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Seaweed biofilters as regulators of water quality in integrated fish–seaweed culture units

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Abstract

The water-quality characteristics of a new system for the integrated culture of fish (*Sparus aurata* L.) and seaweed (*Ulva lactuca* L.) were examined. Seawater was recirculated between intensive fishponds and seaweed ponds. The seaweed removed most of the ammonia excreted by the fish and oxygenated the water. A model consisting of several tanks and a pilot consisting of two 100-m^3, 100-m^2 ponds were studied. In both, the metabolically dependent water-quality parameters (dissolved oxygen, NH_4^+-N, oxidized-N, pH and phosphate) remained stable and within safe limits for the fish during over 2 years of operation. The design allowed significant increases in overall water residence time (4.9 days), compared with conventional intensive ponds, and produced a high yield of seaweed in addition to the fish. The design provides a practical solution to major management and environmental problems of land-based mariculture.

Keywords: Sustainable-mariculture; Seaweed-biofilters; Effluents; Nutrients; Recirculating; Water-quality; Fish

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1. Introduction

Many farmed fish assimilate less than 30% of the supplied nitrogen (Porter et al., 1987; Hall et al., 1992). Hence, in fish-cages (Gowen et al., 1989; Watanabe, 1991) and in intensive fishponds (Rimon and Shilo, 1982; Neori et al., 1989; Boyd, 1990; Cripps, 1991; Bergheim et al., 1991) most nutrients are released to the environment and contribute to water pollution. This is of particular concern in oligotrophic warm-water coastal seas (Ziemann et al., 1992), such as in Eilat on the Red Sea. Furthermore, strict limits are being set on the release of nutrients from mariculture facilities (see in Cowey and Cho, 1991).

In previous studies with phytoplankton-dominated intensive seawater fishponds in Eilat (Neori et al., 1989) extremes of dissolved oxygen (DO), high dissolved ammonia and high pH were identified as the key problems of water quality. Frequent crashes of the phytoplankton populations, driven by protozoan grazing, led frequently to events of high ammonia levels and low DO.

Seaweed biofilters constitute a logical alternative to phytoplankton and bacterial biofilters for the maintenance of water quality in land-based mariculture. Harlin et al. (1978) discussed the theoretical benefits and preliminary results from small indoor closed systems for the culture of marine fish and seaweed. At the National Center for Mariculture (NCM), we have modified, upscaled and studied the use of such systems to minimize the water-quality problems of land-based fish-culture in an environmentally sustainable way. In the seaweed ponds, the proper algal biomass and rate of nutrient-uptake could be controlled better than in phytoplankton ponds (Cohen and Neori, 1991). The seaweed biofilters removed nitrogen without the anaerobic conditions required in nitrification–denitrification N-removal biofilters. Unlike the latter, the seaweed biofilters also produced a biomass which could be used in several ways (Kissil et al., 1992), for instance to feed ruminants (Arieli et al., 1993) and molluscs (Tenore, 1976).

Fishpond biofilters with the green seaweed *Ulva lactuca* L. remained clean and functional for years with minimal maintenance while producing high yields (200 g wet weight, 30 g dry weight m^{-2} day^{-1}) using only fish-pond effluents for water and nutrition (Vandermeulen and Gordin, 1990; Cohen and Neori, 1991; Neori et al., 1991). Young gilthead seabream (*Sparus aurata* L.) grew well in the seaweed-treated water (C.P. Porter, D. Popper and A. Neori, NCM report, 1989, unpublished data). In the integrated culture system described below, water was recirculated between ponds of fish and seaweed, as basically described by Harlin et al. (1978) and by Lewis et al. (1978). We report here the long-term performance and dependability of the system with regard to water quality.

2. Materials and methods

Two systems were studied, a model system consisting of several tanks, and a pilot system consisting of two 100-m^3 ponds. The fish were crowded in a fraction of the overall system volume, so that culture space was freed for the seaweed biofilters. Water

