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# Nitrogen pollution in mariculture: toxicity and excretion of nitrogenous compounds by marine fish

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## Contents



## Introduction

Success in intensive aquaculture requires the maintenance of good water quality. Dissolved oxygen (DO) levels > 90% saturation, water pH values between 6.0 and 9.0 depending on the cultured species, and concentrations of suspended solids below 15 mg $l^{-1}$ are preferable in culture systems (review, Poxton, 1990). Sufficient water flow (volume per unit time) through the system is also required to minimize the deleterious effects on water quality of oxygen consumption, carbon dioxide and ammonia excretion by the fish. Consequently, large volumes of farm effluent may be produced with a lower partial pressure of oxygen and higher ammonia content than receiving waters (Gowen *et al.*, 1988). However, effluent is rarely acutely toxic to aquatic life because sufficient dilution of the waste water usually occurs in seawater.

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Concern about the chronic toxicity of farm effluent has led to the development of environmental quality standards (EQS), which must be met before a licence to discharge waste is granted. Although regional variation in the quality standards occurs within Europe (EIFAC, 1982; Highland River Purification Board (RPB), 1987; Seager *et al.*, 1988), the total ammonia and suspended solids concentrations should not exceed about 408 and 6400 mg $kg^{-1}$ fish $day^{-1}$ respectively, while DO consumption by the farm should not exceed 6000 mg $kg^{-1}$ fish $day^{-1}$ (e.g. Highland RPB, 1987). Consequently, receiving waters should have DO values > 80% saturation and the total nitrogen (N) concentration should not exceed 300 $\mu g$ $l^{-1}$ (e.g. Highland RPB, 1987). These EQSs were derived after considering the ecological and toxicological impacts of N-containing effluents in freshwater. Insufficient information on effluent toxicity in seawater, and particularly on ammonia toxicity, has led authorities to apply freshwater EQSs to the marine environment (Mcloughlin and Forster, 1982). The Water Research Centre (UK) suggests an unionized ammonia annual limit of 0.021 mg $l^{-1}$ as $NH_3$-N to protect marine fish life, but argue that insufficient data are available to set an EQS in seawater (Seager *et al.*, 1988).

Despite controls on effluent discharge from aquaculture, deleterious effects on the environment have been reported. These effects are usually localized around the culture system and include the loss of benthic invertebrates arising from the deposition of anaerobic sediment (Leonardsson and Naslund, 1983; Brown *et al.*, 1987; Kaspar *et al.*, 1988). However, several approaches may be employed to improve effluent quality. Firstly, culture systems may be redesigned and/or relocated to allow easier control of farming practices and effluent treatment (Mäkinen *et al.*, 1988; Seymour and Bergheim, 1991), but this is probably only a practical consideration in new or expanding sites. Secondly, discharge consent limits and consequent falls in fish production may be temporarily imposed to allow environmental recovery. Thirdly, and arguably more practicable for existing farms, the feeding practices may be reassessed.

Seymour and Bergheim (1991) identified food wastage as the most important source of N contamination from Norwegian salmonid culture, and similar observations concerning food conversion ratios (FCRs) and wastage have been made in Sweden (Ackefors and Enell, 1990). Nitrogen waste from farms was also compounded by the high N content (8.45% dry weight) of salmonid diets in the 1980s (Ackefors and Enell, 1990). European aquaculture is expanding (Cueff, 1990) and marine fish such as the sea bream (see Appendix Table 1A for family and species names used in this review), sea bass, turbot, Atlantic halibut and sole are being cultured (Cueff, 1990; Garrabé *et al.*, 1990). These new species are also carnivores requiring diets with high N contents. However, the literature on N excretion and feeding in these fish is sparse (Wood, 1958; Birkett, 1969; Sayer and Davenport, 1987; Davenport *et al.*, 1990) compared with that on salmonids (Fromm, 1963; Rychly and Marina, 1977; Paulson, 1980; Wright and Wood, 1985; Houlihan *et al.*, 1986; Brodeur and Pearcy, 1987; Randall and Wright, 1987; Ruggerone, 1989; Milligan *et al.*, 1991). Thus the potential for pollution from developing mariculture is considerable. The UK has adopted a coastal N waste limit for fish culture of 123 kg of N metric $tonne^{-1}$ (t) of fish produced (e.g. Highland RPB, 1987), based on salmonid culture. However, the likely N waste from the culture of many marine species and its relationship to pollution legislation, especially in the Mediterranean countries developing mariculture, is unclear.

This review summarizes the available information on N toxicity and excretion in marine fish and suggests possible contributions to total N waste by farmed fish. In

addition, it identifies those aspects of feeding in finfish culture that can be improved to reduce N pollution.

## Nomenclature of nitrogenous compounds excreted by fish

Fish excrete a variety of nitrogenous compounds including ammonia, urea, trimethylamine, creatine and creatinine (reviews, Forster and Goldstein, 1969; Randall and Wright, 1987). The chemistry of these compounds in both fresh and seawater is complex (Emerson *et al.*, 1975; Fisher *et al.*, 1981; Soderberg and Meade, 1991; reviews, Poxton and Allouse, 1982; Krom and van Rijn, 1989), and particularly in the case of aqueous ammonia, dependent on water pH. We shall not attempt to review N chemistry in natural waters, as excellent treatments are given elsewhere (Fisher *et al.*, 1981; Poxton and Allouse, 1982; Krom and van Rijn, 1989), but some description of terminology is necessary. Total-N refers to the sum concentration of all forms of N present in a particular sample. $NH_3$-N, $NH_4^+$-N, $NO_3^-$-N, $NO_2^-$-N and urea-N refer to the amount of N present as ammonia, ammonium, nitrate, nitrite and urea respectively. Ammonia is a particularly important excretory product of fish and may be excreted as un-ionized ammonia ($NH_3$) or as the ammonium ion ($NH_4^+$). The sum of these two forms of ammonia gives the total ammonia present ($T_{amm}$), while the total amount of nitrogen present in this ammonia is given as TAN (i.e. $T_{amm} = NH_3 + NH_4^+$; TAN = $NH_3$-N + $NH_4^+$-N). Thus distinction is drawn between the forms of aqueous ammonia and those of N, and for example, that the concentration of $NH_3$ is not the same as $NH_3$-N when expressed in mg $l^{-1}$.

## The toxicity and occurrence of nitrogenous compounds in marine finfish culture.

Most fish farms will monitor water quality to ensure good fish husbandry, but also to comply with any discharge consent limits imposed by the regulatory agencies. However, very few of the data which must have been collected have been published. Furthermore, the relationship between farm effluent and the toxicity of N compounds in seawater has not been established.

### *Nitrogen-containing effluents*

Effluent quality from freshwater fish farms has been documented (Bergheim and Selmer-Olsen, 1978; EIFAC, 1982; Penczak *et al.*, 1982; Bergheim *et al.*, 1984; Edsall and Smith, 1989; Foy and Rosell, 1991a, b). Notably, the European Inland Fisheries Advisory Commission (EIFAC) surveyed effluent quality from freshwater fish farms in Europe (EIFAC, 1982). The $T_{amm}$ and $NH_3$ concentrations in effluents were $< 0.3$ and $< 0.01$ mg $l^{-1}$ respectively, well within the recommended EIFAC water quality standard of 0.025 mg $l^{-1}$ as $NH_3$ for freshwater fish (EIFAC, 1982). Clearly, freshwater farms generally produce point-source effluents which can be monitored, and usually comply with EQSs.

