examples of these processes are the invasions of the Asian brown alga *R. okamurae* (Fig. 1) in the Mediterranean [5, 6, 9] and various species of *Sargassum* in the Atlantic [10]. In the first case, the onset of the invasion in 2015 coincides with the highest temperature peak of the last 20 years in the surface waters of the southern Iberian Peninsula [5]. Subsequently, more than 5000 tons of upwelling biomass were collected from the beaches of Ceuta [11].

Some of the impacts of invasive marine algae are economic [12]. In this regard, the negative effects on diving areas, sport infrastructures and fisheries are of particular concern [13]. According to [12], the cost of extracting the algal blooms is the factor that generates most of the economic expenditure, although in the case of *R. okamurae*, it remains to be investigated whether the economic impact generated in the fishing sector exceeds this.

Possible uses for invasive algae should be explored to alleviate the economic costs of massive beach removals. To this end, it is necessary to develop interdisciplinary research that analyzes these algae from a biological and economic point of view. In this sense, some species of seaweeds have been used for biochar generation by pyrolysis obtaining C sequestration rates between 11 and 12% [14].

Fig. 1 *Rugulopterys okamurae*, invasive seawed of Asian origin on the coast of the Strait of Gibraltar

Other research has been directed towards the use of algae tops in the generation of biogas (methane) by anaerobic fermentation, although some technical problems such as the production of corrosive sulfur compounds and low C/N levels can be corrected mixing seaweeds with food waste residues [15] or marine sediments [16]. Also, in many seaweeds, antifouling compounds of industrial use have been detected [17], as well as pollutant absorbers [18], biofuels [19], products useful in cosmetics [20], antimicrobial compounds [21], antivirals [22], anticarcinogens [23] and antioxidant substances [24]. In agricultural sciences, invasive marine algae have been used as nutrients, for agricultural mulching, as water absorbers, bio-stimulants, bactericides, fungicides and in composting [2, 23, 25]. This last use constitutes a simple environmental biotechnology that allows us to transform the large biomass of the upwellings on the beaches into a product for agricultural use that is continuously increasing its demand [26]. In this sense, it is known that the quality of a compost depends on the source material, the method of preparation and the maturation time between other factors [27]. Some seaweed species present several problems for composting such as a high salt content, accumulation of metals or low C/N levels far from the ideal value close to 1/25 [28]. Therefore, the addition of forest residues with high C levels, as well as small amounts of fishery residues to the algal biomass to microbiologically enrich the sample has been recommended [29]. This strategy is ideal if we intend large-scale composting of the above-ground algae that can be arranged in different structures as mounds, windrows, continuous flow devices with or without aeration, rotating machines, compost tumblers, etc. Also, it is possible to prepare mixtures of microorganisms from various waste sources and algal species favoring a faster composting [26]. Another biotechnological strategy is to use seaweed to enrich the compost generated from other substrates such as livestock manure, agriculture residues or food waste. With this methodology, moisture is improved, micronutrient content is enriched, bacterial diversity is increased and seaweed mineral salts balance acidic pH [30, 31]. In any case, the objectives of composting are always the same: that the sample is aerated, with an appropriate moisture level (~ 70%) and a good C/N ratio (~ 20–25) [32]. However, in the case of *R. okamurae* composting poses as additional technical difficulty the high concentration in sesquiterpenes [4–6]. In this sense, research on composting with other materials rich in terpenes, such as waste from aromatic plant factories, can serve us as a technical guide [33, 34]. It has been shown that during the thermophilic phase of composting, emissions of volatile compounds increase enormously and that most of these are terpenes [35]. Volatile terpenes do not have a bad odor and some studies indicate that they are even beneficial to health [36]. In any case, the best methodological developments for the bioremediation of terpene-rich wastes must be aerobic [37].

Due to the unpredictability of composting with free-living microorganisms and the fact that these systems emit greenhouse gases during the first weeks [38] (although the emission is lower than if the waste is not processed) other bioremediation methods have been tested. Among these are the use of invertebrates in seaweed processing which allows the generation of high value-added products such as compost, high quality protein meals and live feed used for animal and even human consumption [39]. Also, these biotechnologies are an environmental good in themselves, as they serve to decrease the greenhouse gases produced by garbage during its transportation, storage and treatment [40]. On the other hand, composting with invertebrates is much less expensive than other organic waste treatments [41]. Several studies have shown that using invertebrates generates compost that is greatly reduced in pathogens and heavy metals compared with compost produced with free-living microorganisms [42]. By this, different invertebrate composting techniques have been proposed, in addition to vermicomposting, such as composting with millipedes (millicomposting) [43], with different non-climbing cockroach species (blatticomposting) (https://www.wormman.blog/Blatticomposting/blatticomposting.pdf), many dipterans and isopods (https://isopodcomposters.weebly.com/index.html).

Vermicomposting of algae has shown excellent results with various earthworm species such as *Eudrilus eugeniae* [44] or *Perionyx excavatus* [45, 46]. In fact, many earthworm species have the ability to detoxify waste, but are sensitive to salts, certain heavy metals, ammonium, methane or various organic compounds [47]. Such elements may be present in seaweed in certain proportions, so that the most appropriate strategy is double composting, i.e. to perform a first composting with free-living microorganisms to degrade toxics during the thermophilic phase and a subsequent vermicomposting to stabilize the samples diminishing the soluble organic matter transforming it in humic acids [32].

Moreover, the treatment of organic waste with insects serves to drive an efficient and desirable circular economy, since a problem (the waste) is transformed into beneficial and economically valued products (proteins, compost, chitin, etc.) [39, 48]. In this regard, studies with black soldier fly (*H. illucens*) larvae (BSFL) stand out [39]. This species presents multiple advantages such as rapid growth, tolerance to overcrowding, high voracity, lack of specificity towards the type of organic matter, presence of bactericidal peptides in its digestive tract, ease of handling, short life cycle that allows for the development of many generations per year, etc. [49]. On the other hand, it requires a certain temperature to reproduce (~ 28 °C), a specific design that allows adult flight and an intense illumination of at least 5500 lumens of blue-white light to favor mating [50]. In return, *H. illucens* generates excellent compost with a high nutrient content, although they tend to produce a large amount of ammonium, which is lost through volatilization [51]. However, the compost generated with *H. illucens* has high contents of soluble organic matter and nitrogen. To stabilize this compost, double composting has been suggested to convert the soluble fraction to humic acids [52]. An added advantage of using algae as *H. illucens* feed is that BSFL are enriched with omega-3, generating an excellent feed for fish farming [53]. Another biotechnological application of BSFL is its detoxifying capacity for the heavy metals contained in algae [54].

Within the insect group, the larvae of various species of tenebrionid beetles (dark beetles) have also been used as consumers of various types of organic waste [55, 56] and even plastics [57]. With a seaweed-based diet, the species *Zophobas morio* showed good consumption and growth results [58].

Finally, we highlight the use of various species of cockroaches in the consumption of organic wastes of different types [59]. Subsequently, guano (blatticompost) and protein from these insects can be used in animal and even human food [60]. In fact, the most commonly used cockroach species in animal feed such as *Blaptica dubia*, *Nauphoeta cinerea*, *Eublaberus* spp., *Blaberus craniifer* or *Pycnoscelus surinamensis* have low fat contents and very high protein levels [61–63].