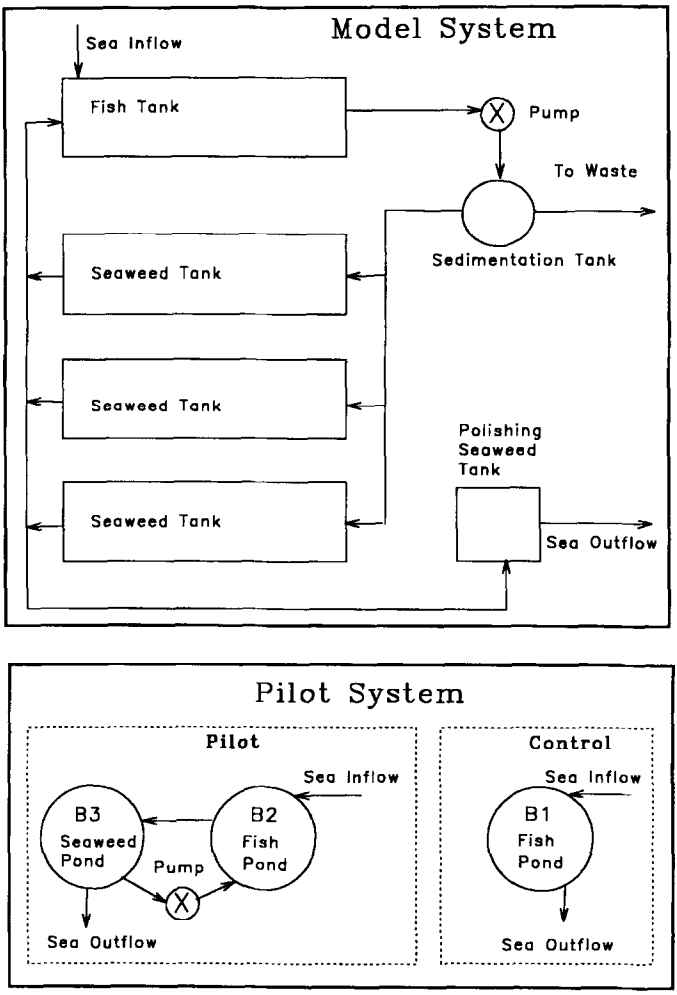

Fig. 1. Schematic configurations of the model and the pilot systems for the integrated culture of fish and seaweed. Arrows mark the directions of water flow.

recirculated between the fish and the seaweed compartments. Fish feeding rate and capacity of the seaweed biofilter to remove nutrients were matched, as described below.

2.1. The model system

The model system (Fig. 1) was aimed to determine detailed nutrient budgets and water quality performance. It consisted of a series of round-bottom fiberglass trough tanks, each with dimensions of $3 \times 1.1 \times 0.9$ m, a nominal volume of 2.5 m^3 and an area of 3.3 m^2. A smaller 600-l seaweed culture tank (as in Vandermeulen, 1989), served for polishing and a 2-m-tall, 400-l tank served for sedimentation.

2.2. Design and operation of the model system

The fish were stocked in one of the trough tanks at densities which required the equivalent of 450 kg^{-1} ha^{-1} day^{-1} of feed. For a total recirculating tank area of 13.3 m^2 (of which the fish occupied only 25%), this ration was 0.6 kg day^{-1}. The food ration was maintained constant for the purpose of nutrient budget determinations and the fish were therefore occasionally culled.

Three trough tanks served as seaweed biofilters and were connected in parallel. The area of 10 m^2 allocated to the seaweed biofilter was determined with respect to the curve for the seaweed NH_4^+-N removal rates (Cohen and Neori, 1991), which could reach 7 g N m^{-2} day^{-1}. The daily food ration of 0.6 kg was expected to produce up to 27 g of excreted combined N (Krom and Neori, 1989), or only 39% of the maximal removal capacity of the biofilter. The seaweed tanks were aerated at a moderate rate by pipes, embedded in the round bottoms. Holes of 2.5–3 mm were spaced at 15-cm intervals along the pipes, so that the large bubbles produced stirred the seaweed gently but effectively. Water was pumped from the fish tank to the seaweed tanks via the sedimentation tank at a rate of 800–1000 l h^{-1}. Fresh seawater (inflow) flowed into the fish tank at a rate of 2000 l day^{-1}. Screens (3–5-mm mesh) at the ends of the seaweed tanks kept the seaweed inside. The water from the seaweed tanks recycled back into the fish tank by gravity via stand-pipes. A water volume equal to the inflow (less evaporation, leakage and sampling) overflowed from the seaweed tanks into the polishing seaweed tank, and from there drained to the sea. The fish tank was shaded to about 15% of full sunlight to reduce phytoplankton growth.

The system was operated as described above from January 1991 to May 1993. The seaweed biomass in excess of 3 kg per tank was harvested weekly. The fish were given their full feed ration (0.6 kg) daily at 08:30, by a demand feeder. In winter, when temperature dropped below 14°C (see Fig. 2) a 3-KW heater was placed in the fish tank and the tank walls insulated to raise daytime temperature to 17–19°C. Below this temperature, gilthead seabream begin to lose appetite (D. Popper, NCM, unpublished observations). Each day, at 08:30 and at 16:30, the inflow valve was opened for 4 h at a flow rate of 250 l h^{-1}. Each day at 08:30, the sedimentation tank was drained for a few seconds to remove accumulated particles.

The following events altered the otherwise constant management protocol of the model: (1) In June 1991, one seaweed tank was disconnected from the system; (2) During February 7–10 1992, clean seawater was accidently undersupplied by an undetermined amount; (3) Due to a severe parasitosis by *Amyloodinium ocellatum*, the fish were removed during July–August 1992. Salts of ammonium and orthophosphate at quantities similar to those in the feed, were then added daily and the water quality parameters continued to be measured; (4) On July 30 1992, fertilizers were accidentally oversupplied; (5) The system was emptied and dried completely during March 1991, September 1992 and March 1993 for technical reasons.

