J Appl Phycol (2016) 28:2427–2433
DOI 10.1007/s10811-015-0741-z

Can the European abalone *Haliotis tuberculata* survive on an invasive algae? A comparison of the nutritional value of the introduced *Grateloupia turuturu* and the native *Palmaria palmata*, for the commercial European abalone industry

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Received: 27 May 2015 / Revised and accepted: 26 October 2015 / Published online: 17 December 2015

Abstract The suitability of two red algae species, the introduced *Grateloupia turuturu* and the native *Palmaria palmata*, as feed for the culture of the European abalone *Haliotis tuberculata*, was compared over a 5-month period. Three experimental diets were tested: (1) *P. palmata*, (2) *G. turuturu*, and (3) a mixed diet of *P. palmata* and *G. turuturu* (1:1). Biochemical composition (proteins, carbohydrates, lipids, ashes) of algae was measured. No mortality was observed during the time of the experiment in any of the treatments. Growth in length and weight was higher for abalone fed with *P. palmata* and the mixed diet. Abalone exhibited a preference for *P. palmata* and showed the highest weight gain with this macroalgae (107.8 ± 7.2 %). *Grateloupia turuturu* disintegrated faster in abalone rearing conditions and was not suitable for significant growth of *H. tuberculata* in a monospecific diet. However, when it is provided in a mixed diet, abalone seem to show a higher lipid content than when fed a *P. palmata* monospecific diet. The invasive *G. turuturu* could be an interesting food supplement for European abalone.

Keywords Aquaculture · Feeding · Growth · *Haliotis* · Macroalgae · Nutrition

Introduction

Haliotis spp. (abalone) are of great commercial value (Shepherd and Steinberg 1992). Their high nutritional value, the flavor of their flesh, and the originality of their perforated shell lined with mother-of-pearl make of them a highly desirable seafood delicacies, particularly in Asia (Cook 2014). Due to the ever increasing demand for this product and the simultaneous overfishing of wild stocks, the farm production of abalone has increased over the past few years and reached a production of 100,352 t and 785.799 billion US dollars in 2012 (FAO 2014). The main obstacle for the production and the economic success of this product is its slow and variable growth rate (Shepherd and Steinberg 1992). *Haliotis* species need between 3 and 4 years to reach market size (Demetropoulos and Langdon 2004b; Shpigel et al. 1996). Abalone growth in the wild is very variable depending on season, food availability, population densities, temperature, and stress conditions (Huchette et al. 2003; Saunders et al. 2008). The growth of cultivated abalone, however, is influenced by factors linked to the culture system such as water quality, tanks design, abalone density, quantity, and quality of feed, of which feed is the most important economically in farms (Fleming and Hone 1996; Mgaya and Mercer 1995; Shpigel et al. 1999; Troell et al. 2006). After nearly 40 years of research on formulated and natural feeds, feeding of cultivated abalone is always a challenge (Fleming et al. 1996; Kirkendale et al. 2010; Mulvaney et al. 2013). This is the case in Europe where the annual production of the European

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abalone, *Haliotis tuberculata* Linnaeus 1758, remains anecdotal (around 10 t for the last 3 years—FAO 2014), nutrition being among the main technical problems encountered by abalone growers. Macroalgae, the natural feed of abalone, which are known to deliver suitable growth rates and condition in abalone (e.g., Bansemer et al. 2014; Kirkendale et al. 2010), could contribute to a more sustainable aquaculture than formulated feed (e.g., Mulvaney et al. 2013). However, macroalgae harvesting is costly and quantitatively limited (Viera et al. 2014; Troell et al. 2006). The use of an introduced prolific macroalgae available most of the year in high quantities could be a cost-effective solution for the development of abalone aquaculture. This would also help with product diversification in some countries where shellfish industry is largely dominated by oyster production and is facing severe financial difficulties due to mass mortalities (e.g., in France—Petton et al. 2013; Segarra et al. 2010).