In comparison, the data available for effluents from marine culture are limited (Figs 1 and 2). This is partly due to the extensive use of marine pens or cages, rather than land-based farms with an identifiable point of effluent discharge. In those land-based farms that have been studied, outflow TAN levels range between 7.0 and 1780 $\mu$g $l^{-1}$ and $NO_2^-$-N concentrations were 0.12–107 $\mu$g $l^{-1}$. However, the flow of water through the culture systems and the final concentrations of ammonia in receiving waters were not

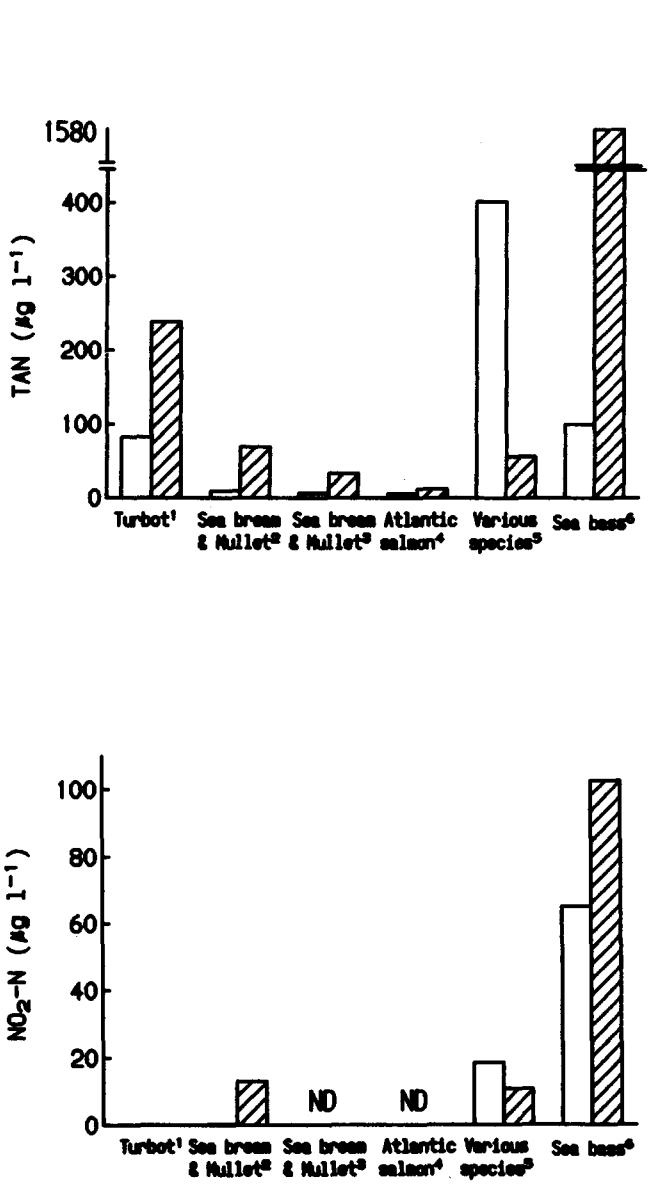



**Fig. 1.** Inflow (open bars) and outflow (shaded bars) water quality in marine fish farms. (a) TAN; (b) $NO_2$-N. ND, no data. [1]Poxton, unpublished data. Land-based farm in the UK. Stock density 32.1 kg $m^{-3}$; pH 7.4; DO 8 mg $l^{-1}$; temp. 15–17 °C. [2]Krom *et al.* (1985b). Marine ponds in Israel. Stock density 0.009 kg $m^{-3}$ (bream), 0.2 kg $m^{-3}$ (mullet); DO 5–15 mg $l^{-1}$; temp. 15–32 °C; salinity 41.5–42.2 ‰. [3]Krom *et al.* (1989). Marine ponds in Israel. Stock density 0.07 kg $m^{-3}$ in winter. [4]Gowen *et al.* (1988). Brackish water cages in the UK. Inflow data collected at a site remote from farm, outflow data collected adjacent to cages. [5]Escaravage (1990). Shallow lagoons in France, filled periodically via sluice gates. DO 2–8 mg $l^{-1}$; temp. 21–28 °C. [6]Saroglia pers. comm. Marine ponds in Italy. Stock density 1.7 kg $m^{-3}$; pH 7.8–8.1; DO 6–10 mg $l^{-1}$; salinity 35–36 ‰.

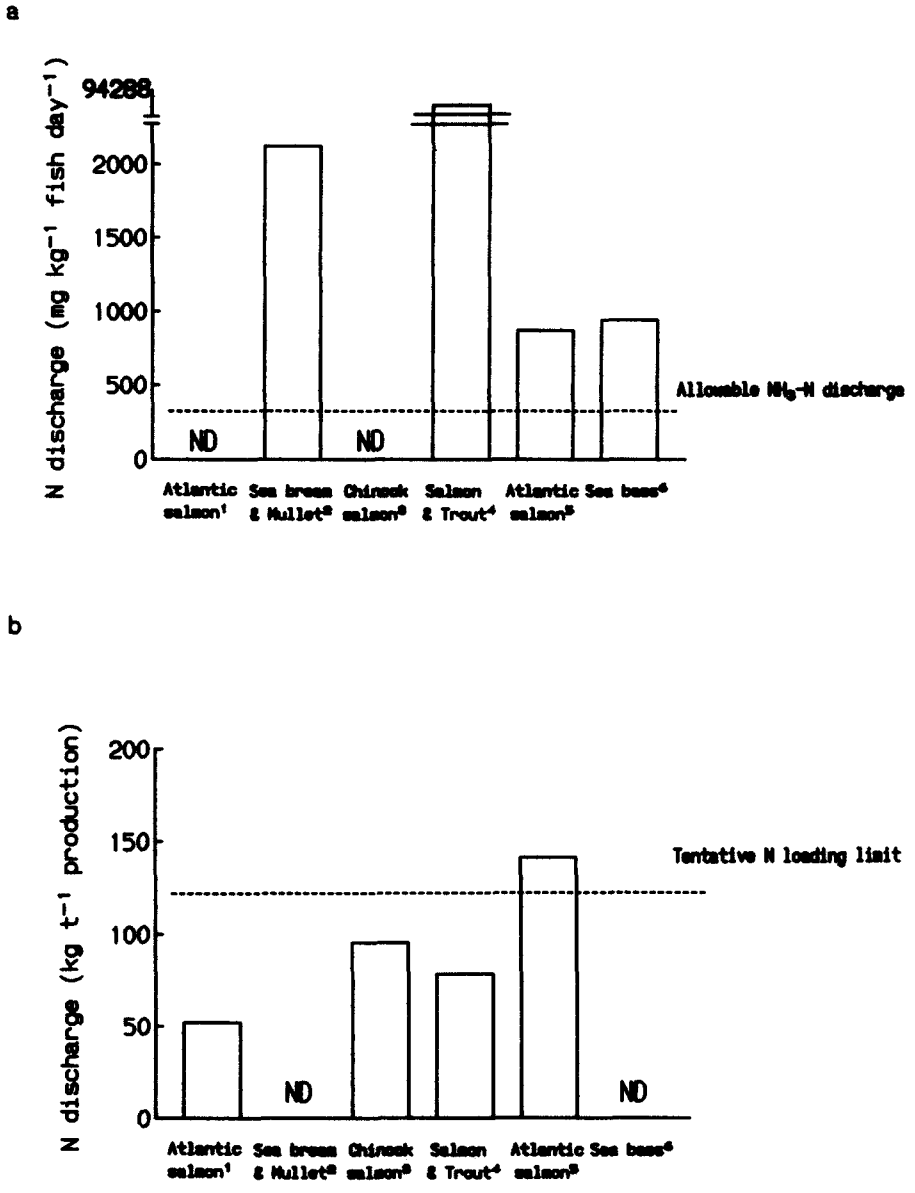



**Fig. 2.** Amounts of nitrogen waste from marine and freshwater farms discharging to seawater. (a) N discharge per kg fish per day; (b) N discharge calculated for each tonne of fish production. Dashed line indicates the daily discharge limit and tentative N loading limit to seawater from UK fish farms respectively. ND, no data. [1]Ibrekk *et al.* (1992). Seawater pens. [2]Krom *et al.* (1985a). Seawater ponds; data calculated from initial stock densities. [3]Kaspar *et al.* (1988). Seawater pens. [4]Ackefors and Enell (1990). Marine and freshwater cages or ponds; data based on annual production and waste rates. [5]Gowen *et al.* (1988). Seawater pens; daily discharge calculated from fish weights and monthly discharge, waste per tonne production calculated from monthly weight gains. [6]Saroglia pers. comm. Seawater ponds.

usually reported (e.g. Krom *et al.*, 1985a), thus the relationship between the amount/quality of effluents and regional EQS is unclear.

The effect of N waste from open culture systems on receiving water quality is difficult to derive, because nutrient inputs from the farm may be masked by other hydrological variables. For example, Gowen *et al.* (1988) measured nitrate concentrations in the vicinity of salmon pens and found levels to be similar to those in other areas in the sea loch. Mixing effects in the water column and the rapid utilization of nutrients by phytoplankton could explain the normal nitrate levels next to cages. However, in the same study, TAN levels were significantly higher next to the farm (Fig. 1), particularly at slack water, but would probably not harm marine life (Wedemeyer, 1980; Seager *et al.*, 1988). Dissolved oxygen levels were low directly below cages, but were normal 30 m away from the farm (Gowen *et al.*, 1988). Thus open culture systems can have very localized effects on water quality, which can be difficult to discern from normal environmental fluctuations.

