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NOTE

THE PERFORMANCE OF SPRAY-IRRIGATED *ULVA LACTUCA* (ULVOPHYCEAE, CHLOROPHYTA) AS A CROP AND AS A BIOFILTER OF FISHPOND EFFLUENTS[1]

Flower E. Msuya

Institute of Marine Sciences, University of Dar es Salaam, P.O. Box 668, Zanzibar, Tanzania

and Amir Neori[2]

Israel Oceanographic and Limnological Research, National Center for Mariculture, P.O. Box 1212, Eilat 88112, Israel

The seaweed *Ulva lactuca* L. was spray cultured by mariculture effluents in a mattress-like layer, held in air on slanted boards by plastic netting. Air-agitated seaweed suspension tanks were the reference. Growth rate, yield, and ammonia-N removal rate were 11.8% · d^{-1}, 171 g fresh weight (fwt) · m^{-2} · d^{-1}, and 5 g N · m^{-2} · d^{-1}, respectively, by the spray-cultured *U. lactuca*, and 16.9% · d^{-1}, 283 g fwt · m^{-2} · d^{-1}, and 7 g N · m^{-2} · d^{-1}, respectively, by the tank *U. lactuca*. Biomass protein content was similar in both treatments. Dissolved oxygen in the fishpond effluent water was raised by >3 mg · L^{-1} and pH by up to half a unit, upon passage through both culture systems. The data suggest that spray-irrigation culture of *U. lactuca* in this simple green-mattress-like system supplies the seaweed all it needs to grow and biofilter at rates close to those in standard air-agitated tank culture.

Key index words: **biofilter; macroalgae; seaweed culture technology; seaweed production cost; spray culture**

Abbreviations: **ANOVA, analysis of variance; DO, dissolved oxygen; IMTA, integrated multitrophic aquaculture; NCM, National Centre for Mariculture; SGR, specific growth rate; SRP, soluble reactive orthophosphate; TAN, total ammonia nitrogen; TAU, Tel Aviv University; TKN, total Kjeldahl nitrogen; ToxN, total oxidized nitrogen**

Most world mariculture is done in coastal waters (FAO 2006). Limited sites and various environmental considerations have raised interest in land-based mariculture and in effluent treatment by seaweed biofilters (Vandermeulen and Gordin 1990, Troell et al. 1999, Neori et al. 2004, FAO 2006). Seaweeds have large profitable markets as food, feed, cosmetics, fertilizers, and more (Critchley et al. 2006, Turan 2009). Seaweed biofiltration is also a key component in integrated multitrophic aquaculture (IMTA) (Chopin et al. 2001). Modern land-based intensive culture of seaweeds consists of shallow ponds, in which fronds are suspended, and where water is agitated for homogeneity and for nutrient diffusion (Ryther et al. 1975, Lüning and Pang 2003) by aeration or paddle wheels (Huguenin 1976, Vandermeulen and Gordin 1990, Bolton 2006). However, ponds and agitation devices entail construction and energy costs (Neori et al. 2004), which can surpass half of the overall seaweed production cost (Huguenin 1976). In nutrient-rich water, seaweeds function well as biofilters with little water agitation (Msuya and Neori 2008). These considerations have brought us to examine the performance of seaweeds in no-pond seaweed spray culture, with the anticipation that it may provide economically attractive low-cost biofiltration modules for land-based IMTA. Documented benefits in seaweed spray culture were related to construction and pumping cost, temperature control, gas (CO_2 and oxygen) exchange, light field, nutrient uptake, pests, and epiphytes, with little attention to the quantitative aspects of biofiltration capabilities (Pickering et al. 1995, Waaland 2004). Reported growth rates of the seaweeds in spray culture have often been low, compared with ponds and tanks. We examined the performance of *U. lactuca* in spray culture with nutrient-rich effluents from intensive fishponds. The deployed design was expected to make the system simple in construction and operation, easily scalable, and applicable for less-developed countries.

U. lactuca was brought in from the neighboring Red Sea (Vandermeulen and Gordin 1990). It was held on 1 m^2 plywood boards with plastic 4 mm mesh netting, creating flat mattress-like squares 3–5 cm thick. Two triplicate mattresses, inclined from the horizontal at 5.7° either due north or due south were placed above six plastic tank units (1 × 1 × 0.6 m) (Figs. 1 and 2). Duplicate

[1]Received 24 December 2008. Accepted 28 January 2010.
[2]Author for correspondence: e-mail aneori@gmail.com.