Grateloupia turuturu Yamada 1941 is an invasive red alga, native from Japan, which has shown considerable expansion along the Atlantic coasts of Europe and North America, in the Mediterranean Sea, as well as in Australian and New Zealand waters (Lafontaine et al. 2011; Janiak and Whitlatch 2012). This species constitutes a resource that is not yet exploited. A recent study has shown that this macroalga was rich in total proteins and had a low total lipids content, respectively 23.0 and 2.6 % dry weight (Denis et al. 2010), comparable to those of *Palmaria palmata* Linnaeus 1805. *Palmaria palmata* allows a higher growth rate of the European abalone *H. tuberculata* when compared to other macroalgae or artificial feeds (Basuyaux 1997; Mai et al. 1995b; Mercer et al. 1993). The biochemical composition of *G. turuturu* seems to match the food requirements of the European abalone which, in dry weight, are below 5 % lipids (Mai et al. 1995a), between 24 and 34.5 % proteins (Mai et al. 1995b), combined with a high level of carbohydrates from 40 to 60 % (Fleming and Hone 1996; Thongrod et al. 2003). Furthermore, its biochemical composition appears to be seasonally more stable than in *P. palmata* (Denis et al. 2010). Mulvaney et al. (2013) showed that *G. turuturu* provided good growth rates of juvenile abalone in *Haliotis rubra* Leach 1814 and *Haliotis laevigata* Donovan 1808.

Food preferences differ between abalone species and are linked to the available food in their natural habitats (Dunstan et al. 1996). Numerous studies on different abalone species have compared survival and growth rates obtained with various macroalgae, mainly in the genera *Laminaria*, *Ulva*, *Gracilaria*, *Sargassum*, *Ecklonia*, and *Palmaria* (Alcantara and Noro 2006; Demetropoulos and Langdon 2004a; Mai et al. 1996; Naidoo et al. 2006; Qi et al. 2010; Shpigel et al. 1999; Taylor and Tsvetnenko 2004; Troell et al. 2006; Viera et al. 2005). Different abalone species fed with identical diets have shown variable growth rates due to differences in nutritional requirements (Taylor and Tsvetnenko 2004). Mai et al. (1995a) also showed that responses of same species to different diets vary according to the physical properties and chemical composition of diets. This is particularly important given that chemical composition of algae varies with species, geographic area, season, or environmental conditions (Ito and Hori 1989).

The aim of this study was to estimate the suitability of *G. turuturu* as food for the abalone *H. tuberculata*. Consumption, growth, and mortality of *H. tuberculata* fed with *P. palmata* and *G. turuturu* were compared.

Materials and methods

Experimental culture conditions

The study was conducted between May 15th and October 15 2010, in a shellfish farm in Le Croisic (47°17′38″ N 2°30′33″ W), a seaside town in the northwest of France. Four 300 L polygonal tanks designed for abalone aquaculture containing PEHD (high density polyethylene) plastic cages (50 × 50 × 5 cm) were used. Aerated tanks were provided with sand-filtered and UV-treated seawater. The experiment was conducted in the dark to not disrupt abalone; light was only used during feedings and measurements. Water temperature was measured daily and varied from 13.2 to 19.0 °C during the experimental period.

Experimental animals and diets

Two hundred and seventy abalone *H. tuberculata* (≈2 years old) with an initial shell length of 42.6 ± 1.7 mm (mean ± standard deviation) and an initial body weight of 11.3 ± 1.5 g were purchased from the Labadie abalone hatchery/farm in Bouin (France). In the hatchery, abalone was fed with a mixture of fresh macroalgae (e.g., *Ulva* spp., *Laminaria* spp., *Palmaria palmata*). Thirty abalones were randomly assigned to each triplicate of three dietary treatments. They were fed one of three experimental diets consisting of the following: (a) *P. palmata*, (b) *G. turuturu*, and (c) a mixture of *P. palmaria* and *G. turuturu* with a mass ratio of 1:1. These seaweeds were harvested every 3 days at Batz-sur-mer (47°16′34.82″ N–2°29′ 36.64″ E; Atlantic Coast, France). Immediately after each algal harvest, abalone were fed freshly harvested algae ad libitum to ensure feed availability and quality and as to not limit abalone feeding.

Algal consumption and growth of abalone

Seaweeds were weighed before being distributed. To estimate algae biomass loss, due to degradation, six plastic cages containing algae without abalone were used as controls. When uneaten algae remained at the next feeding time, it was removed, weighed

Table 1 Mean biochemical composition of the two macroalgae provided to abalone throughout experiment

	G. turuturu	*P. palmata*	*P value*
Proteins (% dw)	22.7 ± 2.7	16.2 ± 1.7	$P < 0.001$
Carbohydrates (% dw)	51.3 ± 4.1	63.4 ± 7.4	$P < 0.001$
Lipids (% dw)	2.6 ± 0.2	2.0 ± 0.3	$P < 0.01$
Ash (% dw)	24.3 ± 0.8	27.2 ± 0.4	ns

Data are expressed as mean ± SD ($n = 12$). *P* value obtained after a *t* test
ns not significant, *dw* dry weight

again, and the difference enabled estimation of the amount that had been ingested by abalone. For the mixed diet, each species was weighed separately. During the experiment, degradation of *G. turuturu* was observed (cf. Results); therefore, only the consumption of *P. palmata* could be estimated.