However, the studies in marine culture systems (Fig. 1) are incomplete; nitrate and urea concentrations, and sometimes total-N contents, of effluent or receiving waters are not routinely reported. Furthermore, in some studies insufficient data are available on fish weight, stocking density and water flow rates, to estimate discharge levels in terms of mg $NH_3$-N $kg^{-1}$ fish $day^{-1}$, the units used to define discharge consent limits from fish farms by some UK agencies (e.g. Highland RPB, 1987). Therefore it is often impossible to determine the margin of safety between actual discharge levels and consent limits. Some data describe N waste in terms of fish production (Fig. 2), and values range between 52 and 200 kg N $t^{-1}$ of fish produced for salmonid culture. The effect of farm production levels on the amount of N waste from non-salmonid marine culture is currently unknown.

The physical characteristics of discharge are also poorly described. Some authors differentiate between dissolved N and that associated with suspended solids (e.g. fresh water: Foy and Rossell, 1991a, b; seawater: Krom *et al.*, 1985a), or at least define 'dissolved N' as including suspended particulate matter (Ackefors and Enell, 1990). Many other reports of effluent characteristics are ambiguous (Bergheim and Selmer-Olsen, 1978; Bergheim *et al.*, 1984; Philips and Beveridge, 1986; Gowen and Bradbury, 1987).

The regulatory agencies also consider the biological impact of effluents discharged into waterways. A numerical relationship between effluent quality/quantity and organism diversity/abundance must be established before the ecological effect of a potential discharge can be estimated. However, few of the published surveys of marine benthos close to culture systems have given detailed information on effluent levels or the water quality (pH, DO, salinity, mineral content, N, P, etc.) associated with changes in biota (e.g. Leonardsson and Naslund, 1983; Brown *et al.*, 1987). Clearly, precise reporting of water quality parameters, water flow rates, effluent dilution in receiving waters, and fish biomass, are needed before a realistic evaluation of marine effluents can be made.

### *Toxicity*

The nitrogenous compounds of most concern in aquaculture are $NH_3$, $NH_4^+$, and $NO_2^-$ because of their known or suspected toxicities to freshwater fish (EIFAC, 1970; Lewis and Morris, 1986; reviews, Meade, 1985; Seager *et al.*, 1988; Russo and Thurston, 1991). Nitrate is a related compound but is not significantly toxic to fish (Russo and

Thurston, 1991), except in the context of eutrophication and algal blooms (Jones *et al.*, 1982). Ammonia is the main nitrogenous excretory product of fish and so could potentially build up to toxic levels in culture systems. Nitrite, on the other hand, occurs at trace levels in seawater (Kalle, 1971; Poxton and Allouse, 1982) and is not excreted in significant quantities by fish (Eddy *et al.*, 1983, Russo and Thurston, 1991). Nitrite is therefore unlikely to be an important toxicant in open culture systems. However, in closed or partially open systems the failure of waste water treatment could lead to significant increases in nitrite concentrations (Poxton and Allouse, 1982; Poxton, 1990; Mayo, 1991).

*Ammonia toxicity*

Un-ionized ammonia is acutely toxic ($LC_{50}$, lethal concentrations producing 50% mortality in 96 h or less) to freshwater fish in the range 0.068–2.0 mg $l^{-1}$ $NH_3$-N (EIFAC, 1970; Seager *et al.*, 1988; Russo and Thurston, 1991). Given such high toxicity, surprisingly few data are available for marine fish (Table 1). Ammonia is acutely toxic between 0.09 and 3.35 mg $l^{-1}$ as $NH_3$-N in seawater for the few species that have been investigated (Table 1). Toxicity is also dependent on salinity, temperature, and water pH (Hazel *et al.*, 1971; Alabaster *et al.*, 1979, 1983; Alderson, 1979; Miller *et al.*, 1990; Soderberg and Meade, 1991; Wajsbrot *et al.*, 1991).

Environmental quality standards cannot be derived from the data in Table 1 because of the varying experimental conditions used (notably salinity and DO) and the extremely sparse chronic toxicity data. The situation is compounded by an absence of reliable field studies (Seager *et al.*, 1988). However, several aspects of ammonia toxicity in seawater are relevant to aquaculture.

Firstly, the ameliorating effects of high DO on acute toxicity could be exploited, particularly when high stocking densities are necessary (during transport etc.). Alabaster *et al.* (1979) reported 24 h $LC_{50}$ for Atlantic salmon of 0.09 and 0.23 mg $l^{-1}$ $NH_3$-N at DO levels of 3.1 and 9.5 mg $l^{-1}$ respectively; thus the risk of ammonia toxicity may be minimized with DO $>$ 10 mg $l^{-1}$ in seawater. Ammonia toxicity is ameliorated at acidic pH values in freshwater (Russo and Thurston, 1991), but the pH effect in seawater is unclear. Miller *et al.* (1990) reported a non-linear response in ammonia toxicity between pH 7 and 5, and found important species differences in susceptibility, although lethality was generally high at pH 7 (unlike toxicity in fresh water). Thus it is difficult to suggest a suitable pH to protect cultured fish from ammonia toxicity in seawater at present. Full-strength seawater is preferable to brackish water because increased salinity (and ionic strength) appears to reduce toxicity (Hazel *et al.*, 1971; Alabaster *et al.*, 1979; Soderberg and Meade, 1991).

Secondly, the paucity of data on chronic effects suggests that the only sensible course of action regarding low levels of ammonia is caution. Ammonia levels around 0.1 mg $l^{-1}$ as $NH_3$-N must be considered suspect, because this is the threshold for no growth for turbot and sole (Alderson, 1979). Furthermore, subtle metabolic disturbances probably occur before reduced growth becomes apparent.

Thirdly, water quality conditions fluctuate in culture systems (review, Poxton, 1992), particularly after the fish have been stressed by handling, transportation etc. (Wedemeyer, 1980). Ammonia levels will also vary dramatically after feeding (Poxton and Allouse, 1987; Poxton and Lloyd, 1989). When fish are exposed to fluctuating $NH_3$ levels, the resulting toxicity may be higher than expected from the continuous exposure

**Table 1.** Toxicity of un-ionized ammonia to marine fish*

| Common name | Salinity (‰) | [Un-ionized ammonia] (mg $NH_3$-N $l^{-1}$) | Notes | Source |
|---|---|---|---|---|
| **Acute** | | | | |
| Inland silverside (larvae) | 31 | 0.76 (96 h) | pH 7 | Miller *et al.* (1990) |
| | | 1.45 | pH 8 | |
| | | 0.61 | pH 9 | |
| Rockling (larvae) | 34.4–35.7 | 0.46 (24 h) | Temp. 15 °C; pH 7.85 | Brownell (1980) |
| White sea bream | 34.4–35.7 | 0.36 (24 h) | Temp. 15 °C; pH 7.85 | Brownell (1980) |
| Striped bass | | | pH 7.5–8.0 | Hazel *et al.* (1971) |
| | 12 | 0.87 (96h) | Temp. 15 °C | |
| | 12 | 1.12 | Temp. 23 °C | |
| | 35 | 0.66 | Temp. 15 °C | |
| | 35 | 0.87 | Temp. 23 °C | |
| Threespine stickleback | | | pH 7.5–8.0 | Hazel *et al.* (1971) |
| | 12 | 1.50 (96 h) | Temp. 15 °C | |
| | 12 | 1.4 | Temp. 23 °C | |
| | 35 | 3.35 | Temp. 15 °C | |
| | 35 | 1.61 | Temp. 23 °C | |
| Sheepshead minnow (larvae) | 32.5 | 1.72 (96 h) | pH 8.0–8.1 | Miller *et al.* (1990) |
| | 32.0 | 2.29 | pH 7.9–8.1 | |
| | 30.0 | 2.89 | pH 7.6–7.9 | |
| Chinook salmon (parr) | 0.0 | 0.30 (24 h) | DO 8.2–9.8 mg $l^{-1}$; temp. 11.7–13.0 °C | Harader and Allen (1983) |
| | 5.2 | 0.72 | | |
| | 9.6 | 1.80 | | |
| | 16.9 | 1.14 | | |
| | 27.6 | 0.95 | | |
| Rainbow trout (yearlings) | 0.0 | 0.46 (24 h) | pH 7.45; temp. 13.6 °C | Herbert and Shurben (1965) |
| | 5.0 | 0.66 | | |
| | 10.0 | 1.06 | | |
| | 36.0 | 0.59 | | |
| Atlantic salmon (smolts) | 0.0 | 0.23 (24 h) | pH 7.51–7.81 | Herbert and Shurben (1965) |
| | 18.0 | 0.29 | | |
| | 27.0 | 0.27 | | |
| Atlantic salmon (smolts) | 0.0 | 0.12 (24 h) | DO 9.6 mg $l^{-1}$ | Alabaster *et al.* (1979) |
| | 10.2 | 0.23 | DO 9.5 mg $l^{-1}$ | |
| | 0.0 | 0.07 | DO 3.5 mg $l^{-1}$ | |
| | 10.2 | 0.09 | DO 3.1 mg $l^{-1}$ | |
| Spotted seatrout (juveniles) | 13–14 | 1.38–1.98 (24 h) 0.98–1.72 (96 h) | pH 7.8–8.0; temp. 26–27 °C | Daniels *et al.* (1987) |
| Sea bream (juveniles) | 40.5 | 1.59 (96 h) | DO 93% sat. | Wajsbrot *et al.* (1991) |
| | | 1.05 | DO 61% sat. | |
| | | 0.80 | DO 33% sat. | |
| | | 0.34 | DO 26% sat. | |

