

Effects of wild and farm-grown macroalgae on the growth of juvenile South African abalone *Haliotis midae* Linnaeus

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Abstract

The effect of various macroalgal diets on the growth of grow-out (> 20 mm shell length) South African abalone Haliotis midae was investigated on a commercial abalone farm. The experiment consisted of four treatments: fresh kelp blades (Ecklonia maxima [Osbeck] Papenfuss) (~ 10 % protein); farmed, protein-enriched Ulva lactuca Linnaeus (~26 % protein) grown in aquaculture effluent; wild U. *lactuca* (\sim 20 % protein); and a combination (mixed) diet of kelp blades + farmed U. *lactuca*. Abalone grew best on the combination diet (0.423 \pm 0.02% weight day⁻¹ SGR [specific growth rate]; $59.593 \pm 0.02 \,\mu m \, day^{-1}$ DISL [daily increment in shell length]; 1.093 final CF [condition factor]) followed by the kelp only diet (0.367 ± 0.02 % weight day⁻¹ SGR; 53.148 ± 0.02 µm day⁻¹ DISL; 1.047 final CF), then the farmed, protein-enriched *U. lactuca* only diet (0.290 \pm 0.02% weight day⁻¹ SGR; 42.988 \pm 0.03 μ m day⁻¹ DISL; 1.013 final CF) that in turn outperformed the wild U. *lactuca* only diet (-0.079 \pm 0.01 % weight day⁻¹ SGR; 3.745 \pm 0.02 μ m day⁻¹ DISL; 0.812 final CF). The results suggest that protein alone could not have accounted for the differences produced by the varieties of *U. lactuca* and that the gross energy content is probably important.

Key words: abalone, *Ecklonia maxima*, farm-grown, growth, *Haliotis midae*, mixed diet, protein content, *Ulva lactuca*

Introduction

Kelp is the major macroalgal feed for farmed abalone in South Africa (Troell et al. 2006). With the expansion of the abalone industry in recent years, the demand for fresh kelp has steadily grown (Anderson et al. 2006, Rothman et al. 2006, Francis et al. 2008a). In 2003, more than 7000 tons of fresh kelp fronds were harvested (Robertson-Andersson et al. 2008). By 2009, however, this demand dropped to about 5500 tons (Marine and Coastal Management, South African Department of Agriculture, Forestry and Fisheries, unpublished data), this largely due to the

incorporation of formulated feeds into abalone diets over the past few years (P. Britz, Department of Ichthyology and Fisheries Science, Rhodes University, *pers. comm.*). Despite this reduction in kelp for feed, many kelp beds were still approaching limits of sustainable harvesting, particularly in kelp concession areas with high numbers of abalone farms (Anderson et al. 2003, 2006, Rothman et al. 2006, Troell et al. 2006).

There are other drawbacks to the use of kelp as a fresh feed. While kelp is cheaper than formulated feeds on a price per ton basis, its future availability as the primary abalone fresh feed is uncertain (Troell et al. 2006). Kelp harvesting is also dependent on sea conditions; this complicates farm management and increases the risk of such ventures (Dixon 1992, Britz 1995). The use of kelp was considered by some farmers to be costly and labour intensive when the expenses of harvesting, transport and storage were taken in account (W. Barnes, Abalone Farmers Association of South Africa [AFASA], *pers. comm.*). Other, less desirable properties of kelp include its low protein (5 - 15 %) and high water (68 - 83 %) content (Hahn 1989), and its unbalanced amino acid profile (Britz 1996a, Erasmus et al. 1997, Rosen et al. 2000, Troell et al. 2006). As an alternative to kelp, some South African farms already grow certain species of macroalgae for use as abalone feed in their aquaculture systems.

Farm-grown macroalgae have been shown to have comparatively higher protein contents than their wild counterparts (Neori and Shpigel 1999, Shpigel et al. 1999, Neori et al. 2003, 2004, Robertson-Andersson et al. 2008). This is because macroalgae remove dissolved nitrogen from aquaculture effluent resulting in a considerable increase in the alga's phosphorous and protein content (Robertson-Andersson et al. 2008). Of all macroalgae grown in aquaculture environments, *Ulva* spp. have been shown to be the best candidates for integrated aquaculture practices largely because they are fast-growing, have a high nitrogen concentration, are generally resistant to epiphytes, and have simple life cycles that are easily controlled (Shpigel et al. 1996, Neori and Shpigel 1999, Shpigel et al. 1999, Neori et al. 2003, 2004).