The present work proposes a method of bioremediation by invertebrate composting to solve the problems generated by the large biomass of the seaweed *R. okamurae* in the Mediterranean coasts of southern Spain. Unlike other seaweed, *R. okamurae* presents high toxicity due to the presence of sesquiterpenes [64, 65]. As mentioned above terpenes are not easily degraded forming the major fraction of volatile organic compounds (VOC) during waste recycling processes by both aerobic composting and anaerobic fermentation. In consequence, this forces us to look for other biotechnological alternatives testing various invertebrate species to determine their composting potentialities and assess whether any of them can resist the high concentration of terpenes of the algae. For this purpose, we estimated the seaweed consumption (fresh and desalted) of three species of insects (*H. illucens*, *Eublaberus* spp. "Ivory" and *T. molitor*) and two species of earthworms (*E. fetida* and *D. veneta*). Although some studies have used different invertebrate species for algae composting, none have used so many species and the use of cockroaches for these purposes is especially novel. We believe that these types of insects have excellent prospects in bioremediation and should be explored. In this paper, we analyze in detail the first stage of the composting process, which is consumption. In future research we will analyze the nutritional and microbiological quality of the compost generated, as well as its viability for agricultural use. Our results could contribute to mitigate the environmental problems, the effects on public health, the impact on the landscape and the economic losses (due to the costs of the removal of the upwelling and the drop in tourism) generated by the enormous amount of biomass that ends up stranded each year on the coasts of southern Spain.

Materials and Methods

The animal species used in this research were obtained from approved exotic animal dealers and none of them are protected under the CITES convention, the IUCN or the Spanish Catalog of Threatened Species, nor do they violate the Spanish Invasive Species Act (Royal Decree 216/2019, of March 29, BOE-A-2019-4675). The average of some biological characteristics of these species were tested previously by us under laboratory conditions (Table 1).

Laboratory Experimental Design

Three replicates of each species were taken for the control group (no seaweed), three replicates for the desalted *R. okamurae* seaweed and three replicates for the fresh seaweed. The algae were obtained from recent upwelling on the coast of Tarifa (Andalusia, Spain). For desalting, they were submerged in fresh water tanks for 1 week with water changes every 24 h.

Table 1 Biological characteristics of the five invertebrate species studied under laboratory conditions

Species	Weight (g)	Sexual maturity (days)	Annual reproduction rate	Longevity (days)
Dendrobaena veneta	0.91–1.20 adults	40–65	73–146 cocoons	1470
Eisenia fetida	0.29–0.55 adults	28–30	128–475 cocoons	1551
Eublaberus spp. "Ivory"	2.64–4.19 adults	141	72 nymphs	548
Hermetia illucens	0.34–0.67 larvae	48	412–1060 eggs	62
Tenebrio molitor	0.01–0.23 larvae	132	500 eggs	365

Data of weights are referred to the commercial stages of each species

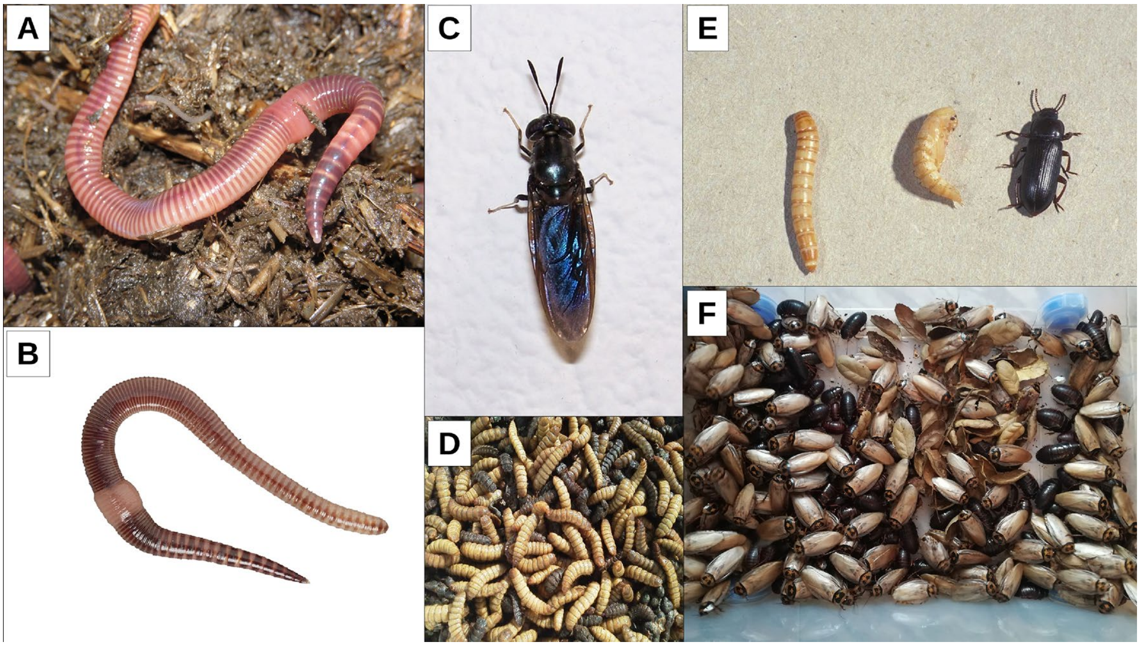


Fig. 2 Invertebrate species studied in the present work. **A** *Eisenia fetida*. **B** *Dendrobaena veneta*. Adult (**C**) and larva (**D**) of *Hermetia illucens*. **E** Metamorphosis stages of *Tenebrio molitor*. **F** Adults (light) and nymphs (dark) of *Eublaberus* spp. "Ivory"

The annelids *E. fetida* and *D. veneta* (Fig. 2) were kept in 25-L plastic boxes, removing the substrate once a week to avoid anaerobiosis or ammonium concentration because they are poison for these animals [28]. Every 15 days, the vermicompost generated was extracted by placing the substrate on a grid assisted by intense light, with a 5 mm mesh size, which the worms passed through, thus reaching the underlying substrate. The worms were quantified and the vermicompost was dried and weighed. At the same time, continuous flow and tray vermicomposters were maintained as reservoirs for replacement animals. The control group was fed with various household wastes such as coffee grounds, fruits, vegetables, bread, non-plasticized and non-tinted paper, cardboard, etc. Only the desalted and fresh seaweed group received this feed. There was no need to hydrate the substrate as the vermicomposters were closed.

The rearing of *T. molitor* (Fig. 2) was carried out in a system with trays. The upper one was bottomless and the pupae were placed on a platform. When they transformed into adults and moved, they fell to the lower tray. This had a bottom with a 1 mm wire mesh that retained the adults while the eggs fell into a third tray. When the eggs hatched and the larvae were large enough, they were screened with 1 mm hand screens and transferred to lower trays where they were sorted by size until they pupate and the cycle began again. This system produced sufficient larvae for the trials and allowed them to be sorted by size for batch design in the three feeding types. The larvae were transferred to open plastic boxes where 50 specimens were placed in each. Each week the average weight, mortality, transformation to pupae and adults were measured. The control group was fed a mixture of chicken feed, breadcrumbs and olive oil in equal parts. The desalted and fresh seaweed groups were also monitored in plastic boxes. Once a week the larvae from the three groups were given some carrot or apple to hydrate.