**Table 1.** continued.

| Common name | Salinity (‰) | [Un-ionized ammonia] (mg $NH_3$-N $l^{-1}$) | Notes | Source |
|---|---|---|---|---|
| **Sublethal** | | | | |
| Turbot | ND | 0.09 | No effect on growth | Hampson (1976) |
| Turbot | 34 | 0.11 (11 days) | Threshold for no effect on growth | Alderson (1979) |
| | | 0.3–0.9 | No growth; pH 6.9–7.9 | |
| Dover sole | ND | 0.04 | No effect on growth | Hampson (1976) |
| | | 0.75 | No growth or feeding | |
| Dover sole | 34 | 0.066 (11 days) | Threshold for no effect on growth | Alderson (1979) |
| | | 0.38–0.77 | No growth; pH 6.9–7.9 | |

*Table modified from Seager *et al.* (1988) and updated. Figures in parentheses indicate duration of acute $LC_{50}$ test or exposure duration in sublethal experiments where known. ND, no data.

$LC_{50}$ value, and more difficult to predict (Brown *et al.*, 1969; Ruffier *et al.*, 1981; Thurston *et al.*, 1981). Thus an additional safety margin should be included to account for the variability of ammonia levels in culture systems.

*Nitrite toxicity*

Nitrite is acutely toxic to freshwater-adapted salmonids in the range 0.19–0.88 mg $l^{-1}$ as $NO_2^-$-N, while largemouth bass are among the most tolerant freshwater fish with a 96 h $LC_{50}$ value of 140.2 mg $l^{-1}$ $NO_2^-$-N (Colt and Tchobanoglous, 1976; Palachek and Tomasso, 1984; Lewis and Morris, 1986; Russo and Thurston, 1991). The literature on $NO_2^-$ toxicity to marine fish is very sparse, with 24 h $LC_{50}$ for $NO_2^-$-N ranging from 675 mg $l^{-1}$ for the milkfish in brackish water, to > 4000 mg $l^{-1}$ for rockling larvae in 100% seawater (Table 2). Few data are available on water pH, temperature and salinity effects on lethality (Table 2). The effect of temperature on nitrite toxicity to most marine fish is unknown. However, Saroglia *et al.* (1981) reported an increase in toxicity to sea bass with an increase in temperature from 17 to 27 °C. High salinity may protect fish from toxicity; Crawford and Allen (1977) found that nitrite was far less toxic to chinook salmon in seawater than in freshwater. In one study (Almendras, 1987), $NO_2^-$–was more toxic to milkfish in freshwater than in brackish water. Elevating salinity from 0 to 36 ‰ increases the 168 h $LC_{50}$ value for the European eel from 84 to 974 mg $l^{-1}$ $NO_2^-$-N (Saroglia *et al.*, 1981). Various explanations have been offered for the ameliorating effects of salts on $NO_2^-$ toxicity (review, Lewis and Morris, 1986). These include $Ca^{2+}$ induced changes in gill permeability to $NO_2^-$ and the competitive inhibition of $NO_2^-$ uptake by $Cl^-$ in freshwater-adapted fish (Crawford and Allen, 1977; Eddy *et al.*, 1983; Lewis and Morris, 1986). Nitrite uptake kinetics across the gills of stenohaline marine fish and the associated physico-chemical effects of seawater have not been studied.

There are no studies on the chronic toxicity of $NO_2^-$ in seawater. Sublethal effects

**Table 2.** Toxicity of nitrite to marine and brackish water fish

| Common name | Salinity (‰) | $[NO_2\text{-}N]$* (mg $l^{-1}$) | Notes | Source |
|---|---|---|---|---|
| **Acute** | | | | |
| Spotted seatrout (larvae) | 25–30 | 980 (24 h) | pH 7.8–8.0; temp. 26–27 °C | Daniels *et al.* (1987) |
| Milkfish (juveniles) | 0.0 | 12 (48 h) | pH 7.9–8.3 | Almendras (1987) |
| | 16 | 675 | pH 8.0–8.5; temp. 27 °C | |
| Rockling (larvae) | 34.4–35.7 | > 4000 (24 h) | pH 7.79–7.85; temp. 14.8–15.2 °C | Brownell (1980) |
| White sea bream (larvae) | 34.4–35.7 | 1360 (24 h) | pH 7.79–7.85; temp. 14.8–15.2 °C | Brownell (1980) |
| Chinook salmon | 32.5 | 325.6 | 10% mortality in 48 h | Crawford and Allen (1977) |
| Sea bass | 36 | 274 (96 h) | Temp. 17 °C | Saroglia *et al.* (1981) |
| | 36 | 220 | Temp. 23 °C | |
| | 36 | 154 | Temp. 27 °C | |
| European eel | 0–36 | 84–974 (168 h) | Temp. 20 °C; pH 8.0–8.2 | Saroglia *et al.* (1981) |
| **Sublethal** | | | | |
| Sea bass | 36 | 87.2 (96 h) | 96 h †$EC_{50}$ for reduction in blood [haemoglobin] | Scarano *et al.* (1984) |
| | 36 | 12.9 | 10.2% methaemoglobin in 96 h | |
| Chinook salmon | 37.5 | 37.5 (48 h) | Threshold for methaemoglobin formation | Crawford and Allen (1977) |
| Rainbow trout (fingerlings) | 16 | 315 (24 h) | 50% methaemoglobin formation in 12 h | Eddy *et al.* (1983) |

*Figures in parentheses indicate duration of acute $LC_{50}$ test or the exposure period of the sublethal test.
†$EC_{50}$ is the concentration of toxicant required to reduce 50% of the blood haemoglobin to methaemoglobin.

include methaemoglobin formation, which causes hypoxia and may be a principal cause of death. The threshold level for methaemoglobin formation in chinook salmon is 37.5 mg $l^{-1}$ $NO_2^-$-N (Crawford and Allen, 1977; Table 2), but sea bass may be more sensitive, with methaemoglobin formation with exposure to 12.9 mg $l^{-1}$ $NO_2^-$-N (Scarano *et al.*, 1984; Table 2). In freshwater, ionoregulatory disturbances occur at 3.0–7.7 mg $l^{-1}$ $NO_2$ $O_3^-$-N (Williams and Eddy, 1986). In the absence of significant quantities of data for chronic effects on marine fish, nitrite levels one-tenth of that known to produce methaemoglobinaemia should be considered potentially toxic.

The toxicity of ammonia and nitrite to marine fish is clearly an area in need of research, preferably before water reuse systems and land-based mariculture develop further.