2.3. Budget of the model system

The water volume, and the rate of evaporation and other water losses, were determined for the different components of the model system. The measurements were

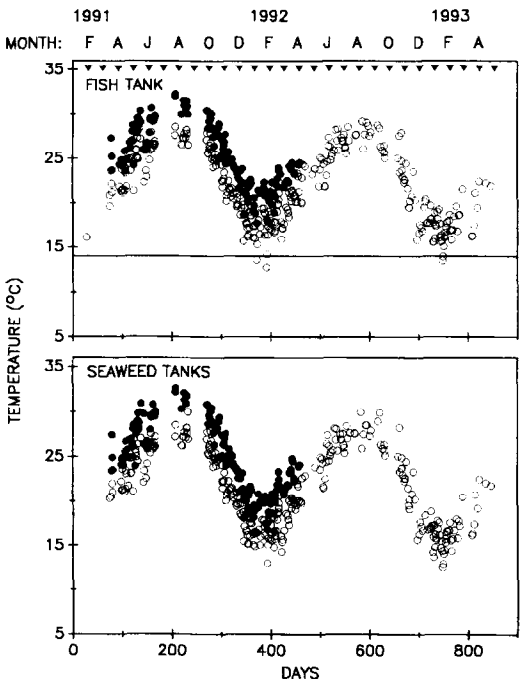

Fig. 2. Temperatures in the model system, measured once or twice a day (8:30 h, open circles, and 13:30 h, closed circles) during 2 years of system operation. The horizontal line marks 14°C.

conducted on a clean system filled by seawater to operating capacity, with the recirculation pump switched off. Due to the large volumes of water involved, the volume of each tank was determined by dilution. A KNO_2 solution of known concentration was introduced into the tank and mixed by aeration for 30 min before sample collection (in duplicates). The KNO_2 concentration was then determined by autoanalyzer and the tank volume was calculated as follows: $V_{tank} = C_{original} \times V_{original}/C_{tank}$ (V_{tank} = tank volume; $C_{original}$ = concentration in original solution; $V_{original}$ = volume of original solution; C_{tank} = concentration of solute measured in the tank).

Evaporation rate was determined according to the rate of salinity increase. The measurements were carried out in June 1992. Samples for salinity determination were collected from each of the system tanks every 2 h from 11:00 to 17:00 and again from 08:00 to 12:00. Sample conductivity was measured with an inductively coupled salinometer and salinity was calculated using the International Oceanographic tables (UNESCO and National Institute of Oceanography, Australia). Samples were calibrated against a vial of standard sea water with chlorinity of 19.375 (Institute of Oceanographic Sciences, Wormley, Surrey, UK). The amount of a given salt in a tank remains constant over time, thus:

$$S_{(t)} \times V_{(t)} = S_{(0)} \times V_{(0)} \quad (1)$$

(S = salinity; V = volume of water in the tank, in l; t = time since start of experiment).

Therefore, the $V_{(t)}$ can be determined by solving for it in Eq. (1),

$$V_{(t)} = S_{(0)} \times V_{(0)} / S_{(t)} \quad (2)$$

Assuming a constant evaporation rate E (in l h^{-1}),

$$V_{(t)} = V_{(0)} - E \times t \quad (3)$$

and therefore E is estimated by regressing the computed $V_{(t)}$ against t.

2.4. The pilot system

The pilot system (Fig. 1) consisted of a fishpond of the type described in Gordin et al. (1990) with an area of 100 m^2 and a volume of 100 m^3, and a similar-size seaweed (*Ulva lactuca*) pond. The latter was converted from a fishpond by the installation of an aeration network at the bottom. Water was recirculated between the two ponds at a rate of about 400 m^3 day^{-1}. In addition, 100 m^3 day^{-1} of fresh seawater were added to the system so that the overall water residence time was 2 days for the two-pond system. The seaweed were harvested usually weekly. However, the seaweed density remained always above the optimal range of 1–2 kg m^{-2}.

The pilot system was compared with a neighboring conventional intensive fishpond, also with a water residence time of 2 days. While the conventional fishpond and the seaweed pond were exposed to full sunlight, the fishpond in the integrated system was shaded with a net which screened about 85% of the light, to reduce phytoplankton growth.

The pilot system was operated at two levels of fish biomass, requiring different daily feeding rates. From September to November 1990, 850 kg of fish received a fixed feed ration of 10 kg day^{-1}. The fish were not culled as they grew, and from December 1990 to April 1991 the feed ration was adjusted according to the fish biomass. During the same period the conventional fishpond was stocked with 550 kg of fish, which were culled regularly, and received a constant feed ration of 6.5 kg day^{-1}.