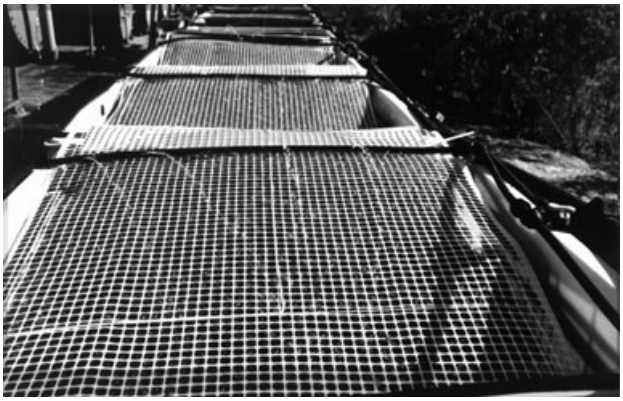


FIG. 1. The series of spray-irrigation units: a wooden board is placed slanted over a tank (used as a drain); the board is covered by a layer of the seaweed *Ulva lactuca*, held in place by a 4 mm mesh plastic net; water is sprayed onto the seaweed through a perforated pipe.

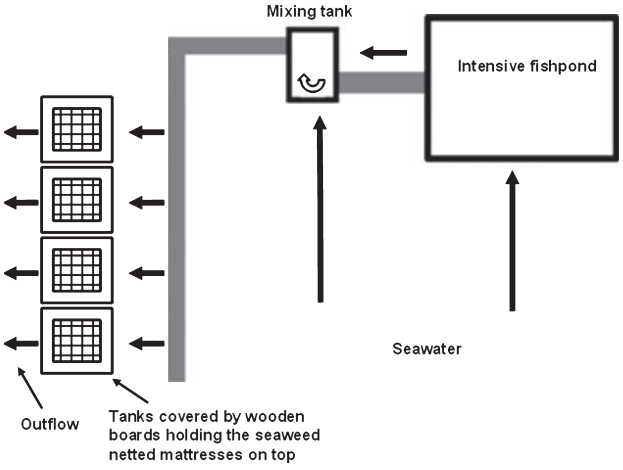


FIG. 2. A layout of the spray-culture seaweed culture system used for the experiments (only four units are shown). Seawater enters the fishpond; nutrient-rich effluent is pumped into a mixing tank, from which, after dilution with seawater, the water is distributed by a second pump into the eight experimental units.

air-agitated $1 \times 1 \times 0.6$ m culture tank units (as in Vandermeulen 1989) were the reference.

Water from an intensive gilthead seabream (*Sparus aurata*) pond (salinity 40.3–41 ppt) was sprayed onto the seaweed mattresses by perforated plastic pipes. Each of the eight units received 12 $m^3 \cdot m^{-2} \cdot d^{-1}$ (0.5 $m^3 \cdot h^{-1}$) pond water. The experiment lasted for 3 weeks in the summer of 2002 in Eilat, Israel.

Two days a week, at 08:00 a.m. and 02:00 p.m., water samples were collected at the inflow to the system and at the outflows from each of the eight units. Total ammonia N (TAN), nitrate and nitrite N (ToxN), and soluble reactive orthophosphate-P (SRP) were analyzed as in Krom et al. (1985), Solórzano and Sharp (1980), and Glibert and Loder (1977), respectively, with detection limits of 1, 1, and 1.5 $\mu mol \cdot L^{-1}$, respectively, after filtration (Whatman GF/C; Whatman International Ltd., Maidstone, England). Nutrient biofiltration rates and efficiencies for each unit were calculated from the differences in nutrient concentrations between the inflow and the outflows.