The cultivation of *Ulva* spp. on South African abalone farms is increasing, with two such farms depending almost entirely on farm-grown macroalgae to meet the bulk of their feed requirements (Bolton 2006, Troell et al. 2006, Robertson-Andersson et al. 2008). The latter farms culture *Ulva lactuca* Linnaeus alongside *Haliotis midae* in an integrated mariculture system where the algae serve not only as a biological filter, but also as feed for the abalone (Bolton 2006, Troell et al. 2006, Robertson-Andersson et al. 2008, Bolton et al. 2009). While data on *H. midae* feed fortification with wild macroalgae exist (e.g. Stepto and Cook1993, Naidoo et al. 2006, Dlaza et al. 2008), information on how *H. midae* may benefit from farm-grown, protein-enriched macroalgae is lacking. The objective of this study was therefore to compare the growth of juvenile grow-out *H. midae* on both farm-grown and wild *U. lactuca*, and study the effects of wild macroalgal feed fortification with the protein-enriched, farm-grown *U. lactuca*.

Materials and methods

Experimental system

The research was conducted at the Jacobsbaai Sea Products (JSP - 17° 53' 12.5" E, 32° 58' 2.5" S, Western Cape, South Africa) commercial abalone farm. Moderately aerated seawater flowing at 700 \pm 100 Lh⁻¹ was supplied at 15.5 \pm 2.5 °C in a flowthrough concrete holding tank (L x B x H; 5500 x 1300 x 550mm) with a total water volume of 4500 L. Table 1 details water quality variables measured. Abalone were grown in polyethylene culture baskets (L x B x H; 1037 x 517 x 540mm) subdivided with four vertically-orientated ABS (acrylonitrile butadiene styrene) plates (L x B x H; 760 x 4 x 310 mm) to increase the surface area to approximately 1.8 m² in each basket available for attachment. A horizontal polyethylene feeder plate (L x B x H; 600 x 4 x 380mm) was positioned centrally above the vertical plates. This design provided optimum access to feed with no visible feed wastage. Replicate (N = 4)baskets were arranged in a single holding tank according to a Latin square model (Zar 1984). In addition, the flow direction in the tank was alternated weekly to further compensate for end effects. End effects refer to the potential negative impacts (e.g. reduced water flow-rate, accumulation of faeces and silt, etc) that may arise from a unidirectional flow. Both the flow-through tank and culture baskets were cleaned every two weeks.

Experimental animals

Hatchery-reared grow-out (abalone with a shell length > 20mm) abalone (supplied by the JSP commercial abalone farm), approximately 22 months old from a single brood stock pool, were subdivided into four diet treatments of approximately 2.5 kg (approximately 250 individuals) abalone per basket per diet treatment totaling 4000 animals used for the study. The stocking density in the tank was approximately 10 kg m⁻³. Initial shell length and body weight were 36.04 ± 0.16 mm and 8.69 ± 0.12 g respectively. After four months, stocking density of each basket was reduced by random removal of animals to 150 individuals to reduce feed competition.

Treatments

Four dietary treatments were tested, each with four replicate baskets:

- 1. Fresh kelp (*Ecklonia maxima* [Osbeck] Papenfuss) blades. Kelp was chosen as a seaweed control because it is this seaweed that is most commonly used as fresh abalone feed in South Africa.
- 2. Wild *U. lactuca* collected from the adjacent bay.
- 3. Farmed *U. lactuca* obtained from the JSP farm from a cultured stock grown in both abalone and fish (turbot, *Scophthalmus maximus* Linnaeus) effluent.
- 4. A mixed diet of fresh kelp blades and farmed *U. lactuca* supplied in equal quantities.

All feeds were spread evenly among the vertically-orientated plates and supplied daily *ad libitum* according to standard farm feeding practices with the total weight of

macroalgae not exceeding 150 g per basket per day. At each feeding, any leftover macroalgae were removed and fresh macroalgae added. Table 2 details the approximate nutritional composition of the diets.

Sampling and data collection

Representative animals were randomly selected for measurement from each basket at monthly intervals during the eight-month experiment (n = 30 at 0-2 months, n = 40 at 3-7 months and n = 50 at 8 months to compensate for increasing differential growth). Before measuring, abalone were blotted dry to remove excess water. Body weight was recorded to the nearest 0.01 g using an electronic balance, and shell length along the longest axis of the shell was measured to the nearest 0.01 mm with electronic Vernier calipers. Daily increment in shell length (DISL, μ m day⁻¹) was calculated using the formula of Zhu et al. (2002): DISL = [(SL_t - SL_i)/t] x 1000 where SL_t = final mean shell length (mm), SL_i = initial mean shell length (mm), and t = 1 the feeding period in days.