## Nitrogen excretion in marine fish

Although N excretion in fish has been extensively studied (reviews, Forster and Goldstein, 1969; Randall and Wright, 1987), much of the earlier work focused on freshwater species (Smith, 1929; Fromm, 1963; Fromm and Gillette, 1968; Savitz, 1969, 1971; Gerking, 1971; Brett and Zala, 1975; Rychly and Marina, 1977; Savitz *et al.*, 1977), with the notable exceptions of Wood (1958), Birkett (1969), and Guérin-Ancey (1976a, b). Basal N excretion rates are about 1.35–23.05 mg N $kg^{-1}$ $h^{-1}$ in starved or unfed freshwater fish (Savitz, 1971; Brett and Zala, 1975; Sayer and Davenport, 1987; Saha and Ratha, 1989), but may be an order of magnitude higher in fed animals (Dabrowski and Kaushik, 1984; Poxton and Lloyd, 1989), and are also dependent on temperature (Ramaballav and Baran, 1990; Forsberg and Summerfelt, 1992). Most freshwater fish excrete ammonia as the chief N waste, but can also excrete urea (Forster and Goldstein, 1969; Randall and Wright, 1987). In a few species, urea-N can make a substantial contribution to total-N waste (*Chalcalburnus tarichi*: Danulat and Kempe, 1992; lungfishes: Saha and Ratha, 1989; tilapia: Sayer and Davenport, 1987). One species of tilapia in Lake Magadi, Kenya (*Oreochromis alcalicus grahami*) is exclusively ureotelic (Wood *et al.*, 1989). Freshwater fish excrete N waste from the gills (Wright and Wood, 1985; Randall and Wright, 1987), renal N loss being negligible (Fromm, 1963) although the urine contains both ammonia and urea (Smith, 1929; Curtis and Wood, 1991). Nitrogen excretion in marine teleosts is broadly similar to that of freshwater species, although there are some important differences.

### *Nitrogenous excretion rates from marine fish*

The available data on N excretion rates in marine fish are summarized in Table 3. The basal total-N excretion rates for unfed fish range between 1.35 and 34.93 mg $kg^{-1}$ $h^{-1}$. Interestingly the lower values are associated with sessile benthic species (e.g. Gulf toadfish, blenny) while the highest values are from salmonids (e.g. Arctic charr). The ingestion of food has a marked effect on N excretion (Table 3). Turbot fed on strips of fish-flesh had elevated excretion rates lasting for about 16 h (Poxton and Allouse, 1987). Post-prandial increases in N excretion last 19–95 h in Atlantic cod (Ramnarine *et al.*, 1987) and about 10 h in American eels (Gallagher and Mathews, 1987). High TAN excretion rates are also evident in lemon sole, Atlantic halibut and Japanese flounder 24 h after feeding (Davenport *et al.*, 1990; Kikutchi *et al.*, 1991). Maximum post-feeding TAN excretion rates vary between 6 and 140 mg $kg^{-1}$ $h^{-1}$, with the notable exception of the Cape anchovy which excretes an incredible 600 mg $kg^{-1}$ $h^{-1}$ (Table 3). Post-prandial N excretion rates are, not surprisingly, dependent on ration size (Ramnarine *et al.*, 1987) and the protein content of the diet (Jobling, 1981; Gallagher and Mathews, 1987).

Fish are poikilotherms and so N metabolism (and therefore excretion) will depend on the weight-specific metabolic rate and the body temperature of each species (Jobling, 1981). Small fish have higher excretion rates than large fish (plaice: Birkett, 1969; Jobling, 1981; sea bream: Porter *et al.*, 1987). This may not be true for all size ranges of fish (sole: Birkett, 1969).

The few reports of temperature effects on N excretion in marine fish (Table 3) suggest that N loss increases with temperature (Guérin-Ancey, 1976a; Jobling, 1981), similar to the responses of freshwater fish (Savitz, 1969; Forsberg and Summerfelt, 1992). The rate of N excretion also appears to depend on the thermal range of the fish. Jobling (1981)

**Table 3.** Excretion rates of nitrogenous compounds from marine fish

| Common name | Nitrogenous excretion | Excretion rate (mg $kg^{-1}$ $h^{-1}$) | Notes | Source |
|---|---|---|---|---|
| Blenny | Total-N | 2.05 | Unfed for 6 days; 13 °C | Sayer and Davenport (1987) |
| | TAN | 1.53 | | |
| | Urea-N | 0.53 | | |
| Dab | Total-N | 7.36 | Unfed for 6 days; 13 °C | Sayer and Davenport (1987) |
| | TAN | 6.86 | | |
| | Urea-N | 0.51 | | |
| Plaice | Total-N | 2.33 | Basal excretion (16–28 g fish) | Birkett (1969) |
| | | 8.66 | Basal excretion (0.7–3.7 g fish); 17 °C | |
| Sole | Total-N | 6.20 | Basal excretion (6–53 g fish) | Birkett (1969) |
| | | 5.00 | Basal excretion (0.6–1.8 g fish); 17 °C | |
| Gulf toadfish | TAN | 0.95 | Unfed; 15 °C | Goldstein *et al.* (1982) |
| Cape anchovy | Total-N | 34.93 | Unfed 48 h | James *et al.* (1989) |
| | TAN | 24.31 | Unfed 48 h | |
| | | 600 | Maximum after feeding | |
| | Urea-N | 60–80 | Maximum after feeding | |
| Atlantic cod | TAN | 12.34–37.5 | Maximum excretion rate; ration 0.5–3.5% bw | Ramnarine *et al.* (1987) |
| Japanese flounder | | | Average value 0–24 h after feeding | Kikuchi *et al.* (1991) |
| | TAN | 5.37–7.91 | Ration 0.5–1.5% bw | |
| | Urea-N | 0.75–1.04 | Ration 0.5–1.5% bw | |
| Mudskipper | TAN | 7.66 | Unfed for 16.5–24 h | Gregory (1977) |
| | Urea-N | 1.29 | | |
| Peruvian anchovy | Total-N | 21.12 | Starved for 24 h | McCarthy and Whitledge (1972) |
| | | 29.16 | Fed | |
| | TAN | 10.0 | Starved for 24 h | |
| | | 11.70 | Fed | |
| | Urea-N | 3.45 | Starved for 24 h | |
| | | 3.70 | Fed | |
| | Creatine | 4.92 | Starved for 24 h | |
| | | 4.63 | Fed | |
| Lemon sole | TAN | 3.26 | Unfed for 6 days | Davenport *et al.* (1990) |
| | | 6.37 | 24 h after feeding; 10 °C | |

**Table 3.** continued.

| Common name | Nitrogenous excretion | Excretion rate (mg $kg^{-1}$ $h^{-1}$) | Notes | Source |
|---|---|---|---|---|
| Atlantic halibut | TAN | 2.32 | Unfed for 6 days | Davenport *et al.* (1990) |
| | | 5.08 | 24 h after feeding; 10 °C | |
| Atlantic cod | TAN | 0.81 | Unfed 48 h; 8 °C | Lied and Braaten (1984) |
| | | 8.76 | Post-feeding peak | |
| | | 5.66 | 9–10 h post-feeding | |
| American eel | TAN | | 24 h after feeding | Gallagher and Mathews (1987) |
| | | 57.64 | P/E ratio 70 mg $kcal^{-1}$ | |
| | | 98.82 | P/E ratio 80 mg $kcal^{-1}$ | |
| | | 140.0 | P/E ratio 90 mg $kcal^{-1}$ | |
| Starry flounder | Total-N | 67.04 | Probably fed; recalculated data for one fish; 12 °C | Wood (1958) |
| | TAN | 57.82 | | |
| | Urea-N | 7.70 | | |
| | TMA-N* | 0.74 | | |
| | TMAO-N* | 0.35 | | |
| | Creatine plus creatinine | 0.17 | | |
| Sea bream | TAN | | Maximum after feeding; 24.2 °C | Porter *et al.* (1987) |
| | | 70 | 3 g fish | |
| | | 36.4 | 40 g fish | |
| | | 25.2 | 90 g fish | |
| Japanese flounder | | | 20 °C, unfed for 24–72 h | Kikuchi *et al.* (1990) |
| | TAN | 7.62 | 1.8–5.1 g fish | |
| | | 2.25 | 15–49 g fish | |
| | | 2.00 | 163–575 g fish | |
| | Urea-N | 0.87 | 1.8–5.1 g fish | |
| | | 0.71 | 15–49 g fish | |
| | | 0.42 | 163–575 g fish | |
| Sea bass | TAN | 2.08 | 12–14 °C | Guérin-Ancey (1976a) |
| | | 9.16 | 16–18 °C | |
| | | < 1.25 | > 20 °C | |
| | Urea-N | 1.16 | 12–14 °C | |
| | | 0.66 | 16–18 °C | |
| | | 0.83 | > 20 °C | |
| Gulf toadfish | TAN | 1.04 | Unfed for at least 3 days | Walsh *et al.* (1990) |
| | Urea-N | 0.31 | | |
| | Total-N | 1.86 | Re-immersion after 8 h aerial exposure; unfed fish | |
| | TAN | 1.67 | | |
| | Urea-N | 0.18 | | |