For the experimental design with the black soldier fly (*H. illucens*) (Fig. 2), its biological particularities were taken into account, according to the guidelines of [50]. *H. illucens* was maintained at 28 °C, with photoperiods of 8 h daily of blue-white light (6500 K) of 8000 lm intensity and in Exo-terra terrariums (http://www.exo-terra.com) of 90 × 45 × 90 cm for adult mating (this is done on the floor), with layers of stacked cork bark that present cracks where adult females can deposit their eggs. The newly hatched larvae seek darkness, so they sink into the substrate, which should be at least 15 cm deep and kept relatively moist to avoid dehydration. Pupae, on the other hand, seek a dry environment, which is provided by the bark piled among which they take refuge. Once sufficient numbers of larvae were obtained, they were separated into three batches of 50 specimens for each type of diet: control, desalted seaweed and fresh seaweed. As a control diet, the same household waste was used as for the two species of worms.

Eublaberus spp. "Ivory" cockroaches (Fig. 2) were kept in Exoterra terrariums (90 × 45 × 90 cm). Bark was placed to generate a taller structure to simulate a rocky bat cave wall, a habitat where this species lives in nature (www.roachcrossing.com). Since *Eublaberus* spp. "Ivory" is a burrowing species (especially the nymphs), a 20-cm layer formed by cypress leaves and compost in equal parts was maintained. After a few months, nymphs of at least 2 cm were separated by screening and distributed into groups of 50 individuals for the three batches of each type of diet. These batches were kept in plastic boxes with sufficient aeration to avoid condensation, as this species prefers a dry environment. The control group was also fed domestic waste, although 100 g of dog food was added weekly to correct possible nutritional deficits. In this way, we prevented individuals from eating each other's wings, since this species has a higher protein requirement than other cockroach species [66]. Once every 15 days, guano was removed with a 1 mm sieve and part of the substrate was replaced.

All species were maintained under strict temperature and humidity control (Table 2), with *ad-libitum* feeding and in complete darkness after feeding and turning or substrate change operations.

Quantification and Statistical Analysis

For each species studied and at the end of the 5-week experimental period, the number of dead specimens in each batch was identified and the average was transferred to mortality percentages per treatment (control group, desalted seaweed and fresh seaweed). On the first day of the trial, the weight of feed fed and the number of animals in each batch were counted. Every two or three days throughout the 5 weeks of the trial, the weight of the remaining feed and the number of animals, as well as their total weight, were determined. Small animals at high densities such as invertebrates pose some technical difficulties such as the impossibility of calculating consumption per individual in isolation [67]. Therefore, we determine intake levels as the difference in weight of food provided at a given time (t) interval by the number of animals and days elapsed (1).

$$\text{Feeding rate}(\text{mg}/\text{animals} * \text{days}) = \frac{\text{Food weight}_t - \text{Food weight}_{t-1}}{\text{number of animals} * \text{days}} \tag{1}$$

Table 2 Average humidity and temperature parameters over the 5 weeks of testing in the terrariums and containers for each species

Species	Humidity	Temperature
Dendrobaena veneta	83.75 ± 1.97	27.88 ± 0.10
Eublaberus biolleyi	62.31 ± 7.36	25.46 ± 0.39
Hermetia illucens	72.10 ± 16.57	25.95 ± 0.72
Tenebrio molitor (adults)	58.20 ± 1.87	26.01 ± 0.23
Tenebrio molitor (larvae)	61.42 ± 1.94	24.05 ± 0.74

Eisenia fetida is absent from the table, as its mortality was almost immediate upon addition of the algae

All consumption data per individual were subjected to Dunn's non-parametric analysis of variance with post-hoc estimation [68]. In the case of the adult *T. molitor* and due to their slow movement and small size, it was possible to apply Elton's "cafeteria test" [69] of food preference between desalted and fresh seaweed. This test is determined by offering two or more separate food sources with equal probability of access by the animals [70]. The number of specimens observed on the two types of algae was counted. Five repetitions of this test were done by changing the location of the substrates. The data were analyzed using the Wilcox test [71]. The cafeteria experiment was not conducted with soldier flies because of their high mobility and high larval density, nor with cockroaches because of their larger size and speed of movement.

The average differences in weight per individual in the species *T. molitor*, *H. illucens* and *Eublaberus* spp. "Ivory" were analyzed by Dunn's test. In the case of the earthworms *E. fetida* and *D. veneta*, the weight was not recorded, since they presented a high adherence of the substrate to their bodies, which had high water contents. However, the presence of egg sacs and juveniles was recorded, as well as the possible presence of *clitellum* as a sign of reproduction [72]. In *H. illucens*, the weights in the last larval stage (pre-pupation), identifiable by its darker color were measured (Fig. 2D). Additionally, a non-parametric analysis of variance with Scheirer–Ray–Hare intercept was performed to test the influence of treatment over the 5 weeks of the trial [73]. Finally, to functionally explain the differences in composting efficiency among the invertebrates studied, we performed a multivariate analysis. The technique used was Non-Metric Multidimensional Scaling, since it is a very flexible methodology that adapts to different data sources [74]. As variables we used the microbiota taxa of the five invertebrate species according to bibliographic data [75].

Results

The temperature and humidity values measured in all the compost consumption and production experiments carried out are shown in Table 2.

A very different tolerance to the algae was observed among the various invertebrate species tested during the 5 weeks of the trial. In the earthworm *E. fetida* the mortality rate reached 100% of the population within a few days (Fig. 3). This occurred for both dry and desalted algal feeding, but not for the control group. In the *D. veneta* earthworm, no mass mortality was observed at the beginning of the experiment and no unusual mortality was observed throughout the trial. However, very low earthworm densities were detected with both desalted (101.64 individuals/m^2) and fresh (49.69 individuals/m^2) algae (Fig. 3). These