Specific growth rate (SGR in % body weight day⁻¹) was calculated using the formula of Britz (1996b): SGR = ([In(W_f)-In(W_i)]/t) x 100 where In(W_f) = the natural log of the final mean weight, In(W_i) = the natural log of the initial mean weight, and t = the feeding period in days. The condition factor (CF), which is an index developed to account for the relationship between the weight of the abalone per unit shell length, was calculated using the formula of Britz (1996b): CF = [BW / SL ^{2.99}] x 5575 where BW = the body weight (g) and SL = the shell length (mm).

Feed conversion ratio (FCR) was calculated using the formula of Britz (1996b): FCR = R/G where R = ration, defined as the blotted wet feed intake (g), and G = growth, defined as the blotted wet weight (g) gained. To calculate FCR, the weight of all algae placed into the baskets was recorded and any uneaten algae that was removed from the baskets was recorded. Kelp was allowed to drip-dry in empty culture baskets for no more than 5 min, while all *U. lactuca* samples were simply blotted dry.

Statistical analysis

Treatment average values for each of the four replicate baskets were analysed by means of a one-way analysis of variance (ANOVA), which assumes equal variances and normality of residuals. To test for this, a Levene's test for homogeneity of variances and the Shapiro-Wilk test for normality were performed for data from each month. All underlying assumptions were met. Pair-wise comparisons between treatments were analysed using Tukey's test for multiple comparison of means. Differences amongst treatments were considered statistically significant at p < 0.05. Unless otherwise stated, data are expressed as means \pm SE.

Results

Abalone grew fastest (SGR = 0.423 ± 0.02 % weight day⁻¹; DISL = 59.593 ± 0.02 μ m day⁻¹) on a combination diet of kelp and farm-grown, protein-enriched *U. lactuca* (weight ANOVA: $F_{(3,12)}$ = 387.29; p < 0.001) (length ANOVA: $F_{(3,12)}$ = 542.23; p < 0.001) (Figures 1 and 2, Table 3). Abalone fed farm-grown *Ulva lactuca* produced significantly better growth (SGR = 0.290 ± 0.02 % weight day⁻¹; DISL = 42.988 ± 0.03 μ m day⁻¹) than those fed wild *U. lactuca* (SGR = -0.079 ± 0.01 % weight day⁻¹; DISL = 3.745 ± 0.02 μ m day⁻¹) (weight T-test: t = 66.32; p < 0.001) (length T-test: t = 205.61; p < 0.001. Despite the improved protein content, farm-grown *U. lactuca* did not result in improved abalone growth compared with kelp as a single feed diet (SGR = 0.367 ± 0.02 % weight day⁻¹; DISL = 53.148 ± 0.02 μ m day⁻¹, p < 0.001) (weight T-test: t = 22.43; p < 0.001) (length T-test: t = 10.63; p = 0.002), which resulted in superior growth.

While all animals had CF values >1 at the start of the experiment, only abalone cultured on a mixed diet of kelp and farm-grown *U. lactuca* improved their CF values, producing comparatively 'fatter' individuals (Table 2). The remaining diets resulted in a reduction of CF values (Table 3) suggesting that abalone grown on these feeds gained more length relative to weight. This trend was particularly strong in the wild *U. lactuca* that showed a negative specific growth rate. CF ranking for all diets followed those of the SGR and DISL. Similarly as before, although farm-grown *U. lactuca* had higher protein contents than kelp, FCR for this alga was higher and thus feed conversion efficiency (FCE) lower, i.e. substantially more protein-enriched *U. lactuca* was required to produce comparable growth.

Discussion

While many studies (Owen et al. 1984, Day and Fleming 1992, Fleming 1995a, Simpson and Cook 1998, Naidoo et al. 2006, Dlaza et al. 2008) have shown the benefits of variability in the diets (e.g. mixed and rotational diets) of abalone, no studies exist to show the benefit of feeding farm-grown macroalgae over that of their wild counterparts. This study is the first to show that farm-grown *U. lactuca*, whether fed as a single diet or as part of a mixed diet, produced comparatively good growth in farmed *H. midae*. This was likely due to the increased protein content of the macroalga as they were farmed under aquaculture conditions.