**Table 3.** continued.

| Common name | Nitrogenous excretion | Excretion rate (mg $kg^{-1}$ $h^{-1}$) | Notes | Source |
|---|---|---|---|---|
| Atlantic salmon | Total-N | 9.06 | Cultured fish; density | Fivelstad *et al.* |
| | TAN | 6.00 | 108 kg $m^{-3}$; 12 °C | (1990)† |
| | Urea-N | 0.90 | | |
| Arctic charr | Total-N | 22.8 | Cultured fish; density | Fivelstad *et al.* |
| | TAN | 11.70 | 64–86 kg $m^{-3}$; 6 °C | (1990)† |
| | Urea-N | 1.32 | | |

*TMA-N and TMAO-N are trimethylamine and trimethylamine oxide nitrogen respectively.
†Data from Fivelstad *et al.* (1990) were calculated from inflow and outflow water quality.

noted that the largest $Q_{10}$ value for plaice was recorded between 5 and 10 °C, temperatures typical of UK waters. Ammonia excretion rates decrease in two-year-old sea bass when temperature exceeds the preferred thermal range, causing an apparent shift towards ureotelism above 20 °C (Guérin-Ancey, 1976a).

Ammoniotelism is the predominant mode of N excretion in marine teleosts (Table 3), even though most fish have the enzymes necessary for urea excretion (Forster and Goldstein, 1969). However, some marine fish are capable of significant ureotelism (Table 4), most notably elasmobranchs which retain urea to maintain osmotic balance (Forster and Goldstein, 1969). There appears to be no taxonomic-related trend in urea excretion for marine teleosts (Tables 3 and 4), but the extent of ureotelism is greater than previously suggested for fish (Forster and Goldstein, 1969; Randall and Wright, 1987). Notably, the Gulf toadfish will excrete 90% of its N waste as urea if ammonia loss is restricted by aerial exposure (Walsh *et al.*, 1990). If fish are grouped on an edibility basis, the species most likely to be cultured by humans produce the least urea (Table 4). Trimethylamine oxide (TMAO) was suggested to contribute a 'relatively large fraction of the N excreted by marine fish' (Forster and Goldstein, 1969). This is not true for at least three species of marine teleost (Wood, 1958), and unlikely in 12 other species where TAN and urea-N constitute most of the total-N loss (Tables 3 and 4). Marine teleosts are thus ammoniotelic with perhaps a broader capacity for ureotelism than freshwater species.

*Routes of nitrogenous excretion in marine fish*

The literature on branchial, renal, faecal, and cutaneous routes of N excretion in marine fish is sparse (Table 5). Only a handful of studies have attempted to quantify branchial contributions to N excretion (Goldstein *et al.*, 1982; Sayer and Davenport, 1987; Evans and More, 1988; Milligan *et al.*, 1991), and in those experiments fish have remained unfed. Basal excretion rates across the gills range between 2.45 and 7.00 mg $kg^{-1}$ $h^{-1}$ as TAN, assuming that N excretion from fish heads is mostly branchial (Table 5). However, values may be higher in ammonia-infused fish where excretion across the gills can reach 44.8 mg $kg^{-1}$ $h^{-1}$ as TAN (Milligan *et al.*, 1991). The mechanism of branchial ammonia loss is by diffusion in coho salmon, because elevated blood ammonia increases excretion

**Table 4.** Ureotelism in marine teleost fish

| Common name | Percentage of total-N as urea-N (%) | Source |
|---|---|---|
| **Non-edible fish** | | |
| Corkwing wrasse | 4.5 | Sayer and Davenport (1987) |
| White steenbras | 6–8 | Cockcroft and Du Preez (1989) |
| Pogge | 16.4 | Sayer and Davenport (1987) |
| Sea scorpion | 17.40 | Sayer and Davenport (1987) |
| Sculpin | 21.5 | Wood (1958) |
| Blenny | 25.8 | Sayer and Davenport (1987) |
| Sea perch | 38.0 | Wood (1958) |
| Gulf toadfish | 10–90 | Walsh *et al.* (1990) |
| **Edible fish** | | |
| Arctic charr | 5.7 | Fivelstad *et al.* (1990) |
| Dab | 6.9 | Sayer and Davenport (1987) |
| Atlantic salmon | 9.9 | Fivelstad *et al.* (1990) |
| Starry flounder | 11.5 | Wood (1958) |

rates (Milligan *et al.*, 1991). Evidence also exists for $NH_4^+$ excretion in exchange for $H^+$ or $Na^+$ (Evans, 1977; Goldstein *et al.*, 1982; Evans and More, 1988).

Urea excretion from the head region of marine teleosts is low (Sayer and Davenport, 1987), and negligible across the gills of at least one marine teleost (Goldstein *et al.*, 1964). Urea has a low oil–water partition coefficient and therefore will not diffuse readily across fish gills (Forster and Goldstein, 1969). The excretion of other forms of N (TMA, TMAO, etc.) across the gills of marine fish has not been investigated.

Urinary N losses are unknown for many species, partly because of the difficulty in collecting representative urine samples from fish (Fromm, 1963; Curtis and Wood, 1991). Urinary N excretion varied between 54.1 and 6.25 mg N $kg^{-1}$ $h^{-1}$ with progressive starvation in freshwater rainbow trout (Fromm, 1963). Curtis and Wood (1991) found much lower urinary N losses of 0.0188 and 0.0540 mg $kg^{-1}$ $h^{-1}$ as TAN and urea-N respectively, for unfed trout using an improved method (external catheter). Urinary N losses have been measured in one marine teleost, the goosefish; TAN and urea-N output were 0.084 and 0.007 mg $kg^{-1}$ $h^{-1}$ respectively using the composite data of Hickman and Trump (1969). Renal N loss is considered negligible in many marine teleosts because of low glomerular filtration rate (GFR) and urine flow. When rainbow trout are transferred to seawater, urine flow drops to $> 1$ ml $kg^{-1}$ $h^{-1}$ and GFR is almost zero (Rankin and Davenport, 1981). Similarly, when the euryhaline flounder, *Paralichthys lethostigma*, is in 100% seawater, urine flow drops to 0.108–0.59 ml $kg^{-1}$ $h^{-1}$ (Hickman, 1968), compared with 2–4 ml $kg^{-1}$ $h^{-1}$ in freshwater fish (Hunn, 1982; Eddy and Talbot, 1985). Glomerular development is also poor in marine fish with GFR around 1 ml $kg^{-1}$ $h^{-1}$, compared with 4 ml $kg^{-1}$ $h^{-1}$ or more in freshwater fish (Hickman and Trump, 1969).