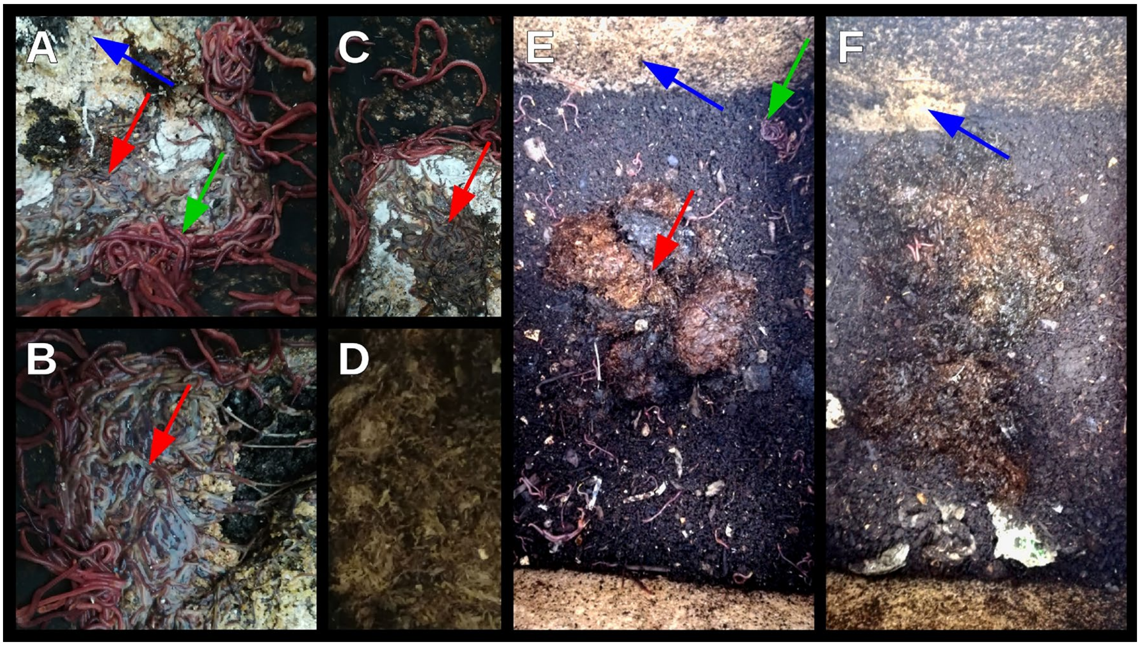


Fig. 3 Effect of feeding *Rugulopteryx okamurae* on *Eisenia fetida* mortality using desalted (**A** 24 h; **B** 48 h) and fresh (**C** 24 h; **D** 48 h) seaweed. The effect on *Dendrobaena veneta* was much lower during the 5 weeks of the trial for both desalted (**E**) and fresh (**F**) seaweed. The green arrows show live specimens, the red arrows show dead specimens and the blue arrows show accumulations of mineral salts from the algae and excreted by the worms. The vermicompost observed in the images is prior to the experiment, due to the high mortality observed when administering the algae

densities were lower than those of the continuous flow composters or trays where more than 4000 individuals/m^2 were obtained. In both algae treatments, no egg sacs or new individuals were detected during the 5 weeks of the trial. In the control group plots, an average of 1465.48 cocoons/m^2 was reached.

Neither cockroaches *Eublaberus* spp. “Ivory”, nor black soldier flies (*H. illucens*) showed appreciable mortality during the test period. No differences were observed among the three feeding treatments. On the other hand, *H. illucens* had an average development time of 31.09 days with 65.82% survival (transformation to adults) with no significant differences due to feeding type.

For the mealworm (*T. molitor*), the mortality rate of the control group was 18.34% in larvae, 24.86% in pupae and 1.03% in adults. In contrast, 51.02% of larvae died with desalted seaweed and 90.91% with fresh seaweed (Fig. 4). The larvae that survived in the two seaweed treatments were much smaller in size and none of them transformed into pupae or adults. The behavior of the *T. molitor* larvae was different in the two seaweed treatments. It was observed how the larvae consumed the desalted seaweed, dispersing it throughout the container and leaving accumulations of mineral salts. This behavior was not observed in the fresh seaweed, but consumption was low (Fig. 4). In the *T. molitor* beetles (obtained separately) there were no differences between treatments, and the mortality rate was less than 2% in all cases. In the “cafeteria test” ($n=5$), for both groups of algae, the results are close to significance ($W=22$, $p=0.059$). A total of 69.09% of adults preferred desalted seaweed.

Consumption rates per individual showed significant differences between treatments for all species tested (Table 3), but these differences did not occur between the two types of algae. That is, seaweed (desalted or not) is less consumed than standard feed (Figs. 5, 6). Only in *D. veneta* were there significant changes in seaweed consumption over the trial period (Table 3). The species with the highest consumption of seaweed per individual was *Eublaberus* spp. “Ivory” (Figs. 5, 6). Since there were no significant differences in consumption between the two seaweed treatments for either species, in the subsequent analyses the seaweed batches were grouped as a single group. In this sense, *Eublaberus* spp. “Ivory” consumed an average of 21.84 mg/animal * day of seaweed for the set of batches studied while with standard feeding the consumption of this species reached 668.1 mg/animal * day. This important difference in consumption had hardly any effect on the changes in weight of the nymphs, which went from 1141.0 mg with standard feeding to 1138.1 mg with seaweed feeding (desalted and fresh) along the experimental period of 5 weeks. We also saw no difference in the subsequent growth of the nymphs that developed into adults in all cases. Months after the trial, these adults reproduced without any problem. The percentage changes in

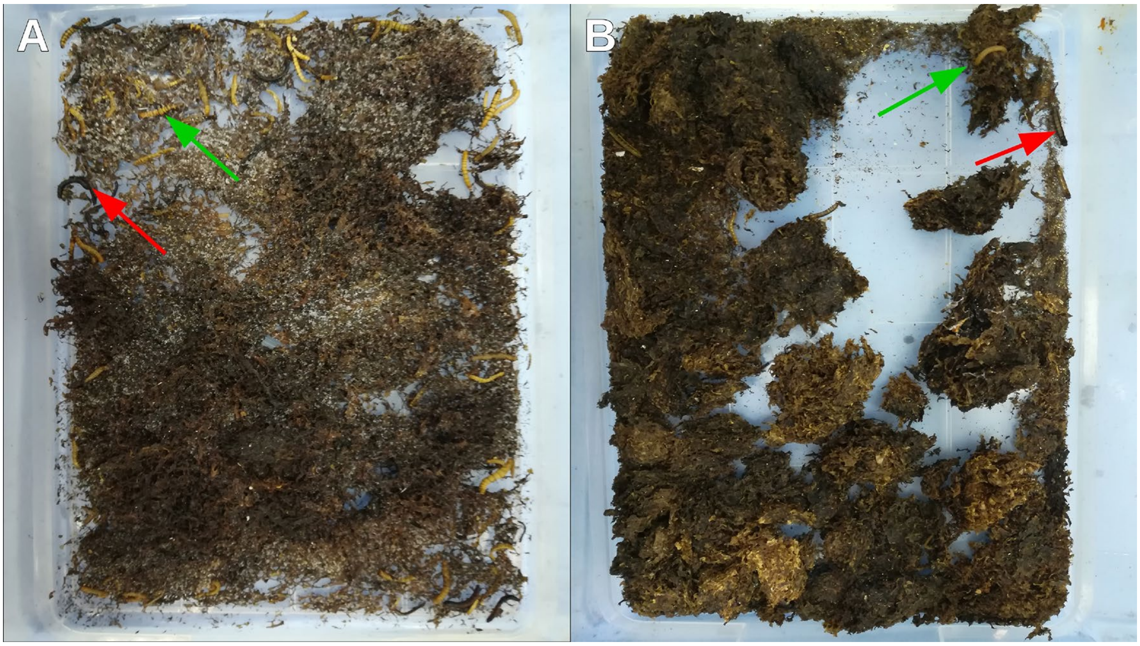


Fig. 4 Effect of feeding *Rugulopteryx okamurae* on the mortality of *Tenebrio molitor* larvae in desalted (**A**) and fresh (**B**) seaweed after the 5 weeks of testing. Red arrows indicate dead specimens (dark), green arrows indicate live specimens (light). Note the difference in food dispersal and mineral salt accumulation (white)

Table 3 Results of the non-parametric variance test with Scheirer–Ray–Hare interaction

Species	Weeks	Treatment	Weeks × treatment (ns)
Dendrobaena veneta	11.266*	42.450***	0.331
Eublaberus biolleyi	2.697 ns	14.864***	1.068
Hermetia illucens	2.144 ns	5.999*	0.857
Tenebrio molitor (adults)	8.057 ns	4.175 ns	0.339
Tenebrio molitor (larvae)	11.928 ns	16.529***	1.368

Eisenia fetida is absent from the table, as its mortality was almost immediate upon addition of the algae

ns non-significant differences

*p value < 0.05

***p value < 0.001

consumption and weight between standard and algae feeding are shown in Table 4. Although the life span of this species is 18 months and it reaches sexual maturity at 105 days, reproduction under laboratory conditions is continuous. At ideal densities and extrapolating to a large scale, the consumption of this species was the maximum observed (Table 4).