2.5. Water sampling and analysis

Water samples were taken two to five times a week, from January 1991 to June 1992 at 08:30 and 13:30 h, and from August 1992 to May 1993 at 08:30 h. DO and temperature were measured inside the culture systems by a Yellow Springs Instruments oxygen electrode. Samples were collected into bottles via a 1-mm screen and divided into two aliquots. One served for immediate electrode analyses of pH and NH_4^+-N and the second was refrigerated for autoanalyzer nutrient analyses, which were made less frequently. The pH electrode was calibrated daily while the ammonia electrode (Ingold NH_3 electrode type 15 230 3000) was calibrated weekly. All autoanalyzer analyses were carried out in duplicates. In cases of duplicate disagreement, frozen replicated samples were also analyzed in duplicate.

The calibration of the ammonia electrode was confirmed by the autoanalyzer

measurement of NH_4^+-N in the same samples. With these data we generated the following long-term linear correlation for the less accurate electrode determinations:

$$C_{aa} = 1.087 \times C_e$$

(C_{aa} = NH_4^+-N concentration by autoanalyzer; C_e = NH_4^+-N concentration by electrode; $n = 274$; $r^2 = 0.90$). The autoanalyzer methods employed for nutrient analyses were described in Krom et al. (1989). Analyses of total dissolved N and P (TDN and TDP) were performed simultaneously by a modification of the persulfate oxidation procedures described by Solorzano and Sharp (1980) and by Valderrama (1981). The pH of each sample was first raised above 12.6 and autoclaved with potassium persulfate for total oxidation of organic N compounds. After cooling the samples were acidified to below a pH of 2.6 and autoclaved again for total oxidation of organic P compounds. After cooling again the samples were analyzed for NO_3^- and orthophosphate by the autoanalyzer methods described above. The coefficient of variation (CV) of the modified method ranged from 3% at 120 μM to 17% at 10 μM for N, and from 12% at 60 μM to 20% at 10 μM for P.

3. Results

3.1. The model system

3.1.1. Hydrological balance

Salinity increased quasi-linearly with time, with only a slight variation between day and night. Therefore, a single evaporation rate was defined for the 24 h. The salinity values in the fish tank, seaweed tanks and the polishing tank were 41.395, 41.438 and 41.136, respectively at $t = 0$ and 42.620, 42.597 and 43.323, respectively, at $t = 25$ h. Evaporation rates (Table 1) totaled 247 l day^{-1} and the tank volumes (Table 1) totaled 9200 l. Thus, less than 3% day^{-1} of the total volume evaporated. Estimated precision for the volume estimates was 2.2%. The precise volumes measured here, the predetermined water inflow of 2000 l day^{-1} and the estimated outflow through the polishing tank of about 1750 l day^{-1} were used to calculate precise water residence times for each

Table 1
The hydrology of the model system

Component	V (l)	E (l day^{-1})	RT (h)
One seaweed tank	2130	55.7	6.5–7.9
System (three tanks)	6390	167.1	
Fish tank	1790	50.9	1.8–2.2 (daily average)
Sedimentation tank	400	11.0	0.4–0.5
Polishing tank	600	29.0	8.2 (daily average)
Whole system	9200	247	4.9 (days)

V is volume; E is evaporation rate; RT is water residence time.

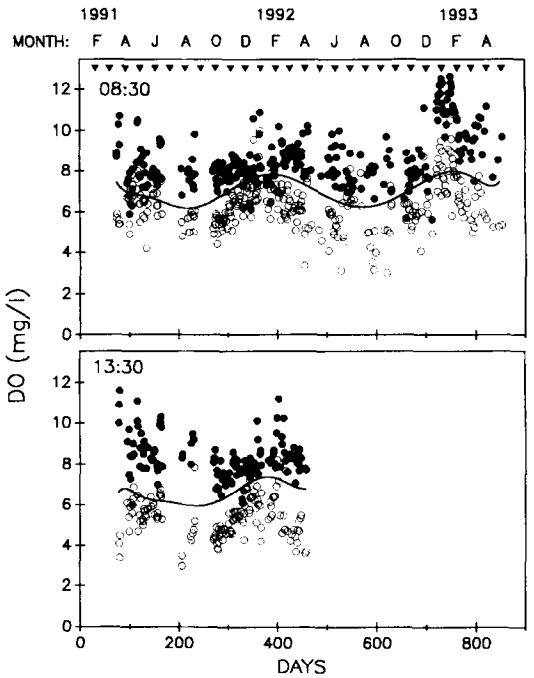

Fig. 3. Concentrations of DO in the model system, measured once or twice a day (8:30 h and 13:30 h) during 2 years of system operation in the fish-tank (open circles) and in a seaweed tank (closed circles). A solid curve marks DO at 100% saturation.

component (Table 1). These results show that the fish tank experienced 11–14 water exchanges day^{-1}, of which over 90% was recycled water.

3.1.2. Water quality

The long-term water quality data are presented without time-averaging or smoothing, since even short-term deterioration in water quality can be stressful to fish. The water quality measurements in the sedimentation tank are not presented because of their similarity to fish-tank data. The CV of the replicates was below 5% and smaller than the size of the symbols in the figures. The data from the three seaweed tanks were very close to each other, with a CV of below 5%. Therefore only the data from one seaweed tank are presented in the figures.