One kilogram of the fresh biomass was stocked in each unit each week. The entire seaweed layer was harvested after each week, centrifuged to remove excess water, and then weighed. Specific growth rate: SGR, $\% \cdot d^{-1} = 100 \cdot [\ln (w_t/w_0)] \cdot t^{-1}$; $w_0 = 1$ kg; w_t = fresh biomass after t (7) culture days. Biomass yield ($g \cdot m^{-2} \cdot d^{-1}$) is reported for the entire biomass of each mattress and is the difference $(w_t - w_0) \cdot t^{-1}$. Dry weight (dwt) content: subsamples from the harvests were rinsed, shaken dry, and oven-dried. The surface sublayer and the bottom sublayer of each of the north- and south-slanting mattresses were sampled separately; the results are presented in Table 1 for ''north surface,'' ''north bottom,'' ''south surface,'' and ''south bottom'' layers. When not statistically different, both sublayers of each mattress were reported as ''north-sum'' and ''south-sum.'' TKN (total Kjeldahl N) protein was determined according to Blaedel and Meloche (1957). Ash content was determined after incineration of dried seaweed samples for 24 h at 550°C in a muffle furnace. Phosphorus content was determined on the ash by the vanado-molybdate method, with the resulting color determined at 400 nm relative to standards. Irradiance was measured above the tanks, at 8:30 a.m. and at 2:00 p.m., by a calibrated LI-1000 Data Logger (LI-COR, Lincoln, NE, USA), equipped with a spherical sensor. Dissolved oxygen (DO) and temperature of the water were measured by a Handy Oxygen Meter Mk III (OxyGuard, Birkerød, Denmark). Air temperature was measured in the shade by a hand thermometer. Water flow was measured using a 5 L beaker and a stopwatch. The pH of the water was measured with a HI 8424 pH meter (Hanna Instruments, Leval, QC, Canada).

Analysis of variance (ANOVA) of the data compared the effect of the treatments on the measured parameters. Pearson correlation coefficient and regression analyses were used to test relationships between variables that were assumed to have direct effects on each other, from the biotic and abiotic variables measured. Data that were measured as percentage (biofiltration efficiency), which were out of the range of 30%–70%, were arcsine transformed to ensure normality before statistical tests were performed on them. The data were analyzed using SPSS (SPSS 11.0 for Windows, SPSS Inc., Chicago, IL, USA), XLSTAT (Addinsoft, New York, NY, USA), and Excel (Microsoft Corp., Redmond, WA, USA).

Air temperature varied from 29°C at 8:00 a.m. (average 32.7 ± 2°C) to 49°C (average 43.8 ± 2.3°C) at 2:00 p.m., with a mean daily temperature of 38.3 ± 2.2°C (data not shown). Water temperature

TABLE 1. Abiotic factors, specific growth rate (SGR), fresh yield, and protein content of the seaweed *Ulva lactuca*.

Treatment	Parameter					
	T (°C)	DO ($mg \cdot L^{-1}$)	pH	SGR ($\% \cdot d^{-1}$)	Yield ($g \cdot m^{-2} \cdot d^{-1}$)	Protein content (% in dwt)
Inflow water	28.2 ± 1.34 a	5.7 ± 0.33 a	7.8 ± 0.18 a			
Mattress spray irrigated (south + north)	28.7 ± 0.07 a	8.8 ± 0.32 b	8.0 ± 1.19 a	11.8 ± 1.5 a	171 ± 29 a	24.1 ± 4.5 a
Aeration (reference)	29.5 ± 1.66 a	9.3 ± 0.53 b	8.2 ± 0.22 b	16.9 ± 0.2 b	283 ± 33 b	24.7 ± 6.6 a
Spray, south inclined, sum					158 ± 32 a	20.6 ± 6.1 a
Spray, north inclined, sum					183 ± 25 a	23.5 ± 5.1 a
Spray, south inclined, bottom						25.9 ± 0.03 b
Spray, south inclined, surface						15.3 ± 0.8 a
Spray, north inclined, bottom						27.0 ± 1.1 b
Spray, north inclined, surface						20.0 ± 5.3 a
Spray, surface, sum of north + south						18.5 ± 4.8 a
Spray, bottom, sum of north + south						26.6 ± 1.0 b

South, thalli on south-slanted board; north, thalli on north-slanted board; surface, thalli on the surface of the seaweed mattresses, next to the netting; bottom, thalli on the bottom of the seaweed mattresses, next to the board; T, temperature; DO, dissolved oxygen; dwt, dry weight.

All values in Tables 1–3 are averages with SD.

ANOVA results: means with the same letters represent significant differences at $P < 0.05$. Separate analyses were made in each subsection (separated by blank lines).

averaged ~28.2°C in the inflow from the fishpond, and 28.7°C–29.5°C in the outflows of the eight units (Table 1). The temperature variation (in the inflow and the eight outflows) was insignificant ($P > 0.05$). Daily variation of temperature in the inflow water was between 0.5°C and 3.5°C.