Farm-grown, protein-enriched *U. lactuca* had produced good growth in abalone species such as *H. tuberculata* Linnaeus (Neori et al. 1998, Shpigel et al. 1999) and *H. discus hannai* Ino (Shpigel and Neori 1996, Neori and Shpigel 1999, Shpigel et al. 1999). Wild macroalgae on the other hand, are known to have a comparatively low protein content ranging from 4 - 20 % (Mercer et al. 1993, Fleming et al. 1996, Fleurence et al. 1999, Neori and Shpigel 1999, Shpigel et al. 1999, Tahil and Juinio-Menez 1999, Rosen et al. 2000, Bautista-Teruel et al. 2002, Demetropoulos and Langdon 2004a, 2004b, Dlaza et al. 2008, Robertson-Andersson et al. 2008) that result in relatively slow growth in abalone (Fleming 1995b, Fleming et al. 1996, Neori and Shpigel 1999, Shpigel et al. 1999, Rosen et al. 2000, Kruatrachue et al. 2004, Lee

2004, Neori et al. 2004). Previous growth studies on *H. midae* (Cook and Claydon 1991, Owen et al. 1984, Stepto and Cook 1993, Simpson and Cook 1998) that used macroalgae as feed, have used only wild, relatively low-protein macroalgae that whether fed as single-species, or in combination as mixed diets, have never been able to produce growth comparable to that obtained with feeds relatively high in crude protein (Viana et al. 1993, Fleming 1995a,b, Fleming et al. 1996, Bautista-Teruel and Millamena 1999, Bautista-Teruel et al. 2002, Kruatachue et al. 2004, Lee 2004). To overcome this deficiency, Shpigel et al. (1999) suggested that it would be necessary to feed protein-enriched *U. lactuca* together with wild macroalgae as part of a mixed diet in order to achieve commercially acceptable growth rates. This was suggested because mixed diets essentially compensate for nutrients and attractants that are generally lacking in single-species diets.

Research into abalone protein requirements gave optimal protein levels of 36 % for H. midae (Sales et al. 2003a, 2003b). Although studying larger abalone of an initial size of around 50 mm shell length, Green et al. (2011) showed that the protein content of formulated feed for *H. midae* can be dropped as low as 18 % given that the digestible energy of the feed is not lower than 13.5 MJ kg⁻¹. The digestible energy content of food is that portion of the energy that is available to the animal after taking into account the energy costs associated with excretion i.e. that portion of the feed gross energy available to the body after the energy costs from excretion have been removed (Fleming 1995b, Britz and Hecht 1997). In H. midae, energy loss in the form of excretion has been recorded to range from being negligible (accounting for < 1 % of consumption; Barkai and Griffiths 1988), to a maximum of 15 % (Green et al. 2011; determined from Table 1). Thus, the digestible energy from feed available to H. *midae* can be assumed to be approximately equal to, or very close to the gross energy content. Bearing this variability in mind, and since Green et al. (2011) did not test diets with energy levels between 13.5 and 11.6 MJ kg-1, we would argue that the farmed *U. lactuca* probably met the minimum energy requirements for optimal *H.* midae growth.

The protein contents of wild and farmed *U. lactuca* used in this study both meet the minimum percentage requirement proposed by Green et al. (2011), suggesting that protein alone could not have accounted for the differences observed in the growth rates experienced from these diets. To account for these very different growth rates, we propose two, but not necessarily mutually exclusive, scenarios. Firstly, both the protein and energy contents of the farmed *U. lactuca* were within the suggested "optimal range" and we suggest that the increased energy content of the farmed *U. lactuca* probably accounted for the marked differences observed between the wild and farmed varieties of the alga. Secondly, the fact that the abalone fed wild *U. lactuca* were unsuitable as a feed source. This being the case, any number of factors, e.g., amino acid profile, presence/absence of specific bacterial coatings, lack of attractants, toughness of the thallus, etc., may have contributed to the poor growth rates of abalone fed the wild *U. lactuca*.

While the results of this study are consistent with previous studies, there is one exception. Of the single-species diets tested, fresh kelp out-performed even the protein-enriched *U. lactuca*. This was surprising as both the protein and gross energy contents for kelp were significantly less than that recorded for the farm-grown *U. lactuca*. Furthermore, the kelp-only feed produced a FCR considerably lower (and thus higher feed conversion efficiency) than the farm-grown *U. lactuca* i.e. substantially more farm-grown *U. lactuca* was required to produce comparable growth. Despite this better performance, kelp in this study performed considerably poorer than that achieved in the South African abalone industry (Hattingh 2006) where FCR values ranging from 9.20 - 15.40 have been reported. Equally surprising is that the wild *U. lactuca* and kelp performed so differently, particularly as energy contents were very similar and protein content was higher in the wild *U. lactuca*. Theoretically, both wild and farmed *U. lactuca* should have performed better than kelp. The better performance of fresh kelp as a single feed diet might be explained by one of three possible reasons, or a combination thereof.