The polishing seaweed tank removed only a little of the nutrients (data not shown) and was redundant with respect to water quality in the fishpond.

Temperature (Fig. 2) varied seasonally and diurnally, but the differences between the tanks were minor. During over two full annual cycles, the daily temperature maxima in the fish tank ranged from 17°C to 32°C. The daily minima ranged from 12°C to 27°C, but only rarely dropped below 14°C. The temperature difference between the morning and the afternoon was up to 10°C, and was larger in winter than in summer. DO (Fig. 3) was higher in the morning than in the afternoon. It remained in the fish tank within a range safe for the fish (4–8.5 mg l^{-1}) throughout the entire 2-year period. (The high DO

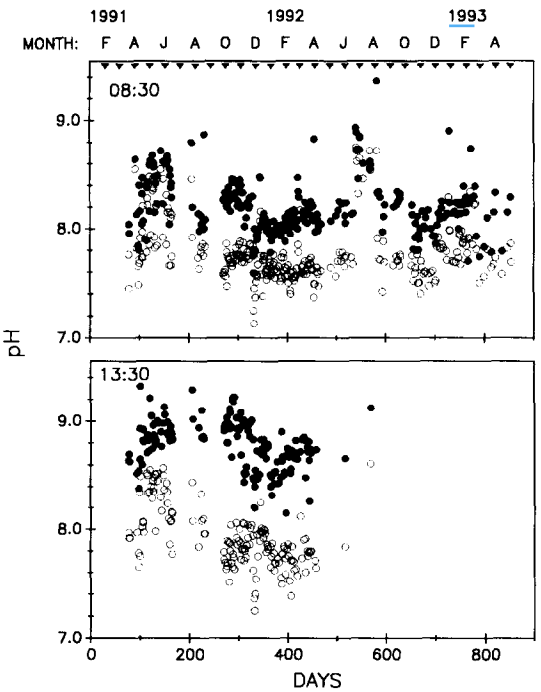

Fig. 4. pH values in the model system, measured once or twice a day (8:30 h and 13:30 h) during 2 years of system operation in the fish-tank (open circles) and in a seaweed tank (closed circles).

values in January 1993 are attributed to a bad DO electrode.) DO supersaturation occurred only in the seaweed tanks, especially in the afternoons. This water helped to keep good DO levels in the fish tank. The disconnection of one seaweed tank (June 1991) did not alter the DO levels. However, when fresh seawater was undersupplied (February 7–10 1992), DO levels in both tanks increased by 1–2 mg l^{-1}. Without fish (July 1992), when nutrient salts were added instead of organic feed, DO levels in the fish tank (but not in the seaweed tanks) were higher by about 2 mg l^{-1} than in both the preceding and the following months.

The pH levels at the same period without fish also rose relative to both the preceding and the following months, by up to one unit (Fig. 4). This difference was larger in the seaweed tanks than in the fish tank. Also when fresh seawater was undersupplied (February 7–10 1992), a small pH increase occurred in both tanks. However, throughout most of the 2-year period, the pH levels in the fish tank remained in the range of 7.3 to 8.6, with a maximum of 8.9. This situation remained even when one seaweed tank was disconnected (June 1991). In the seaweed tanks, the pH was nearly every day 0.5–1 unit above that in the fish tank. This difference was larger in the afternoon than in the morning.

The main feature in the NH_4^+-N data (Fig. 5) was the absence of extremely high values, in contrast to the high peaks observed (Neori et al., 1989) in our phytoplankton-based intensive fishponds with comparable rates of feeding. In the morning, NH_4^+-N

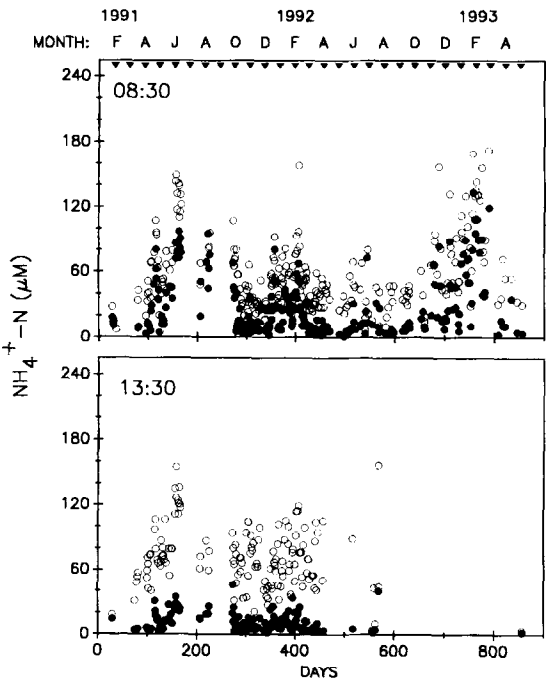

Fig. 5. Concentrations of NH_4^+-N in the model system, measured once or twice a day (8:30 h and 13:30 h) during 2 years of system operation in the fish-tank (open circles) and in a seaweed tank (closed circles).