In the case of the *H. illucens* species, very similar larval weights were also observed between the standard feeding (220.0 mg) and the feeding with seaweed (219.7 mg) for the last larval stage. Again, in the algae-fed batch, a much lower consumption (6.5 mg/animal*day) was observed than in the standard-fed batch (448.8 mg/animal*day). As with the previous species, this represented a very low percentage decrease in weight, but very high in consumption with respect to the standard feeding (Table 4). *H. illucens* has a complete biological cycle of 46 days, of which 1 month corresponds to larval development. In other words, under ideal conditions we can obtain eight complete cycles per year. Taking into account this seasonality and the ideal density of the species, we would have somewhat lower consumption, although similar to *Eublaberus* spp. "Ivory" (Table 4).

Tenebrio molitor larvae did not show differences in weight between the two groups of algae according to Dunn's test, but did show differences with the control group (Fig. 6). Grouping the weights of larvae fed with both types of algae (average 86.13 mg) and comparing them again with the control group (average 160.08 mg) we observed highly significant differences according to the Wilcox test (W = 0, p value = 2.4E-04). These larvae, fed with *R. okamurae*, reached the last molting stage, but did not transform into pupae and all died at the end of their development. In contrast, adult *T. molitor* beetles (obtained separately) showed no difference in weight between the control group (mean 136.3 mg) and both seaweed treatments (mean 135.02 mg). However, seaweed intake (20.4 mg/animal*day) were well below the standard feeding (477.2 mg/animal*day). Regarding seasonality, *T. molitor* can have two complete annual cycles. This implies that the adult (beetle) phase, which is the only one that

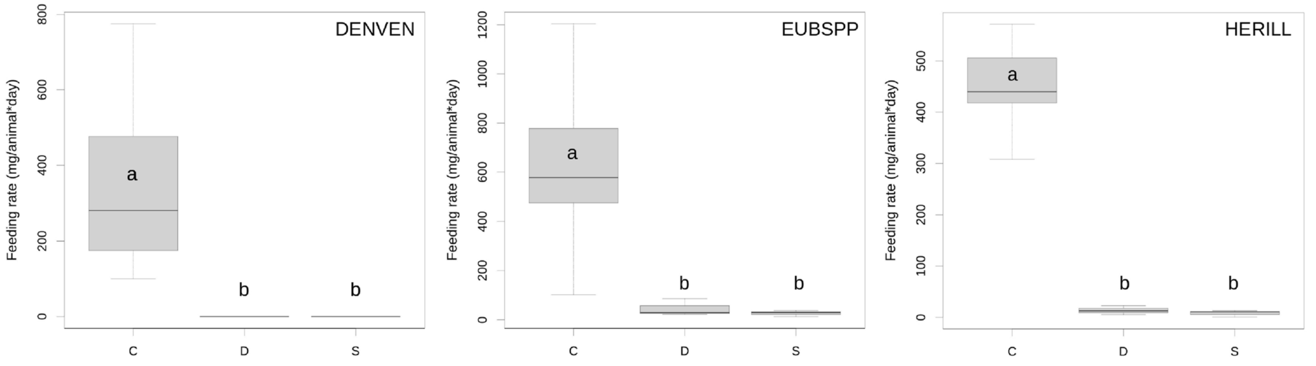


Fig. 5 Consumption per animal per day according to standard feeding (C), desalted seaweed (D) and fresh seaweed (S) in the earthworm *Dendrobaena veneta* (DENVEN), in the cockroach *Eublaberus* spp. "Ivory" (EUBSPP) and in larvae of the black soldier fly *Hermetia illucens* (HERILL). Lowercase letters indicate significant differences according to Dunn's non-parametric *post-hoc* test of variance

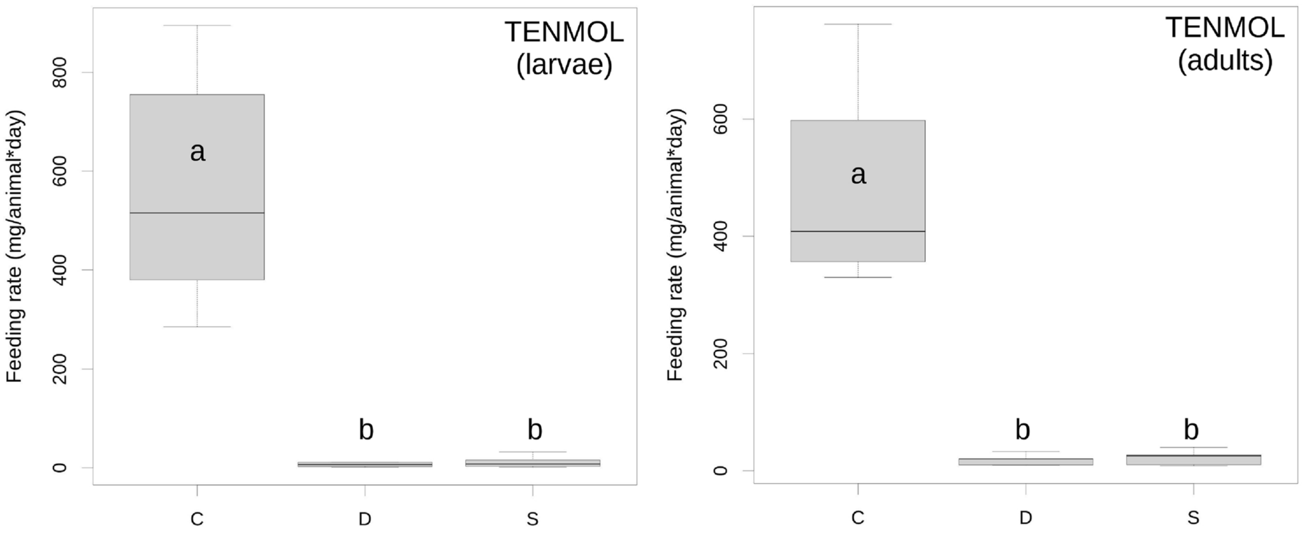


Fig. 6 Consumption per animal per day according to standard feed (C), desalted seaweed (D) and fresh seaweed (S) in larvae and adults of *Tenebrio molitor* (TENMOL). Lowercase letters indicate significant differences according to Dunn's non-parametric *post-hoc* test of variance

Table 4 Percentage changes in weight and consumption rate of the three species that consume *Rugulopteryx okamurae* seaweed on a sustained basis

Parameter	*Eublaberus* spp.	*Hermetia illucens*	*Tenebrio molitor* (adults)
Body weight (%)	− 0.3	− 0.1	− 0.1
Feeding rate (%)	− 96.7	− 98.6	− 95.7
Optimal density (individuals/m^2)	~ 5000	~ 25,000	~ 10,000
Consumption of algae (Tm/ha*month)	397.9	390.0	244.8

The expected averages of total seaweed consumption per hectare at the optimum density and taking into account the seasonality of each species are shown

consumes the algae on a sustained basis, would remain active 4 months per year. Although due to the asynchrony in spawning a supply of adults can be maintained every month. This means maintaining two feedings: a standard one for larvae and another one for adults. Therefore, at the ideal density of adults, the consumption of algae was lower for this species (Table 4).