Shell length (L) and body weight (W) of each abalone were measured twice a month. The following abalone growth variables were calculated for all treatments:

- ΔL (μm day^{-1}) = $(L_t - L_i)$/day
- SGR_W (% day^{-1}) = 100 [(ln W_t − ln W_i) /day]
- SGR_L (% day^{-1}) = 100 [(ln L_t − ln L_i)/day]
- Weight gain (%) = 100 [(W_t − W_i/W_i]
- Survival (%) = 100 (n_t/n_i)

where ΔL is the increase in length, L_i is the initial shell length (mm), L_t is the shell length (mm) at time *t*, (day) is duration of experiment in days, n_i and n_t are respectively initial and final numbers of abalone, *SGR* is the specific growth rate, W_i is the initial body weight (g), and W_t is the body weight (g) at time *t*.

Biochemical analysis

Once a month, certain algae thalli were set aside, cleaned of epibionts, rinsed successively with seawater, tap water, then distilled water and frozen at −20 °C. At the end of the experiment, five abalone from each replicate of the three dietary treatments were also frozen at −20 °C. All seaweed and abalone samples (after shell removal) were freeze-dried and ground into a powder with liquid nitrogen before being homogenized with phosphate buffer (20 mM; pH 7.1). The suspensions were then centrifuged (25,000×*g*, 20 min, 4 °C). The resulting supernatants were the aqueous crude extract (CE) containing all the water-soluble compounds. Each sample was analyzed in triplicate for the biochemical analysis. Water-soluble proteins in the CE were analyzed following the method of Bradford (1976), and total protein content was estimated by multiplying the nitrogen content quantified by the Kjeldhal method, by a factor of 6.25 (Miller and Miller 1948). Total lipids were extracted with a mixture of dichloromethane:methanol (2:1, v:v) and were determined by the gravimetric method as described by Bligh and Dyer (1959). Ash content was determined by incineration of 1 g of each sample at 450 °C for 24 h. Total water-soluble carbohydrates in the CE were analyzed using the modified colorimetric phenol-sulphuric acid method (White et al. 1986).

Statistical analyses

Statistical analyses were performed using SigmaStat software (3.1). Biochemical compositions of algae and abalone, biometrics, and growth parameters were compared with *t* test or one-way ANOVAs. When ANOVA showed a statistical difference, a Holm-Sidak procedure was used for pairwise comparisons. For each data sample, means and standard deviations are given.

Results

Algal biochemical composition

Grateloupia turuturu and *P. palmata* showed significant differences ($p < 0.001$) in their biochemical composition except for ash (Table 1). Protein content was significantly higher in

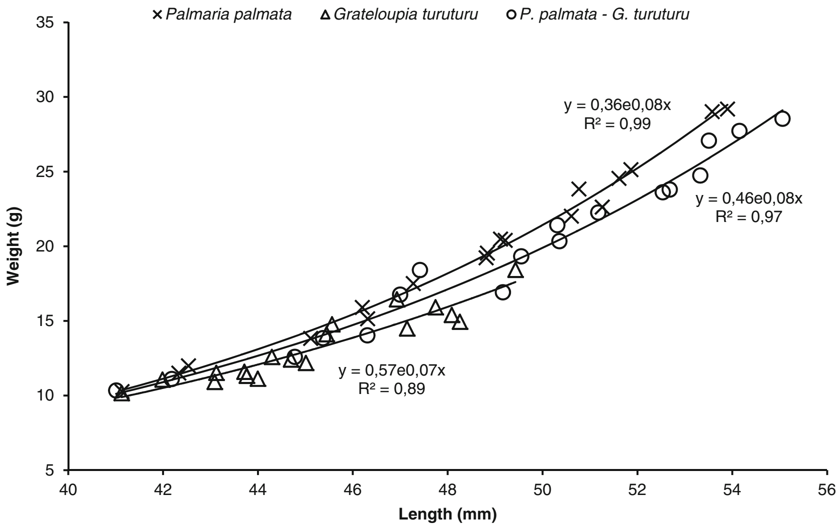
Table 2 Biometrics of the European abalone (*H. tuberculata*) fed with the three macroalgae diets for 5 months