Few measurements of cutaneous N loss exist for marine fish. In Sayer and Davenport's (1987) divided box experiment it is possible that a large portion of the N loss was cutaneous. The fish were starved so faecal loss would be small, and because urine flow is

**Table 5.** Routes of nitrogenous excretion from marine fish

| Common name | Route | Nitrogenous excretion | Excretion rate (mg $kg^{-1}$ $h^{-1}$) | Notes | Source |
|---|---|---|---|---|---|
| **Unfed** | | | | | |
| Coho salmon | Gills | TAN* | 3.78 | Control | Milligan *et al.* (1991) |
| | | | 44.8 | $NH_3$ infusion | |
| | | | 7.00 | Exhaustive exercise | |
| Starry flounder | Gills | TAN* | 2.45 | Control | Milligan *et al.* (1991) |
| | | | 22.40 | $NH_3$ infusion | |
| | | | 3.36 | Exhaustive exercise | |
| Gulf toadfish | Gills | | | Isolated head | Goldstein *et al.* (1982) |
| | | TAN | 2.72 | Perfusate pH 6.8 | |
| | | | 3.47 | Perfusate pH 7.8 | |
| Dogfish pup | Gills | TAN | 2.25–2.71 | Isolated head | Evans and More (1988) |
| Dab | Head | Total-N | 3.83 | Divided box experiment; 13 °C; unfed for 6 days | Sayer and Davenport (1987) |
| | | TAN | 3.57 | | |
| | | Urea-N | 0.26 | | |
| | Body | Total-N | 3.53 | | |
| | | TAN | 3.29 | | |
| | | Urea-N | 0.25 | | |
| Blenny | Head | Total-N | 1.08 | Divided box experiment; 13 °C; unfed for 6 days | Sayer and Davenport (1987) |
| | | TAN | 0.72 | | |
| | | Urea-N | 0.36 | | |
| | Body | Total-N | 0.97 | | |
| | | TAN | 0.81 | | |
| | | Urea-N | 0.17 | | |
| Goosefish | Urine | TAN | 0.084 | Derived from composite data of various studies | Hickman and Trump (1969) |
| | | Urea-N | 0.007 | | |
| **Fed** | | | | | |
| Sea bream | Faeces | | | Calculated from daily excretion values at 24 °C | Porter *et al.* (1987) |
| | | Total-N | 13.76–10.73 | 3 g fish; ration 4–5% bw $day^{-1}$ | |
| | | | 3.20–1.4 | 90 g fish; ration 1.4–2% bw $day^{-1}$ | |
| Japanese flounder | Faeces | Total-N | 1.29–1.41 | Ration 0.5–1.5% bw $day^{-1}$ | Kikuchi *et al.* (1991) |

*Estimated values for cannulated fish derived from flux histograms.

low in marine fish, the skin remains the probable route of N excretion. Indeed, in the dab experiment the faecal and urinary openings were in the anterior chamber and 47% of the total-N loss was attributed to cutaneous excretion (Sayer and Davenport, 1987; Table 5). Nitrogen may be lost with secreted body mucus, because mucus from fish contains both ammonia and urea (Handy, 1989). The blenny excretes 70% of its ammonia output via the body surface mucus during exposure to air (Davenport and Sayer, 1986; Sayer and Davenport, 1987).

There have been numerous studies on N nutrition and protein uptake by the gut of fish (Grove *et al.*, 1985; Houlihan *et al.*, 1988, 1989; Cockcroft and Du Preez, 1989; James *et al.*, 1989; McMillan and Houlihan, 1989; Spyridakis *et al.*, 1989; reviews, Brett and Groves, 1979; Fange and Grove, 1979; Bowen, 1987; Hardy, 1989), but only a few reports of faecal N losses in marine fish (Table 5). Workers have determined N 'assimilation efficiencies' (also termed N 'digestibility coefficients'; see Fange and Grove, 1979, p. 192; Hardy, 1989, p. 540) for marine teleosts (Grove *et al.*, 1985; Jobling, 1986; Cockcroft and Du Preez, 1989; James *et al.*, 1989; Spyridakis *et al.*, 1989), and must have estimated the total amount of faecal N waste during their experiments (directly or with a marker, e.g. chromic oxide). However, faecal N loss may be presented as a percentage of N intake, and the data from which the percentage was calculated are sometimes omitted (Cockcroft and Du Preeze, 1989; Spyridakis *et al.*, 1989). Faecal N loss was determined in the sea bream fed pelleted food over a 24 h period, and values ranged between 1.4 and 13.76 mg N $kg^{-1}$ $h^{-1}$ (Table 5), representing 5.5–19.6% of the total N lost by the fish (Porter *et al.*, 1987). In the Japanese flounder (Tables 3 and 5), faecal N excretion contributes 13.3–37.8% of the total-N loss, with faecal losses notably higher in the 24–48 h period after feeding (Kikuchi *et al.*, 1991), probably relating to the gut transit time of flatfish (Davenport *et al.*, 1990). Thus for at least two marine fish, faecal N loss contributed significantly to the total waste produced.

Faecal N output may be derived from measurements of gastric evacuation rates and N assimilation efficiencies (Table 6), assuming that the average emptying rate of the stomach is reflective of the emptying time of the whole gut. This assumption is probably true given the gastric retention times (Olson and Mullen, 1986; Jobling, 1987) and short intestinal length of carnivorous fish. Ration size multiplied by the gastric evacuation rate will give an estimate of the gut transit time for a particular meal. 'Faecal' N content can then be calculated, if the N assimilation efficiency and N content of the food before digestion are known. Faecal N content divided by the gut transit time will give a faecal N excretion rate. These rates range from $< 1$ mg N $kg^{-1}$ $h^{-1}$ at high assimilation efficiencies, to about 15 mg N $kg^{-1}$ $h^{-1}$ when absorption is poor (Table 6). Cultured fish will normally be fed formulated diets in controlled conditions and can expect to have N assimilation efficiencies of around 95% (e.g. Grove *et al.*, 1985). Thus faecal N excretion in cultured fish is more likely to be around 1–3 mg N $kg^{-1}$ $h^{-1}$ (Table 6) which is comparable with the few measured values (Table 5). Excretion estimates of 15 mg N $kg^{-1}$ $h^{-1}$ are somewhat unrealistic under normal circumstances, but do represent the 'worst-case scenario' where assimilation efficiency is low owing to factors such as poor food formulation (Jobling, 1986) or disease.

*Relevance of nitrogen excretion physiology to farm effluents*

The N excretion rates for marine fish (Table 3) may be used to estimate the likely farm output of N due to fish metabolism (Fig. 3). Many edible marine teleosts have daily N

**Table 6.** Calculated faecal nitrogen excretion rates for marine fish. The N content of the gut after digestion and absorption are estimated from the dry weights of the rations and N assimilation efficiencies. Average gut clearance times are calculated from meal size divided by the gastric evacuation rate, except for the data of Davenport *et al.* (1990) which are direct measurements of gut transit time. N assimilation efficiencies represent 'best' and 'worst' values reported in the literature, while an efficiency of 95% is typical of carnivorous fish under controlled conditions

| Common name (average weight kg)* | Meal size (g) (ration as percent body weight)*† | Gastric evacuation rate ($g\ h^{-1}$) (temp. °C)*‡ | Estimated gut clearance time for meal (h) | N assimilation efficiency (%) | N remaining in gut contents after meal digestion and adsorption (mg N) | Faecal excretion rate (mg N $kg^{-1}\ h^{-1}$) | Source |
|---|---|---|---|---|---|---|---|
| Atlantic cod | 16 | 0.44 | 36.36 | 68 | 512.0 | 17.49 | Santos and Jobling |
| (0.805) | F, 1.98%) | (1.2–2.6) | | 95 | 80.0 | 2.73 | (1991) |
| | | | | 99 | 16.0 | 0.54 | |
| Turbot | 20.8 | 0.75 | 27.73 | 68 | 665.6 | 4.62 | Bromley (1987) |
| (5.2) | (F, 0.4%) | (16) | | 95 | 104.0 | 0.72 | |
| | | | | 99 | 20.8 | 0.144 | |
| Turbot | 0.739 | 0.094 | 7.86 | 68 | 23.6 | 7.16 | Bromley (1987) |
| (0.42) | (F, 3.7%) | (16) | | 95 | 3.7 | 1.12 | |
| | | | | 99 | 0.7 | 0.22 | |
| Coho salmon | 8.02 | 0.112 | 71.60 | 68 | 256.6 | 10.54 | Brodeur and Pearcy |
| (0.34) | (SF, 2.36%) | (11.1) | | 95 | 40.1 | 1.65 | (1987) |
| | | | | 99 | 8.0 | 0.33 | |
| Atlantic halibut | 76 | – | 120§ | 68 | 163.2 | 0.98 | Davenport *et al.* |
| (1.383) | (F, 5–6%) | (10) | | 95 | 38.0 | 0.23 | (1990) |
| | | | | 99 | 7.6 | 0.05 | |

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| Lemon sole | 14.48 | – | 72[§] | 68 | 463.3 | 8.88 | Davenport *et al.* |
| (0.724) | (F, 2%) | (10) | | 95 | 72.4 | 1.39 | (1990) |
| | | | | 99 | 14.5 | 0.27 | |
| Dab | 0.44 | – | 22.65[§] | 68 | 14.1 | 14.06 | Jobling *et al* (1977) |
| (0.0442) | (SD, 1%) | (16.4 & 8.5) | | 95 | 2.2 | 2.19 | |
| | | | | 99 | 0.4 | 0.44 | |
| Plaice | 1.75 | 0.325 | 5.38 | 68 | 56.0 | 59.47 | Basimi and Grove |
| (0.175) | (SD, 1%) | (9.5) | | 95 | 8.8 | 9.29 | (1985) |
| | | | | 99 | 1.8 | 1.86 | |

*Values in parentheses in columns 1, 2 and 3 are fish wet weights, ration size as a percentage of wet body weight, and temperature respectively.
[†]F, = fish; SD, = synthetic diets; SF, = shellfish. Food is estimated to contain 10% nitrogen (Pandian and Marian, 1985).
[‡]Gastric evacuation rates are based on wet weights of food ingested and stomach contents rather than on a dry weight basis.
[§]Experimental measurement of gut transit time for a single ration.