- 1. The diet prior to the start of the experiment was fresh kelp alone. This may explain the comparatively poor performance of the farmed *U. lactuca* as abalone in this size range often become habituated to kelp and are slow to change (P. Britz, *pers. comm.*).
- 2. The contribution of bacteria associated with fresh kelp may have added to the digestibility and assimilation of nutrients in the kelp (P. Britz in Troell et al. 2006: 274).
- 3. For some time, only protein contents and amino acid profiles of feeds were considered limiting factors (Britz 1996a, b, Fleming et al. 1996b, Britz and Hecht 1997, Troell et al. 2006). Research by Green et al. (2011) showed that digestible energy is also important. It is thus possible that some other, as yet unidentified variable or combination of variables, may also account for such differences.

Ulva lactuca has long been known to be a good candidate for aquaculture. This species has a high nutrient uptake capacity (Neori et al. 1998, 2004, Neori and Shpigel 1999, Shpigel et al. 1999), a rapid growth rate (Neori et al. 1996, Shpigel et al. 1999, Robertson-Andersson et al. 2006), and a relatively simple life cycle that is easy to control (Shpigel et al. 1999, Neori et al. 2004, Robertson-Andersson et al. 2006, 2008). Seaweeds such as *U. lactuca* that are co-cultured with abalone in an integrated aquaculture system therefore add considerable value to aquaculture because not only do they serve as biological filters that reduce the filtration costs by recycling the nutrients within the system, but they are a potential high-protein feed (Shpigel et al. 1999, Neori et al. 2003, 2004, Troell et al. 2003, 2006, Robertson-Andersson et al. 2006, 2008, Nobre et al. 2010).

In conclusion, this study is the first to document the effect of farm-grown, proteinenriched *U. lactuca* on the growth of the abalone *H. midae*. *Ulva lactuca* grown in aquaculture effluent produced significantly better growth in *H. midae* than their wild counterparts. While the protein-enriched *U. lactuca* on its own was not a good substitute for kelp in this study, when fed in combination with kelp as a mixed diet, however, it produced the best growth in *H. midae*. The potential for on-farm cultivation of *U. lactuca* may become even more important as many kelp beds have approached limits of sustainable harvesting, especially in kelp concession areas with high numbers of abalone farms (Anderson et al. 2003, 2006, Rothman et al. 2006, Troell et al. 2006). Furthermore, farms that feed only formulated feeds may at some stage have to feed macroalgal diets to reduce their overall FFER¹. In light of these challenges, those farms with reduced access to abundant fresh kelp and those located substantial distances away from any kelp resource, as well as those that rely heavily on formulated feed, may find it necessary to resort to on-farm cultivation of macroalgae such as *U. lactuca*. Co-culturing *U. lactuca* alongside *H. midae* in integrated aquaculture systems clearly hold benefits for the South African abalone farming industry.

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¹Feed Fish Equivalency Ratio (FFER, also referred to as Forage Fish Efficiency Ratio) is defined by the WWF (http://www.worldwildlife.org/what/globalmarkets/aquaculture/feedfaq.html#2) as a means of estimating the amount of wild forage fish used to produce a unit of farmed fish. The calculation takes into account the yield of forage fish live weight to dry fishmeal weight, the efficiency of feed use (the feed conversion ratio or FCR) and the inclusion rates of fishmeal and fish oil in feed. In the context of the Aquaculture Dialogues ("fishmeal" debates), FFER rather than FCR is being considered as a potential indicator for individual farm performance.

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Table 1. Water quality variables of the experimental system under investigation.

Variable	Mean ± standard deviation	Range
Salinity (‰)	34 ± 0.91	29 – 40
Temperature (°C)	15.5 ± 2.50	9.8 – 19.2
pН	8.24 ± 0.22	7.1 - 9.1
Dissolved O ₂ (mg L ⁻¹)	8.51 ± 0.67	6.7 - 10.3
Flow rate (L h-1)	700 ± 100	850 - 1300

Table 2: Proximal analysis (based on dry weights) of the feeds tested in this study. Feed samples were sent to the Animal Production Laboratory, Institute for Animal Production, Department of Agriculture: Western Cape, Elsenberg for nutritional analyses. Comparative values with the same superscript within a column are not statistically different (ANOVA; $p \ge 0.05$).