Diet fed to abalone			
	G. turuturu	*P. palmata*	*G. turuturu*—*P. palmata* (1:1)
Initial biomass (g)	353.3 ± 61.2^{a}	336.8 ± 26.9^{a}	356.1 ± 67.6^{a}
Final biomass (g)	402.6 ± 49.8^{a}	658.0 ± 96.2^{b}	715.3 ± 66.2^{b}
Initial length (mm)	42.9 ± 2.3^{a}	42.0 ± 0.8^{a}	42.9 ± 2.3^{a}
Final length (mm)	47.3 ± 2.0^{a}	52.7 ± 1.7^{b}	54.2 ± 0.6^{b}
Initial weight (g)	12.7 ± 2.2^{a}	10.3 ± 0.1^{a}	11.8 ± 1.8^{a}
Final weight (g)	16.5 ± 1.8^{a}	27.3 ± 3.0^{b}	27.8 ± 0.7^{b}

Data are expressed as mean ± SD ($n = 3$ for biomass and $n = 90$ for length and weight). Statistical results were analyzed after a one-way ANOVA followed by a Holm-Sidak test

^{a,b} Values in the same row with different letters are significantly different ($P < 0.05$)

Fig. 1 Abalone weight/length relationship depending on the dietary treatment



G. turuturu (22.7 ± 2.7 % dw) than in *P. palmata* (Table 1). However, *P. palmata* showed the highest carbohydrate content with 63.4 ± 7.4 % dw. Both, *G. turuturu* and *P. palmata*, were low in lipid contents, 2.6 and 2.0 % dw, respectively.

Consumption, survival, and growth of abalone

In abalone aquaculture tanks, *G. turuturu* deteriorated rapidly, resulting in very small pieces which made the calculation of algae consumption difficult. No conservation problem was encountered with *P. palmata*. Daily average intake of *P. palmata* per abalone was 17.6 ± 2.6 g day^{-1} during the entire feeding trial period.

During the entire experiment, abalone mortality was not observed; the survival rate was 100 % in all treatment groups. Initial biomass of all abalone triplicates was similar, whereas final biomass was significantly higher with *P. palmata* and the mixed diet (Table 2). The initial and final biomass in abalone fed *G. turuturu* showed a difference of only 49.25 g, whereas abalone fed *P. palmata* showed a difference of 359.17 g. Biometrical and growth parameters in *H. tuberculata* were higher with the *P. palmata* diet than with *G. turuturu* (Fig. 1 and Table 3). *Palmaria palmata* and the mixed diet induced a significantly higher SGR in abalone compared to animals fed with *G. turuturu* (Fig. 2). No significant differences were observed in SGR for length and weight between abalone fed with the mixed and those fed with *P. palmata* (Fig. 2).

Biochemical composition of abalone

Abalone fed with *G. turuturu* showed the lowest protein, carbohydrate, and lipid content with 0.18 ± 0.0, 0.7 ± 0.1, and 27.6 ± 1.8 % dw, respectively (Table 4). However, these abalones showed the highest ash content with 11.8 ± 1.5 % dw. The mixed diet and the *P. palmata* diet were not significantly different from each other but were significantly different to the *G. turuturu* diet (Table 4).

Discussion

The biochemical composition of the two red algae *G. turuturu* and *P. palmata* harvested on the French Atlantic coast was within the range of values reported for other species of seaweeds used as feed for abalone (Mercer et al. 1993; Shpigel

Table 3 Growth and survival of juvenile European abalone (*H. tuberculata*) fed with the three macroalgae diets for 5 months

Diet fed to abalone			
	G. turuturu	*P. palmata*	*G. turuturu*—*P. palmata* (1:1)
DL (μm day^{-1})	0.01 ± 0.01^{a}	0.08 ± 0.01^{b}	0.06 ± 0.02^{b}
SGRW (% day^{-1})	0.07 ± 0.02^{a}	0.64 ± 0.03^{b}	0.60 ± 0.10^{b}
SGRL (% day^{-1})	0.21 ± 0.01^{a}	0.62 ± 0.03^{b}	0.62 ± 0.11^{b}
Weight gain (%)	8.3 ± 2.3^{a}	107.8 ± 7.2^{b}	97.5 ± 21.6^{b}
Survival (%)	100	100	100