Discussion

The invertebrates studied in the present work are species that are easy to rear in laboratory conditions and in some cases (mealworms, soldier flies and earthworms) form the basis of emerging industries [76]. Therefore, many aspects of their humidity and temperature requirements are known and maintaining these is critical to the success of any rearing program. In fact, the microclimatic conditions required by mealworms, soldier flies and earthworms were easily maintained in the laboratory, but we believe that extrapolating them to an industrial scale may be a limiting factor for some species. In that sense, earthworms can withstand temperatures that would not be viable for insects. Although they do not consume fresh or desalted seaweed, we must take this aspect into account. Mealworms are viable at temperatures close to 20 °C although its optimum is around 28 °C. The humidity in this species should not fall below 50%, which is a danger for eggs and young larvae in the summer season [77], when the most numerous upwelling arrives. Occasional irrigation and give some fresh vegetables solves easily the problem. The black soldier fly larvae, as the tropical species that it is, adapts perfectly to the south of Spain as demonstrated by the fact that there are already viable farms [76].

In the case of the cockroach *Eublaberus* spp. "Ivory", information was obtained mainly from pet breeders and judging by the success achieved in rearing, we validate that ideal conditions were maintained. This species, despite living in bat caves, needs a dry environment, but access to water through drinking devices or the use of water gel crystals. Regarding temperature, the species is more tolerant, requiring at least 17 °C (www.roachcrossing.com) or a few degrees more if consumption and reproduction are to be increased. Because of these considerations, we believe that the best alternative for the composting of *R. okamurae* is the *Eublaberus* cockroach. Not only is it not affected by ambient humidity, but it prefers a very dry environment similar to bat caves in tropical areas where live in nature. Also, being an ovoviviparous species, they are very easy to maintain at high temperatures even close to 40 °C, which would cause severe dehydration in mealworm or black soldier fly larvae.

Both BSFL, dark beetles and cockroaches showed very strong changes in consumption between the control group and the algae feeding. However, this did not translate into significant differences in weight due to several non-excluyent reasons. The first is that although seaweed has sesquiterpenes it is rich in nutrients. A second reason is that the experimental period of 5 weeks is too short to observe relevant changes in weight in these species. However, outside

Table 5 Seaweeds used in composting

Species	Methods	Composters	References
Ahnfeltiopsis devoniensis	CC	MC	[100]
Arthrospira platensis	SC	MC	[101]
Ascophylum nodosum	IC	HI/ZM	[53, 54, 58]
Ceramium rubrum	CC	MC	[102, 103]
Cladophora glomerata	CC	MC	[104, 105]
Codium vermilara	CC	MC	[103, 106]
Colpomenia peregrina	CC	MC	[100]
Cystoseira baccata	CC	MC	[107]
Dictyota dichotoma	CC	MC	[103]
Dilsea carnosa	CC	MC	[100]
Fucus evanescens	CC	MC	[108]
Fucus serratus	CC/IC	MC/HI	[53, 99]
Gastroclonium ovatum	CC	MC	[100]
Gracilaria corticata	VC	PE	[46]
Gracilaria edulis	VC	PE	[46]
Gracilariopsis funicularis	CC	BC	[109]
Halimeda gracilis	VC	PE	[46]
Himanthalia elongata	CC	MC	[100]
Laminaria digitata	SC/IC	MC/HI	[53, 101]
Laminaria pallida	CC	BC	[109]
Lomentaria articulata	CC	MC	[100]
Palmaria palmata	SC/IC	MC/HI	[53, 101]
Polyedes rotunda	CC	MC	[100]
Polysiphonia fucoides	CC	MC	[105]
Punctaria latifolia	CC	MC	[100]
Rhodomela confervoides	CC	MC	[100, 99]
Saccharina latissima	CC	MC	[100]
Sargassum fluitans	CC	MC	[29, 78, 110]
Sargassum johnstonii	CC	MC	[111]
Sargassum muticum	CC	MC	[78, 100]
Sargassum natans	CC	MC	[29, 78, 110]
Sargassum swartzii	CC/VC	PE/EE	[45, 46, 112]
Sargassum wightii	CC/VC	PE	[44–46]
Spongomorpha aeruginosa	CC	MC	[100]
Turbinaria ornata	VC/CC	PE/MC	[45, 46, 113]
Ulva clathrata	CC	MC	[105, 114]
Ulva fasciata	CC	MC	[114]
Ulva flexuosa	CC	MC	[105]
Ulva lactuca	IC	HI	[53, 115]
Ulva ohnoi	CC	MC	[116, 117]
Ulva pertusa	CC	MC	[114]
Ulva reticulata	VC/CC	PE/MC	[45, 46, 118]
Ulva rigida	CC	MC	[119]
Undaria pinnatifida	CC	MC	[120, 121]

Methods: *CC* co-composting, *IC* insect composting, *SC* soil composting, *VC* vermicomposting. Composting organisms: *EE Eudrilus eugeniae* (worm), *HI Hermetia illucens* (insect), *MC* microorganisms, *PE Perionyx excavatus* (worm), *ZM Zophobas morio* (insect) the experimental period we did not really see increases in mortality or significant differences in weight so this explanation is not very likely. Third, it is quite possible that the gut flora of these invertebrates has some ability to detoxify sesquiterpenes. This should be investigated in depth.

Regarding the background of the use of various algae composting techniques, Table 5 compiles a list of red, green and brown species commonly used in bioremediation. This compilation includes traditional composting with free-living microorganisms, as well as the use of various species of earthworms and insects. However, the list of species is limited and does not include cockroaches, a group with extraordinary possibilities due to their voracity, resistance to toxins and unspecificity. Therefore, it follows that, worldwide, algal composting research with invertebrates is very limited. In order to explore the possibilities offered by composting with invasive macroalgae in the field of circular economy with a higher level of knowledge, we have incorporated five invertebrate species (2 annelids and 3 insects). The Table 5 includes the term co-composting, a process that consists of a strategy of composting algae in compost piles to which other materials of different nature (manure, straw, vegetable waste, fish remains, etc.) are added to maintain an ideal C/N ratio, in some cases using earthworms to reduce pathogens and further stabilize the compost [78]. In this regard, this work is the first to use a battery of insect species as its main strategy.

The two annelid species investigated in the present work, *E. fetida* and *D. veneta,* are widely spread in vermiculture in Europe. It is known that earthworms have a great capacity to process certain organic compounds rich in cellulose, lignin and high C content [79]. However, earthworms should not be used to degrade hospital waste, citrus, meat or industrial oils. This is because they do not tolerate pharmaceutical compounds, acidic materials, salty, ammonium-rich substances or anaerobic environments [41]. In these cases, pre-composting is usually carried out [80]. Some studies show that worms can process toxic materials if they are pre-composted for only 1 week [81]. This strategy would extend the algal processing time by forcing two facilities to coexist: one for pre-composting and another for vermicomposting. This strategy could be promising because it accelerates the final composting process by working the worm on a material that it can process better. Another advantage of double composting is that the volume of substrate is greatly reduced, making the whole installation smaller and more intensive. Pre-composting can even be carried out close to the beaches, so that by having to transport a smaller volume to the vermicomposting plant, transportation costs would be reduced. Double composting was not the objective of this work, but it should be implemented in subsequent research. We have concluded, however, that the algae should not be fed directly to the worms. The effect was especially negative on *E. fetida,* as massive mortality was generated in only 24 h for both desalted and fresh algae. The effect on *D. veneta* was more long-term, but it considerably affected reproduction so that the use of this species would also be unfeasible.