Feed	Dry Matter (%)	Ash (%)	Protein (%)	Fibre (%)	Fat (%)	Carbohydrat e (%)	Gross Energy (MJ kg ⁻¹)
Kelp	88.43 ± 0.45 ^a	26.71 ± 1.96 ^a	9.73 ± 0.68^{a}	8.35 ± 0.14^{b}	0.66 ± 0.13^{b}	62.90 ± 1.15 ^b	10.94 ± 0.20 ^b
U. lactuca (farmed)	88.36 ± 0.98 ^{ab}	23.11 ± 0.71^{a}	$25.57 \pm 1.45^{\circ}$	6.31 ± 0.44^{a}	0.29 ± 0.04^{a}	51.03 ± 1.68a	13.12 ± 0.27^{c}
U. lactuca (wild)	86.17 ± 0.47 ^b	31.20 ± 0.35^{b}	$20.22 \pm 0.56^{\rm b}$	5.74 ± 0.09^{a}	0.19 ± 0.01^{a}	48.40 ± 0.39 ^a	10.55 ± 0.01 ^a

Table 3: Growth parameters of abalone fed the various diets. Specific growth rate (SGR, % body weight day⁻¹), daily increment in shell length (DISL, μ m day⁻¹), feed conversion ratio (FCR) and condition factor (CF) are provided for all feeds. Values with the same superscript within a column are not statistically different from each other (ANOVA; $p \ge 0.05$).

Diet treatment	Mean Final	Mean Final Length (mm)			FCR	Initia l CF	Final CF	Rank		
	Weight (g)		SGR	DISL				SG R	DIS L	CF

Kelp + farmed <i>U</i> lactuca	. 24.308 ± 0.28 ^a	50.521 ± 0.21 ^a	0.423 ± 0.02 ^a	59.593 ± 0.02ª	N/A	1.073 ^a	1.093ª	1	1	1
Kelp	21.194 ± 0.28 ^b	$48.955 \pm 0.23^{\rm b}$	0.367 ± 0.02 ^b	53.148 ± 0.02 ^b	47 ^a	1.072 ^a	1.047 ^b	2	2	2
U. lactuca (farmed)	17.568 ± 0.26^{c}	46.486 ± 0.22°	0.290 ± 0.02^{c}	42.988 ± 0.03°	91 ^b	1.072 ^a	1.013 ^c	3	3	3
U. lactuca (wild)	7.164 ± 0.09 ^d	36.950 ± 0.15 ^d	-0.079 ± 0.01 ^d	3.745 ± 0.02^{d}	-71 ^c	1.073 ^a	0.821 ^d	4	4	4

Figure legends

Figure 1: Mean increase in shell length (\pm standard error) of abalone fed kelp, *U. lactuca*, and a combination of the two macroalgae (ANOVA; p < 0.001); "F" refers to farm-grown, protein-enriched *U. lactuca*; "W" refers to wild *U. lactuca*.

Figure 2: Mean increase in body weight (\pm standard error) of abalone fed kelp, *U. lactuca*, and a combination of the two macroalgae (ANOVA; p < 0.001); "F" refers to farm-grown, protein-enriched *U. lactuca*; "W" refers to wild *U. lactuca*.

Figure 1.

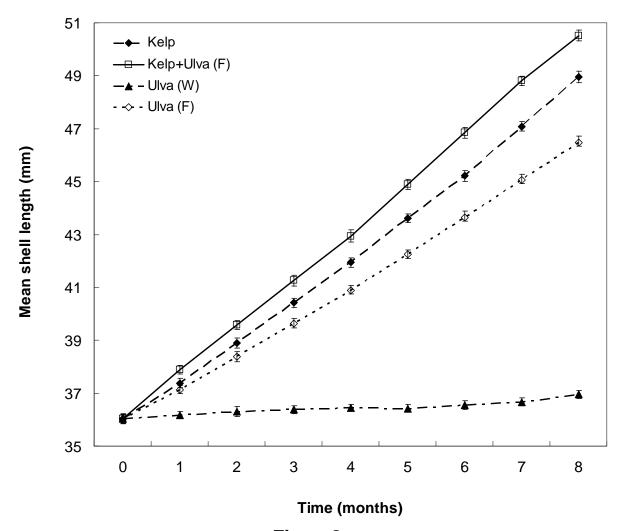


Figure 2.