levels in the seaweed tanks were higher than in the afternoon. The morning levels in the seaweed tanks were higher in winter than in summer, but in the afternoon they always dropped below 50 μM and usually even below 35 μM. In the fish tank, the NH_4^+-N levels were usually slightly lower in the morning than in the afternoon, and generally below 100 μM (1.4 mg N l^{-1}). Exceptional but not dangerous increases in NH_4^+-N levels were observed during June 1991, when one seaweed tank was disconnected, in February 7–10 1992, when the fresh seawater was undersupplied and during winter (especially of 1993), when the weather was cloudy for an extended period. In the latter case, the NH_4^+-N level in the fish tank reached 180 μM.

The oxidized forms of bound N (Fig. 6) were found in the system at levels of up to 230 μM (3.2 mg N l^{-1}) for NO_2^- and 180 μM (2.5 mg N l^{-1}) for NO_3^-. The differences in the levels of these nutrients between the seaweed tanks and the fish tank alternated between positive and negative but were always small (< 10 μM). The combined concentration of the oxidized N-forms was usually between 200–250 μM. Only following the drying of the system (March 1991, September 1992 and March 1993) were NO_3^- and NO_2^- at low concentrations. After each activation of the system, typical accumulation successions occurred. NO_2^- accumulated first, followed in several weeks by NO_3^-. Without fish (July 1992), the levels of both forms of oxidized N approximately doubled compared with the preceding and following months.

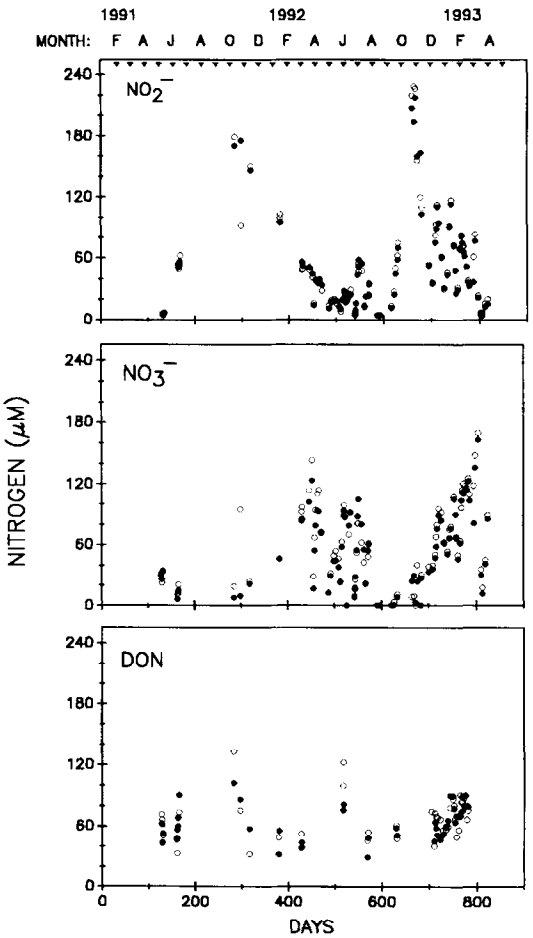

Fig. 6. Concentrations of NO_2^-, NO_3^- and DON in the model system at 08:30 h during 2 years of system operation in the fish-tank (open circles) and in a seaweed tank (closed circles).

The concentration of dissolved organic N (DON) in the system (Fig. 6) was more stable than were the oxidized N forms. Except for two occasions, it ranged between 30 and 100 μM. The DON concentration in the seaweed tanks was usually lower by up to 20 μM than in the fish tank. With no fish in the system (July 1992), DON levels dropped but did not disappear. The DON composition has not been determined.

The concentration of phosphate (Fig. 7) built up slowly, for instance following the drying of the system in March 1991 and September 1992. During regular operation of the system the phosphate levels ranged between 20 and 50 μM. The phosphate concentration in the seaweed tanks was usually slightly lower than in the fish tank. With only two seaweed tanks (June 1991), phosphate concentrations in the system rose by over 10 μM compared with the preceding month. With no fish (July 1992), phosphate concentrations fluctuated.