Data are expressed as mean ± SD ($n = 3$). Statistical results were analyzed after a one-way ANOVA followed by a Holm-Sidak test

SGR shell growth rate, ΔL increase in length

^{a,b} Values in the same row with different letters are significantly different ($P < 0.05$)

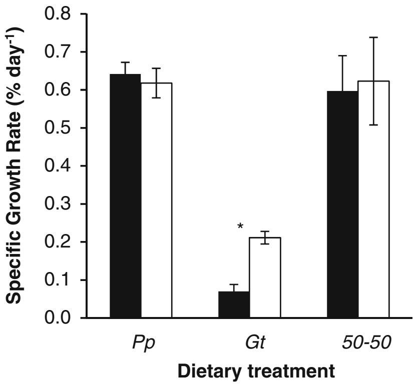


Fig. 2 Specific growth rate (% day^{-1}), for length (*white bars*), and weight (*black bars*), in abalone *H. tuberculata* fed with three dietary treatments over 5 months ($n = 90$). Data with *asterisk* are significantly different from the others (one-way ANOVA, *P* value <0.05)

et al. 1999). Mercer et al. (1993) showed that balanced levels of proteins (>15 %), lipids (3–5 %), and carbohydrates (20–30 %) in macroalgae were essential for optimal growth performance of abalone species. Protein content of *G. turuturu* and *P. palmata* (around 20 %) was within the range reported previously in red seaweeds (Fleurence 1999; Galland-Irmouli et al. 1999; Morgan et al. 1980) and for the protein requirements of *H. tuberculata* which have been estimated between 25 and 35 % (Mai et al. 1995b; Mercer et al. 1993). For *P. palmata*, the total carbohydrates were comparable to those found in the literature, which were from 38 to 45 % dw (Morgan et al. 1980; Morgan and Simpson 1981; Rosen et al. 2000) and were higher than those found in *G. turuturu* (51.3 %). To our knowledge, our paper reports the total carbohydrate content of *G. turuturu* for the first time. The carbohydrate contents of *P. palmata* is higher than the requirements for abalone (20–30 %—Mai et al. 1995b), and *P. palmata* exhibited the best growth of *H. tuberculata*. As previously reported for other species of red seaweeds (Mabeau and Fleurence 1993), lipid contents were low, 2.6 ± 0.2 % dw for *G. turuturu* and 2.0 ± 0.2 % dw for *P. palmata*. The low lipid contents are in agreement with the requirement of abalone (Mercer et al. 1993), where high levels of dietary lipids negatively affect abalone growth (Thongrod et al. 2003). As all the diets used in this study fulfilled requirements of abalone, the different growth performances could not be attributed to the biochemical composition of the algae. In particular, the *P. palmata* diet contained a lower protein content (16.1 %) than the *G. turuturu* diet (22.7 %), suggesting that protein levels in the other diets may not be a limiting factor for abalone growth.

Although survival percentages were not affected by any of the treatments assayed, the abalone fed with *G. turuturu* showed the lowest growth performance compared to those fed with *P. palmata* or the mixed diet. Previous growth trials already demonstrated that *P. palmata* was the best algal diet for *H. tuberculata* (Mai et al. 1996; Mercer et al. 1993), and the lower growth reported in our experiments with *G. turuturu* were certainly due to a lower feed intake due to algal breakup and possible difficulty in feeding. Indeed, consumption rate in abalone could be influenced by multiple factors other than the nutritional quality of algae. Secondary metabolites are factors modifying seaweed susceptibility to herbivores and can make algae unpalatable to abalone (Yates and Peckol 1993). The texture of algae also influences the food intake (Shepherd and Steinberg 1992); in the wild, abalone thus prefer soft texture seaweeds because their radula has a limited ability to exert force against the substrate (Steneck and Watling 1982). This explanation should be rejected as *G. turuturu* is the softer of the two algae used in the present study (D'Archino et al. 2007; Rosen et al. 2000). The preference for *P. palmata* could be explained by the rapid decomposition of *G. turuturu* in the culture tank making it unattractive to the animals.