As previously indicated, the toxicity of *R. okamurae* was probably due to the existence of sesquiterpenes [65, 66) and, in this regard, previous studies with terpenes showed that they had high toxicity to earthworms [82] and some insects [83]. The fact that terpenes from the algae affected *D. veneta* less may have to do with the fact that this species has a much thicker integument or cuticle than *E. fetida*. Although it must be demonstrated through further research, we believe that poisoning occurs more by diffusion through the epithelium than by ingestion, since the worms shun the algae, but cannot escape the algal leachates.

The larvae of the beetle *T. molitor* are used in the biotechnology industry not only for protein production, but also for waste recycling and fertilizer generation (frass). Some studies indicate that they can adapt to very diverse feeding strategies and not only cereal diets, which is the one generally used in the farms of this species [56]. The potential of this species to degrade plant residues should be further exploited since, as noted by [84], it increases the growth rate of larvae. The fact that only adult *T. molitor* consume algae regularly may be due to a shorter developmental time or a difference in the microbial flora between adults and larvae due to changes in their diet [85]. We must also consider the possibility that algal toxicants slowly accumulate in *T. molitor* larvae until causing mass mortality in the last larval stages. The decrease in weight supports this idea and could suggest that the microbial flora of the digestive tract of the *T. molitor*, which consists mainly of *Parabacteroides*, *Clostridium* and *Agrobacterium* (different flora from that of other invertebrates tested in this work) is able to detoxify the algae only partially. *T. molitor*, despite its potential, only consumes the seaweed if it is desalted and not in its entirety, but it does not resist the toxins in *R.okamurae* over the long term. This invalidates this biotechnological alternative for the degradation of algae, since reproduction would be compromised by not being able to reach the pupal stage. It would only be possible to use mealworms with the algae if it is mixed with another food source or if the alga was pre-treated (silage, anaerobic digestion, bacterial aerobic precomposting, etc.…). In addition, the development cycle of *T. molitor* under ideal conditions lasts 140 days and is longer than other alternatives, especially if we consider only the adult stage. Other tenebrionid species of the genera *Zophobas* or *Alphitobius* could be assessed in further studies since, as pointed out by [56], there are differences in the diet of these species which support the idea of a higher resistance to residues of certain toxicity.

No toxic effect was observed on *H. illucens* larvae, and their biological cycle was completed without subsequent effects on adult reproduction. This species is known for its potential in entomoremediation [86]. Several studies link the detoxifying capacity of *H. illucens* to its gut flora, which is dominated by *Bacteroidetes* and *Proteobacteria* [87]. The detoxifying mechanisms of *H. illucens* are complex but the production of phenoloxidases, antimicrobial peptides and H_2O_2 stands out. This is a consequence of its ecology, as it is a species that feeds in nature mainly on decaying carrion where pathogens such as *Staphylococcus* or *Salmonella* dominate [53]. In addition, in favor of the use of this species in algal composting is its productivity, voracity, lack of specificity and its very short biological cycle of only 45 days. On the other hand, in waste treatment with *H. illucens*, factors such as pH, salt content or ammonium level are unimportant [50]. Some studies show that the choice of *H. illucens* gives good results from directly processing (without pre-composting) wastes such as fresh manure, sewage sludge or mill residues [53]. These wastes would be impossible to process directly with earthworms or tenebrionids. On the contrary, some studies show that BSFL compost presents high levels of unstabilized soluble organic matter, which requires double composting to transform it into humic acids [52]. We believe that this strategy could help to generalize the use of entomocompost in agriculture and gardening. Another problem is that *H. illucens* is more difficult to handle because it has a winged phase and requires several hours of intense light *per day* for mating, as well as a breeding temperature of at least 28 °C, which is higher than that observed for other species tested in this study. Another important factor is that *H. illucens* larvae require a certain amount of moisture in the substrate and that the substrate be soft. *R. okamurae* algae meet both conditions, but only for some time. The upwellings end up drying and hardening with the sun in summer, which is when the greatest contributions to the coast occur.

Although *H. illucens* has many factors in its favor, we believe that its conditioning factors would increase the costs of large-scale algal recycling systems in closed environments. However, some designs of waste recycling systems with *H. illucens* in greenhouses have shown great promise [88]. Therefore, if this species is adopted as a biotechnological solution its use should be implemented in stations that receive a lot of sunlight, with bioclimatization systems and close to the upstream areas to avoid unnecessary costs. In such a case, the yields in compost and protein that *H. illucens* would generate could be highly promising, as observed in previous research [89]. In addition, some studies conducted by adding biochar to BSFL compost have shown a marked effect on reducing emissions of volatile compounds and greenhouse gases, which is a plus point for this species [90]. Like cockroaches, BSFL show a great capacity to process food waste that is very difficult to degrade, such as citrus peels [91]. It is not surprising that they are also capable of processing algae with high efficiency.

Cockroaches and especially some genera such as *Blaptica*, *Blaberus*, *Eublaberus* or *Pycnoscelus* are good waste degraders too [66]. This group of insects shows high voracity, ease of handling, unspecificity by food type and high reproductive rates, making them suitable for large-scale waste processing stations [92]. In addition, most cockroaches can withstand very high overcrowding that does not compromise their reproduction as with other invertebrates. Additionally, unlike *H. illucens*, cockroaches do not require light, although they do require high temperatures to generate sufficient rates of consumption and reproduction [93]. However, many cockroach species fly and/or climb so escape risks are an important factor to consider, especially if they are invasive species or have invasive potential. Our experience with several species allows us to select *Eublaberus* spp. "Ivory" as suitable for waste processing. This species is considered an ecotype of *E. distanti* and although its taxonomic status remains unresolved, it is known to be native to South America and to live in caves where it consumes guano and bat carcasses. The peculiar habitat of this species explains many of its excellent waste degrading properties, as it can reproduce at temperatures of only 20° C, which are easily obtained in indoor enclosures in southern Spain if good insulating materials and occasional heating are available. Furthermore, this species can withstand overcrowding of up to 8000 individuals per m^2 without negative effects on nymph growth, consumption rates or reproduction [94, 95]. Unlike other species of the genus *Eublaberus*, individuals do not attack each other, since the protein requirements of this species are moderate and are perfectly satisfied with a diet of plant residues. The species tolerates dry diets if it has water, unlike the larvae of *H. illucens,* which need some moisture in the substrate. This cockroach does not fly, does not climb and does not transmit diseases. It is also a non-invasive species [66] with an enormous detoxifying capacity, since the genus *Eublaberus* presents one of the most varied microbiota found in insects [96]. The compost it generates is of high quality (www.roachcrossing.com), very fine and easy to separate through a 2 mm sieve. Smaller nymphs cannot pass through the sieve, so processing is very easy. In addition, the nutritional values of the genus *Eublaberus* are very good for feeding farm animals and the compost they generate is rich in nitrogen [97]. Finally, it should be pointed out that countries such as China have been using cockroaches for centuries, initially to obtain pharmacological products and more recently to process waste, obtain compost and high-quality proteins which they use mainly in poultry farms [92]. We have observed that this species is highly voracious, consumes more algae than any other, is simple to manage and constantly reproduces. We envision that by moving the use of *Eublaberus* spp. "Ivory" to large scale, algal topsides could be recycled, even mixed with other wastes to lower their toxicity. This would help to mitigate an enormous environmental problem, generate economic resources for municipalities to help alleviate the costs of the removal of seaweed clumps and their impact on tourism and, in addition, biotechnological plants could be installed which can be used to process other waste outside the summer season. In consequence, the methodology shown in this paper has undoubted advantages over the high costs involved in the massive removal of the upwelling. In addition, it is an environmentally recommendable process to avoid the rotting of the above-mentioned uppers. Moreover, when analyzing all the gut microbiota information available in the literature for each species by means of a Non-Metric Multidimensional Scaling Analysis (Fig. 7), it can be seen that the increased consumption of algae clearly points to insects, with the current knowledge, as the most appropriate taxonomic group to degrade the algal uptakes investigated here. Unlike earthworms, the insects used in this study present an exclusively bacterial microbiota with a total absence of fungi. There are more than 4500 species of cockroaches on the planet, more than 20,000 species of *Tenebrionidae* and more than 2700 species of soldier flies (*Stratiomyidae*). Many of these species live in habitats where food sources may be toxic to other species. There remains an enormous field of research that will allow us to find species that can be adapted to consume toxic organic wastes more efficiently without constituting a threat of bioinvasion.