Irradiance on top of the units varied between 1,958 and 2,922 μmol photons $\cdot m^{-2} \cdot s^{-1}$ during midday (average 2,445 ± 57 μmol photons $\cdot m^{-2} \cdot s^{-1}$, data not shown). Morning and afternoon irradiance intensities averaged 2,045 ± 90 μmol photons $\cdot m^{-2} \cdot s^{-1}$, and 2,845 ± 43 μmol photons $\cdot m^{-2} \cdot s^{-1}$, respectively.

All eight culture units significantly raised the DO concentrations in the water from ~6 $mg \cdot L^{-1}$ at the inflow to ~9 $mg \cdot L^{-1}$ at the outflow ($P < 0.01$), as the result of photosynthetic oxygen production (Table 1). The photosynthetic process also raised the pH of the water from 7.7–8.0 to 8.1–8.4 (Table 1). The increase was an insignificant ($P > 0.05$) 0.2 of a pH unit in the six mattress units, but a significant ($P < 0.01$) 0.4 of a pH unit in the two tanks.

The fresh yield and SGR data for the north- and south-facing mattress treatments were combined, since they were similar ($P > 0.05$). The average yield and SGR in the mattress treatment were 30% and 40%, respectively, lower ($P < 0.01$, Table 1) than in the tanks. Biomass yield in all tanks did not correlate strongly with inflow nutrients, maximum temperature, and irradiance levels (Pearson's correlation $r \leq 0.12$; linear correlation $R^2 \leq 0.02$) but correlated strongly with the minimum irradiance and minimum air temperature ($r \leq 0.48$).

Protein constituted ~24% of dwt in all units (Table 1). Protein content varied significantly ($P < 0.01$) between biomass in the surface and the bottom of the green mattresses. The low-protein surface seaweed was light green, while the bottom seaweed was dark green. The surface biomass, however, made only a small fraction of the biomass, and therefore, the overall protein content of the yield was similar ($P > 0.05$) in all units (Table 1). Contents of dry matter and ash (Table 2) also did not vary. Phosphorus content (Table 2) was similar in

TABLE 2. Chemical parameters of the seaweed *Ulva lactuca*, cultured in fishpond effluents.

Treatment, source of the biomass	Nutritional parameters of the biomass			
	DW (% in fwt)	Ash (% in dwt)	P content (% in dwt)	N:P (molar)
Spray, south inclined, surface layer	11.2 ± 0.8 a	20.6 ± 0.3 a	0.18 ± 0.02 a	31.1 ± 2.1 a
Spray, south inclined, bottom layer	10.6 ± 1.4 a	19.9 ± 0.3 a	0.31 ± 0.01 b	29.9 ± 0.7 a
Spray, north inclined, surface layer	11.6 ± 1.6 a	21.3 ± 2.0 a	0.25 ± 0.12 b	30.4 ± 5.6 a
Spray, north inclined, bottom layer	10.0 ± 0.4 a	21.4 ± 0.9 a	0.37 ± 0.10 b	26.6 ± 6.4 a
Aeration suspended, air agitated (reference)	10.9 ± 0.1 a	22.1 ± 0.1 a	0.31 ± 0.11 b	28.3 ± 0.9 a

DW, dry weight content; N:P, N to P molar ratio in the biomass; fwt, fresh weight; dwt, dry weight.

ANOVA results: see Table 1 for an explanation.

the north-facing mattresses and the air-agitated tanks, but 42% lower in the south-facing mattresses. The molar N:P ratio in the biomass (Table 2) was between 26.6 and 31.1 with no significant differences ($P > 0.05$). The low content of N and P in the south-inclined surface biomass, similar to the observations in desiccated or bleached *Gracilaria chilensis* (Pickering et al. 1995), is related to metabolic stress under the heat and the high irradiance, to the rupture of cellular membranes, with the consequent exudation of cellular content, and also to the limited supply of nutrients due to the desiccation (Malta et al. 2003, Figueroa et al. 2009).

The uptake rate per unit area (areal uptake rate) of TAN was 5.1 and 6.8 g $N \cdot m^{-2} \cdot d^{-1}$ for the spray irrigation and the tanks, respectively (Table 3; $P > 0.05$). The biofiltration rates correlated with the inflow TAN concentration ($P < 0.05$, $r^2 = 0.95$, detailed data not shown). Biofiltration efficiency (Table 3) was 63% in the mattresses and 83% in the tanks, with a high variability ($P > 0.05$). Biofiltration of ToxN was low (Table 3), as this *Ulva* species, and most other algae, cease ToxN uptake in the presence of TAN sufficiency (Neori 1996). SRP, on the other hand, was undetected in the system most of the time. Once, SRP was detected in the system at $\sim$2 $\mu mol \cdot L^{-1}$, too low to detect uptake (Table 3).