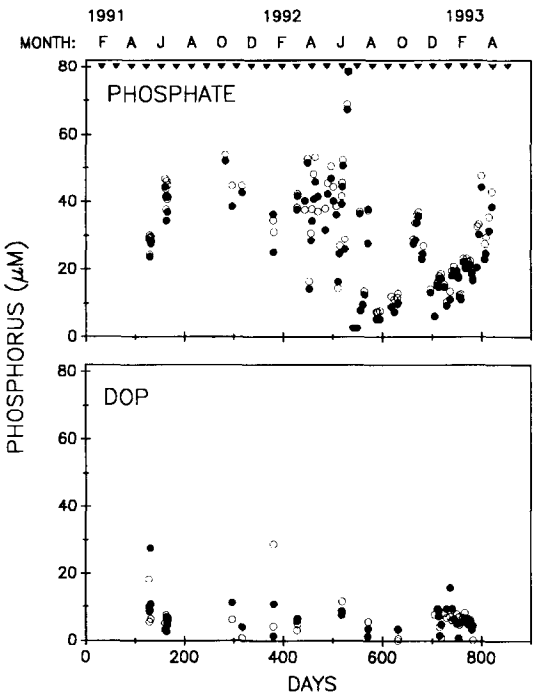

Fig. 7. Concentrations of phosphate and DOP in the model system at 08:30 h during 2 years of system operation in the fish-tank (open circles) and in a seaweed tank (closed circles).

DOP levels were usually low (Fig. 7), and exceeded 12 μM only twice. It dropped slightly with only two seaweed tanks (June 1991) and with no fish (July 1992). The chemical composition and source of the DOP have not been determined.

For the whole system (14 m^2, 9200 l), the cumulative fresh yields of fish and seaweed during about 2 years of operation averaged 15 g m^{-3} day^{-1} and 115 g m^{-2} day^{-1}, respectively.

3.2. The pilot system

As in the model system, the levels of DO and pH (both not shown) in the pilot fish-seaweed system were adequate for the fish at all times. Table 2 summarizes the NH_4^+-N data from the pilot (ponds B2 and B3) and the control phytoplankton-rich conventional fishpond (B1) during the two periods of sampling. The NH_4^+-N concentration in the pilot system was lower and more stable than in the control pond. In the fall of 1990, the NH_4^+-N concentration in the control pond (B1) fluctuated widely and reached 407 μM (5.7 mg NH_4^+-N/l). By contrast, in the fishpond of the pilot system (B2) connected to the seaweed pond, NH_4^+-N concentration remained below 125 μM (1.8 mg N l^{-1}). In the seaweed pond of the pilot system (B3), NH_4^+-N concentration remained below 55 μM (0.8 mg N l^{-1}).

Table 2
Statistical parameters of the NH_4^+-N concentrations (μM) in the pilot system during September–November, 1990 and December–April, 1991. B1 was a conventional fishpond; B2 was a fishpond connected with the seaweed pond B3

	Control, B1, fish	Pilot	
		B2, fish	B3, seaweed
Fall, 1990			
Mean	207	75	22
Min/max	49/407	18/124	2/54
n	59	59	47
s.d.	99	26	15
s.e.	13	3	2
95% confidence	25	7	4
Winter, 1991			
Mean	129	133	65
Min/max	2/571	38/248	14/181
n	98	100	101
s.d.	121	44	33
s.e.	12	4	3
95% confidence	24	9	7

Later, in the winter of 1991, with even more fish and therefore more feed input to the pilot (B2–B3) system than to the conventional (B1) pond, NH_4^+-N levels in all ponds increased. Yet in the pilot fishpond (B2), despite much higher feeding rates, the NH_4^+-N levels were stable (s.d. of 44 and 33 μM in the fishpond and seaweed pond, respectively) and its peaks were below 250 μM (3.5 mg N l^{-1}). Conversely, in the control pond NH_4^+-N concentration fluctuated more (s.d. of 121 μM) and reached a dangerous level of 571 μM (8 mg N l^{-1}).

In a year of operation (1990–1991) this 200-m^2 pilot system produced 1150 kg (16 g m^{-3} day^{-1}) of fish and 2500 kg (35 g m^{-2} day^{-1}) of fresh seaweed biomass.

4. Discussion

The intensive, integrated culture of marine fish with seaweed biofilters took place for several years in two independent systems without the water quality ever deteriorating to levels considered dangerous to the fish. The two principal features that led to this performance were: (1) water recirculation, which provided the fish compartment with many daily exchanges by high quality water from the built-in seaweed biofilters, and (2) photosynthetic assimilatory uptake of nutrients within the seaweed biofilters. This activity counteracted the negative effects of degradative metabolic processes and respiration by fish and microorganisms on water quality. Whereas fish and bacterial metabolism consumed DO, reduced pH and released ammonia and phosphate, the seaweed metabolism, using sunlight, produced DO and increased pH during daytime (which was also the time of maximal oxygen consumption by the morning-fed fish), and simultane-

ously took up NH_4^+-N and phosphate. The system design and operation successfully matched to each other the supply and consumption processes, and therefore maintained a stable water quality. Because of this process matching, the elimination of fish (and its feed) in July 1992 increased only the levels of DO and pH, but not NH_4^+-N, which was supplied then as a salt. On the other hand, the disconnection of a third of the biofiltration capacity in June 1991 led to decreased pH and DO and also increased markedly the NH_4^+-N concentration.