Abalone fed with *G. turuturu* showed the lowest lipid and carbohydrate contents which can be explained by the fact that most of the energy absorbed sustains metabolic needs, and any deficit is drawn from the abalone's nutrient reserves. By the end of the experimental period, abalone fed on *P. palmaria* and the mixed diet had gained an average weight of 17 and 16 g and an average length of 10.7 and 11.3 mm, respectively. Whereas animals fed on *G. turuturu* had grown to an average of 3.8 and 4.4 mm under the same culture conditions. Specific growth rates of the weight were lower, 0.64 ± 0.03 % for abalone fed with *P. palmata* and 0.60 ± 0.10 % for abalone fed with the mixed diet, than those reported by Mai et al. (1996) of

Table 4 Biochemical composition of abalone fed with three different diets throughout experiment

	Abalone *G. turuturu*	Abalone *P. palmata*	Abalone *G. turuturu—P. palmata* (1:1)
Water-soluble proteins (% dw)	0.18 ± 0.00^{a}	0.21 ± 0.00^{b}	0.20 ± 0.00^{b}
Water-soluble carbohydrates (% dw)	0.7 ± 0.1^{a}	2.7 ± 0.2^{b}	2.4 ± 0.2^{b}
Lipids (% dw)	27.6 ± 1.8^{a}	36.9 ± 11.3^{b}	42.4 ± 5.7^{b}
Ash (% dw)	11.8 ± 1.5^{a}	8.3 ± 1.4^{b}	8.0 ± 0.5^{b}

Data are expressed as mean ± SD ($n = 3$). *P* value obtained after a *t* test. Statistical results were analyzed after a one-way ANOVA followed by a Holm-Sidak test

ns not significant, *dw* dry weight

^{a,b} Values in the same row with different letters are significantly different ($P < 0.05$)

1.0–1.3 % for *H. tuberculata* fed with five species of macroalgae (*P. palmata*, *Alaria esculenta*, *Ulva lactuca*, *Laminaria digitata* and *Laminaria saccharina*). Nevertheless, the SGR of the length are among the highest compared to those obtained in 130 diets examined from the peer-reviewed literature (Kirkendale et al. 2010). When comparing the weight gain, a difference of 90–100 % was found between the *G. turuturu* diet and the mixed and *P. palmata* diet. However, when the animals were fed with *G. turuturu* in a mixed diet, they exhibited higher lipid content, although not significantly, than the ones fed only with *P. palmate.* This trend suggests that *G. turuturu* provided complementary nutrients to those found in *P. palmata*.

At present, very little information has been reported on the suitability of *G. turuturu* as a promoter of growth and survival in abalone species. Previous studies have shown that growth was improved when abalone were fed with a combination of different algae compared with those fed a monospecific or formulated feed (Mulvaney et al. 2013; Qi et al. 2010; Viera et al. 2005). In the present study, the mixed diet sustained a slightly lower growth rate than with *P. palmata* alone. But at the same time and as shown above, abalone fed with the mixed diet presented a higher lipid content, suggesting a qualitative improvement of the diet in mixing these two red algae. Therefore, *G. turuturu* cannot be used alone in monospecific diets for the abalone *H. tuberculata*, in contrast to the study by Mulvaney et al. (2013), but could be used in a mixed diet as a dietary supplement. Moreover, various studies have shown that numerous molecules and/or extracts of *G. turuturu* present a biological activity such as antibacterial (Pang et al. 2006) or antiviral ones (Hudson et al. 1998). More specifically, *G. turuturu* has shown an antibacterial activity against the abalone pathogen *Vibrio harveyi* (García-Bueno et al. 2014).

To benefit from its biological activities and as a complementary source of lipids in abalone aquaculture, further investigations are required to test the use of *G. turuturu* (1) as dried fronds, (2) as a component of a formulated food that must be further developed, or (3) as fresh fronds in an integrated coculture system to allow this source of algae to be changed every day. Considering the prolific nature and the wide distribution of *G. turuturu*, this could improve the development of the commercial European abalone industry.

Acknowledgments All authors participated in the collection and interpretation of results. Mireille Amat, who is also a translator, corrected the English of the manuscript. The authors thank Katarzyna Lawreniuk for her technical assistance during feeding experiments. This project was funded by the Fundació "Obra Social la Caixa" through a doctoral scholarship to Nuria García Bueno and by the Syndicat Mixte pour le Développement de l'Aquaculture et de la Pêche (SMIDAP) de la Région des Pays de la Loire.

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