The ''green mattress'' spray-irrigation seaweed culture approach functioned better than in Haglund and Pedersen (1988) and Haglund et al. (1991). Yield and SGR in the mattress units, even though lower than in the tanks, were comparable to yields in air-agitated tanks as reported by DeBusk et al. (1986) and Shpigel and Neori (1996). Whereas nutrients, maximum temperature, and irradiance did not individually influence growth, minimum irradiance and air temperature did. Nutrient sufficiency can reduce the impact of and accelerate recovery from stresses induced by light and high temperature in this species (Figueroa et al. 2009).

TABLE 3. Nutrient concentrations, removal rates, and efficiencies (% of inflow) by *Ulva lactuca* biofilter.

	Concentration in inflow ($\mu mol \cdot L^{-1}$)	Concentration in outflow ($\mu mol \cdot L^{-1}$)	Biofiltration rate ($g \cdot m^{-2} \cdot d^{-1}$)	Biofiltration efficiency (%)
Treatment (north and south mattresses, combined)				
TAN	49 ± 10	18 ± 17	5.1 ± 2.8	63
ToxN	9.3 ± 0.4	8.97 ± 1.4	0.10	4
SRP	2.00[a]	2.75[a]	Negligible	Negligible
Reference (air-agitated culture)				
TAN	49 ± 10	8 ± 7	6.8 ± 1.1	83
ToxN	9.3 ± 0.4	8.2 ± 2.1	0.18	11
SRP	2.00[a]	2.26[a]	Negligible	Negligible

TAN, total ammonia N; ToxN, nitrate and nitrite N; SRP, soluble reactive orthophosphate-P.

Water flow through each tank was 500 $L \cdot h^{-1}$; daily nutrient loads to each tank were $\sim$8.2 ± 0.3 g TAN, 1.6 ± 0.1 g ToxN, and 0.3 g or less SRP.

[a]A single entry; the rest were undetectable.

In turf algae, which are physically similar to the green mattresses, self-shading and nutrient limitation related to biomass seem to limit photosynthesis and impact chemical composition more than temperature, except during the extreme low temperature and light in midwinter, while dense biomass reduced photoinhibition in high light (Copertino et al. 2009). Thus, the dense biomass and nutrient sufficiency enjoyed by the green mattresses may allow them to perform better than tank systems under extremes of temperature and irradiance that are outside the range examined here. Protein content of the mattress seaweed was close to comparable studies that used *Ulva* spp. (e.g., Neori et al. 2000, 28%; and Boarder and Shpigel 2001, 32%). Oxygenation of the water and pH elevation by the green mattresses was also comparable with the air-agitated tanks in Neori et al. (2000) and Schuenhoff et al. (2003). Similar to Cohen and Neori (1991), TAN uptake depended on TAN flux. In addition, the biofiltration rate and efficiency obtained in this regime are similar to those reported from air-agitated tanks. Cohen and Neori (1991), Shpigel et al. (1993), and Shpigel and Neori (1996) used TAN loadings of 4–8 $g \cdot m^{-2} \cdot d^{-1}$ and obtained biofiltration efficiencies of 40%–56% and biofiltration rates of up to 5.6 $g \cdot m^{-2} \cdot d^{-1}$ in *U. lactuca*. Little damage was observed in the green mattress *Ulva*, even when exposed to irradiance levels and drying rates that were possibly comparable only to exposed seaweeds during low tide (cf. Beer and Eshel 1983, Friedlander and Ben-Amotz 1991, Scrosati and DeWreede 1998, Bjork et al. 1999). Apparently, *Ulva* coped with the adverse conditions, thanks to protection by the top layer and to its good recovery from dehydration. The main body of the seaweed thickness was kept moist by the underneath thalli for most of the day. Minor differences associated with the slanting relative to the sun were probably related to the exposure to excessive irradiances and temperatures (Bjork et al. 1999).