The other nitrogenous forms, DON and oxidized N, did not play a direct role in water quality. The amino acid most common in the DON excreted by marine teleost fish is trimethylaminoxide (TMAO), produced by the fish for osmotic control (Forster and Goldstein, 1969). DON did not accumulate and was lower in the seaweed tanks than in the fish tank, indicating that it was bacterially degraded and contributed to the NH_4^+-N supply (see also in Krom et al., 1995). Evidently, not all of the system's DON (and DOP) originated from the fish and their feed, as it did not disappear when the fish were eliminated. Nitrification consumed NH_4^+-N in competition with the seaweed. Short-term experiments described elsewhere (Krom et al., 1995) showed that nitrification was the second largest consumer of NH_4^+-N in the system. The slow succession rates of NO_2^- and NO_3^- accumulation described here are similar to those described by Nijhof and Bovendeur (1990) for nitrifiers in water of high salinity. Even the transient peaks of NO_2^- concentration in the system remained far below the damaging levels for marine fish reported by Crawford and Allen (1977). Oxidized N concentrations in all the tanks remained alike because *Ulva lactuca*, like many other algae, preferred NH_4^+-N as its N-source (Harlin et al., 1978; Thomas and Harrison, 1987). Hence, water outflow and possibly denitrification were the primary processes to consume the oxidized N. The significant increase in oxidized N concentrations in July 1992 possibly happened because denitrification was limited by feed-derived organic matter, that ceased then to be supplied.

Although phosphate was taken up by the seaweed, its concentrations in the different compartments remained relatively high. This resulted from the low molar N/P ratio (about 9) in the fish feed, the major source of nutrients to the system, compared with the N/P ratio in the algae. Sixteen is the Redfield N/P ratio for phytoplankton composition and our seaweed usually had an even higher N/P ratio (see Krom et al., 1995). Phosphate does not constitute a danger to fish, yet it contributes to eutrophication downstream. To make the seaweed (and other algae) effective in removing phosphate, the molar N/P ratio in the fish feed has to be at or above 16.

The stability and control of the seaweed biofilters, unlike the situation with phytoplankton ponds, allows predictable performance for the integrated system. To ensure the stability of a commercial system of this type, the fish metabolism (through feeding rate) should be adjusted to the biofilter capacity for NH_4^+-N removal. When the NH_4^+-N supply falls in the middle of the seaweed NH_4^+-N uptake-rate curve, the system is self-buffering. Any increase in NH_4^+-N supply is then restrained by a proportional increase in the seaweed uptake rate. Due to this feature, even when one-third of the biofilter was intentionally disconnected (June 1991), when ammonia was accidentally oversupplied (July 30 1992), or when clean seawater was undersupplied (February 7–10 1992), we did not observe the dangerously high levels of NH_4^+-N or low DO and the

ensuing mass mortalities, that are so familiar when comparable events occur in conventional intensive fishponds. On the other hand, in the conventional control pond of the pilot the NH_4^+-N concentration climbed during a phytoplankton crash above 400 μM. This level was reported by Wajsbrot et al. (1991) to endanger the gilthead seabream, especially when accompanied by low DO.

The model system maintained good water quality in-spite of the long overall water residence time of 4.9 days, compared with 2 days or less in typical seawater intensive fishponds (Neori et al., 1989; Gordin et al., 1990). It was possible because the fish tank received many daily exchanges by recirculated water of high quality from the built-in seaweed biofilters. The seaweed significantly contributed also to the oxygen balance of the fish compartment during the time of day when oxygen consumption in the fish tank was highest and saturation level of DO was lowest. At a residence time of about 2 h in the fish tank, the water from the seaweed tanks (with a mean DO content of 8 mg l^{-1}) carried in about 96 mg DO l^{-1} day^{-1}. This was at least 27% of the maximal expected daily DO consumption in the fish tank, since according to Boyd (1990), 600 g of feed (introduced daily into this system) would generate respiration of as much as 600 g of oxygen, or 350 mg DO l^{-1} day^{-1}. Therefore, at a time of aeration failure, the photosynthetic generation of oxygen within the fish-and-seaweed culture system could significantly slow the rate of DO depletion in the fishpond.

The separation of the fish from the algae prevented the exposure of the fish to supersaturation of DO, which was common in our conventional phytoplankton-rich intensive ponds (Erez et al., 1990; Gordin et al., 1990). It also prevented the exposure of the fish to high pH, which could increase ammonia toxicity to them and reduce their appetite. Thus, the fish-and-seaweed culture system described here effectively reduced the risks of fish asphyxiation, gas bubble disease and ammonia poisoning. In over 2 years of operation, the only two cases of mass mortality resulted from hardware breakdowns in the experimental tank system, and once fish were intentionally sacrificed during an epidemic.

The integrated culture system described here can improve the feasibility of land-based mariculture, because the reduced risks of deterioration in water quality and of nutrient release to the environment allow significant increases in fish yields. This advantage is augmented by large seaweed yields, while using less fresh seawater or pond area relative to the land-based mariculture as practiced today. The design and operation of such recirculating fish culture facilities is made easier by the mathematical model of this system described in Ellner et al. (1996).

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