Conclusions

There is a lot of information on composting of non-toxic algae with free-living microorganisms [98]. The application of these methods in agriculture is not entirely feasible because of a large accumulation of heavy metals that would pass into the food chain [99]. However, many detritivorous invertebrates (isopods, dipteran larvae, cockroaches, earthworms and tenebrians) can tolerate these metals and accumulate them in their bodies [96]. We have analyzed five invertebrate species (two worms, mealworms, BSFL and tropical cockroaches) and found that two species (*Hermetia illucens* and *Eublaberus* spp. “Ivory”) can consume the toxic alga *Rugulopteryx okamurae* tolerating the high concentration of sesquiterpenes in this species. With the data generated and the mini literature review conducted, we believe that the current knowledge on marine macroalgae composting has been significantly expanded. In fact, we propose the use of beach-side composting cockroach farms of the genus *Eublaberus* as an effective bioremediation technique that also allows.

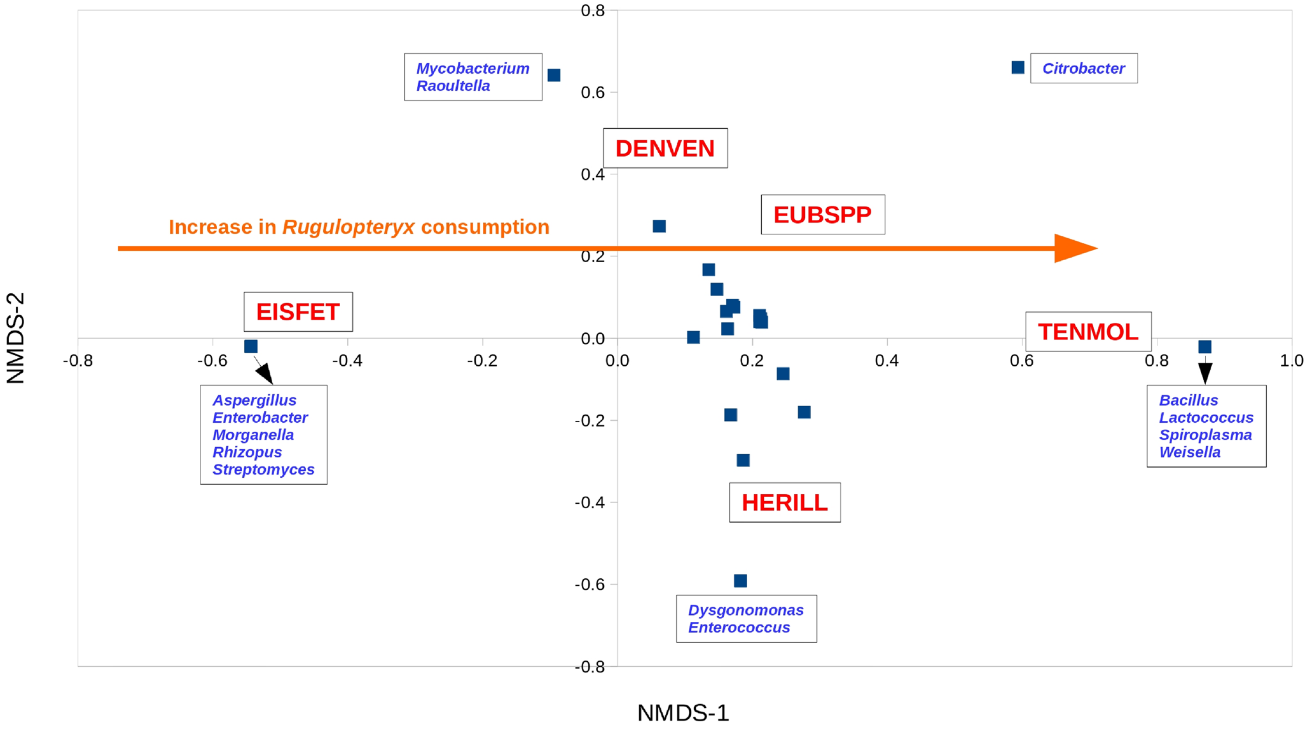


Fig. 7 Ordering of the species studied in the multivariate space of a Non-Metric Multidimensional Scaling analysis on the composition of the intestinal microbiota. The results indicate a higher consumption of *Rugulopteryx* in bacterial flora species. The characteristic microbiological taxa of each species are shown

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Author Contributions In order of signature, the authors' contributions were as follows: DP carried out the analyses of invertebrate consumption in the laboratory, the statistical treatment of the data and was involved in the bibliographic review and writing of the manuscript. JCG-G is the coordinator of the working group that was in charge of finding the necessary resources, preparing the fresh and desalted seaweed materials, reviewing the bibliography on seaweed and writing and correcting the manuscript. JL and AT helped with the literature search and laboratory analyses, as well as providing interesting insights to the manuscript.

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Data Availability The datasets generated during and/or analyzed during the current study are available from the corresponding author on reasonable request.

Declarations

Conflict of interest The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Authors and Affiliations

D. Patón[1] · J. C. García-Gómez[2] · J. Loring[2] · A. Torres[1]

✉ D. Patón
dpaton@unex.es

✉ J. C. García-Gómez
jcgarcia@us.es

[1] Área de Ecología, Facultad de Ciencias, Universidad de Extremadura, Avda. de la Universidad s/n, 06071 Badajoz, Spain

[2] Laboratorio de Biología Marina, Seville Aquarium R + D + I Biological Research Area, Department of Zoology, Faculty of Biology, University of Sevilla, Marine Biology Station of the Strait (Ceuta), Seville, Spain