In conclusion, the growth rate, biomass yield, biomass quality, and biofiltration performance by the green mattresses were a little lower than in the air-agitated reference tanks. Apparently, wet *U. lactuca* in spray culture can take up nutrients, complete all the necessary processes needed for growth, and perform as an efficient biofilter. This finding suggests that the design is useful, where cost, technical complexity, water volume, and labor limit the practicality and the economics of seaweed biofiltration ponds, since in air-agitated seaweed farms, aeration energy constitutes about half of the operating cost (Huguenin 1976, A. Neori, unpublished data).

It is most probable that in a properly engineered system, the advantage of this spray-irrigation approach over air-agitated seaweed ponds will be expressed in a much higher ratio of production to cost. Therefore, large-scale spray-irrigation seaweed systems can be commercially attractive for low-cost

seaweed biofilters and for the production of seaweed biomass as a source of food, feed, phycocolloids, and biomass fuel.

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Beer, S. & Eshel, A. 1983. Photosynthesis of *Ulva* sp. I. Effects of desiccation when exposed to air. *J. Exp. Mar. Biol. Ecol.* 70:91–7.

Bjork, M., Uku, J., Weil, A. & Beer, S. 1999. Photosynthetic tolerance to desiccation of tropical intertidal seagrasses. *Mar. Ecol. Prog. Ser.* 191:121–6.

Blaedel, W. J. & Meloche, V. W. 1957. *Elementary Quantitative Analysis: Theory and Practice*. Row, Peterson and Company, New York, 856 pp.

Boarder, S. J. & Shpigel, M. 2001. Comparative performance of juvenile *Haliotis roei* fed on enriched *Ulva rigida* and various artificial diets. *J. Shellfish Res.* 20:653–7.

Bolton, J. J. 2006. Do we have the vision to integrate our marine aquaculture? *S. Afr. J. Sci.* 102:57–8.

Chopin, T., Buschmann, A. H., Halling, C., Troell, M., Kautsky, N., Neori, A., Kraemer, G. P., Zertuche-González, J. A., Yarish, C. & Neefus, C. 2001. Integrating seaweeds into marine aquaculture systems: a key toward sustainability. *J. Phycol.* 37:975–86.

Cohen, I. & Neori, A. 1991. *Ulva lactuca* biofilters for marine fishpond effluents. I. Ammonia uptake kinetics and nitrogen content. *Bot. Mar.* 34:475–82.

Copertino, M. S., Cheshire, A. & Kildea, T. 2009. Photophysiology of a turf algal community: integrated responses to ambient light and standing biomass. *J. Phycol.* 45:324–36.

Critchley, A. T., Ohno, M. & Largo, D. B. [Eds.] 2006. *Seaweed Resources of the World*, 2nd ed. (DVD). ETI Bioinformatics, University of Amsterdam, Amsterdam.

DeBusk, T. A., Blakeslee, M. & Ryther, J. H. 1986. Studies on the outdoor cultivation of *Ulva lactuca* L. *Bot. Mar.* 29:381–6.

FAO. 2006. *State of World Aquaculture*. FAO Fisheries Technical Paper No. 500, Rome, 134 pp.

Figueroa, F. L., Israel, A., Neori, A., Martínez, B., Malta, E. J., Put, A., Inken, S., Marquardt, R. & Korbee, N. 2009. Effect of nutrient supply on photosynthesis and pigmentation in *Ulva lactuca* (Chlorophyta): responses to short-term stress. *Aquat. Biol.* 7:173–83.

Friedlander, M. & Ben-Amotz, A. 1991. The effect of outdoor culture conditions on growth and epiphytes of *Gracilaria conferta*. *Aquat. Bot.* 39:315–33.

Glibert, P. L. & Loder, T. C. 1977. *Automated Analysis of Nutrients in Seawater: A Manual of Techniques*. Woods Hole Oceanographic Institute Technical Report WHOI 77–47. Woods Hole Oceanographic Institute, Woods Hole, Massachusetts, 46 pp.

Haglund, K., Obledo, D., Garcia-Reina, G. & Pedersen, M. 1991. Increased metal content in spray cultivated seaweed. *In* Garcia-Reina, G. & Pedersen, M. [Eds.] *Proceedings of COST-48-Working Seminar, "Recent Advances in Seaweed Cellular Biotechnology."* University of Las Palmas, Canary Islands, Spain, pp. 283–6.

Haglund, K. & Pedersen, M. 1988. Spray cultivation of seaweeds in recirculating brackish water. *Aquaculture* 72:181–9.

Huguenin, J. E. 1976. An examination of problems and potentials for future large-scale intensive seaweed culture systems. *Aquaculture* 9:313–42.

Krom, M. D., Grayer, S. & Davidson, A. 1985. An automated method of ammonia determination for use in mariculture. *Aquaculture* 44:153–60.

Lüning, K. & Pang, S. J. 2003. Mass cultivation of seaweeds: current aspects and approaches. *J. Appl. Phycol.* 15:115–9.

Malta, E. J., Rijstenbil, J. W., Brouwer, P. E. M. & Kromkamp, J. C. 2003. Vertical heterogeneity in physiological characteristics of *Ulva* spp. mats. *Mar. Biol.* 143:1029–38.

Msuya, F. E. & Neori, A. 2008. Effect of water aeration and nutrient load level on biomass yield, N uptake and protein content of the seaweed *Ulva lactuca* cultured in seawater tanks. *J. Appl. Phycol.* 20:1021–31.

Neori, A. 1996. The form of N-supply (ammonia or nitrate) determines the performance of seaweed biofilters integrated with intensive fish culture. *Isr. J. Aquacult. Bamidgeh* 48:19–27.

Neori, A., Chopin, T., Troell, M., Buschmann, A. H., Kraemer, G. P., Halling, C., Shpigel, M. & Yarish, C. 2004. Integrated aquaculture: rationale, evolution and state of the art emphasizing seaweed biofiltration in modern mariculture. *Aquaculture* 231:361–91.

Neori, A., Shpigel, M. & Ben-Ezra, D. 2000. A sustainable integrated system for culture of fish, seaweed and abalone. *Aquaculture* 186:279–91.

Pickering, T. D., Gordon, M. E. & Tong, L. J. 1995. A preliminary trial of a spray culture technique for growing the agarophyte *Gracilaria chilensis* (Gracilariales, Rhodophyta). *Aquaculture* 130:43–9.

Ryther, J. H., Goldman, J. C., Gifford, J. E., Huguenin, J. E., Wing, A. S., Clarner, J. P., Williams, L.D. & Lapointe, B. E. 1975. Physical models of integrated waste recycling – marine polyculture systems. *Aquaculture* 5:163–77.

Schuenhoff, A., Shpigel, M., Lupatsch, I., Ashkenazi, S., Msuya, F. E. & Neori, A. 2003. A semi-recirculating, integrated system for the culture of fish and seaweed. *Aquaculture* 221:167–81.

Scrosati, R. & DeWreede, R. E. 1998. The impact of frond crowding on frond bleaching in the clonal intertidal alga *Mazzaella cornucopiae* (Rhodophyta, Gigartinaceae) from British Columbia, Canada. *J. Phycol.* 34:228–32.

Shpigel, M. & Neori, A. 1996. The integrated culture of seaweed, abalone, fish and clams in modular intensive land-based systems: I. Proportions of size and projected revenues. *Aquacult. Eng.* 15:313–26.

Shpigel, M., Neori, A., Popper, D. M. & Gordin, H. 1993. A proposed model for "environmentally clean" land-based culture of fish, bivalves and seaweeds. *Aquaculture* 117:115–28.

Solórzano, L. & Sharp, J. H. 1980. Determination of total dissolved nitrogen in natural waters. *Limonol. Oceanogr.* 25:751–4.

Troell, M., Rönnbäck, P., Halling, C., Kautsky, N. & Buschmann, A. H. 1999. Ecological engineering in aquaculture: use of seaweeds for removing nutrients from intensive mariculture. *J. Appl. Phycol.* 11:89–97.

Turan, G. 2009. Potential role of seaweed culture in integrated multitrophic aquaculture (IMTA) systems for sustainable marine aquaculture in Turkey. *Aquacult. Eur.* 34:5–13.

Vandermeulen, H. 1989. A low-maintenance tank for mass culture of seaweeds. *Aquacult. Eng.* 8:67–71.

Vandermeulen, H. & Gordin, H. 1990. Ammonia uptake using *Ulva* (Chlorophyta) in intensive fishpond system: mass culture and treatment of effluent. *J. Appl. Phycol.* 2:363–74.

Waaland, J. R. 2004. Intensive aquaculture of the red seaweed *Chondracanthus exasperatus*. *Bull. Fish. Res. Agen. Suppl.* 1:91–100.