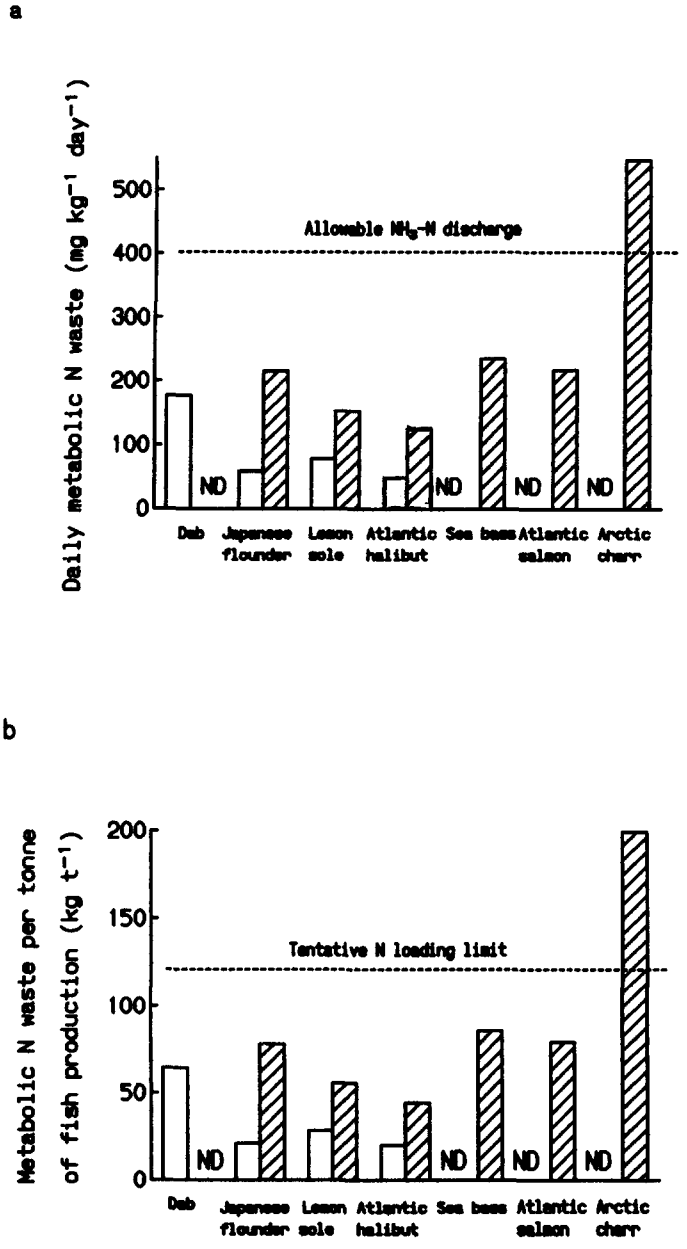



**Fig. 3.** Possible metabolic contributions to nitrogen waste in starved (open bars) and fed (shaded bars) fish. (a) Daily metabolic N waste; (b) metabolic N waste per tonne of fish production. Dashed line indicates the daily discharge limit and tentative N loading limit to seawater from UK fish farms respectively. ND, no data. Data are derived from the nitrogen excretion rates in Table 3. Values for fed fish are taken 24 h after feeding except for the Atlantic salmon (3 h feeds) and Arctic charr (10–12 feeds per hour).

excretion rates below the suggested discharge limits for ammonia, even after feeding (Fig. 3). The metabolic N waste per tonne of fish production is also below the tentative loading limit of 123 kg N $t^{-1}$ for estuarine waters (Highland RPB, 1987), except for Arctic charr (Fig. 3). Some marine fish have the metabolic capacity to exceed N discharge limits (408 mg $NH_3$-N $kg^{-1}$ $day^{-1}$) during short periods of maximal post-prandial N excretion. For example, Atlantic cod can excrete 41.19 mg TAN $kg^{-1}$ $h^{-1}$ after feeding (Ramnarine *et al.*, 1987), a rate equivalent to a daily excretion of 988.5 mg TAN $kg^{-1}$ $day^{-1}$. The American eel can excrete 140 mg TAN $kg^{-1}$ $h^{-1}$ (Gallagher and Mathews, 1987), equal to a daily rate of 3360 mg TAN $kg^{-1}$ $day^{-1}$. However, the magnitude of post-prandial N excretion surges can be reduced by manipulating ration size and feeding times (Poxton and Lloyd, 1989). Thus, while it is unlikely that the species used on a farm will inherently jeopardize imposed discharge consent limits, excessive pollution would probably arise from poor management or farm design rather than from the fish species *per se.*

Temperature and body size effects on metabolic rate also have implications for animal husbandry and effluent control. Small fish will have higher weight-specific metabolic rates (Jobling, 1981) than adults, and are more likely to be held at temperatures in the upper portion of their thermal range to enhance growth (Poxton, 1990). Thus small fish will excrete more N $kg^{-1}$ than adults. Additionally, ammonia could be more toxic to juveniles than adults, therefore enhanced water flow rates and lower stocking densities would provide an additional safety margin in both effluent control and animal husbandry of juvenile stages.

The main routes of N excretion in marine fish are through the gills, skin and faeces. Nitrogen outputs from the gills and skin are likely to be important in the context of fish disease and stress where mucus hypersecretion and damage to the branchial epithelium will enhance N loss. Faecal N loss is about one-third of the N excretion in the few species of fish studied during feeding (Table 5; Porter *et al.*, 1987; Kikuchi *et al.*, 1991). Table 6 suggests that faecal N output will be about 1–3 mg N $kg^{-1}$ $h^{-1}$ if the N assimilation efficiency is 95%; this corresponds to 8.76–26.28 kg N $t^{-1}$ of fish production and represents a quarter or less of the likely metabolic waste from marine fish in culture conditions (Fig. 3).

## Nitrogen pollution from feeding

Farmers should aim to provide sufficient dietary N to promote good growth in immature fish stocks, and establish a suitable N ration to maintain the body weight of animals at marketable size. Feeding in excess of these requirements will waste expensive feeds and cause deterioration in water quality (Poxton, 1992). Nitrogen pollution arising from the feeding of fish can be broadly attributed to three main factors: (1) food wastage owing to poor farming practice, e.g. supplying too much food at the wrong time; (2) the poor stability and high solubility of fish foods in water; (3) limited absorption and retention of ingested N by the fish, or combinations of the above factors.

### *Nitrogen pollution from food wastage*

There are few published estimates of food wastage in finfish culture and the limited available data are also exclusive to salmonids (review, Beveridge *et al.*, 1991; Seymour

and Bergheim, 1991). Evaluation of food wastage is hampered by the difficulty of separating uneaten food from the other solid wastes in the culture system, nevertheless values range between 1 and 40% depending on the type of food and the feeding method (Thorpe *et al.*, 1990; Beveridge *et al.*, 1991).

The underlying cause of good wastage is a mismatch of farming practice with the feeding behaviour and nutritional physiology of the species being cultured. The marine teleosts likely to be cultured have diverse feeding habits, but several criteria should be considered to reduce N pollution from food wastage.

Many marine species show feeding periodicity (Collins, 1981; Macpherson, 1985; Brodeur and Pearcy, 1987; Hall, 1987; Sagar and Glova, 1988; Tanasichuk *et al.*, 1991), so feeding times should occur when fish have maximal appetites. The dab feeds mostly at dusk, while the haddock feeds primarily during the day (Hall, 1987). The walleye pollock will feed continuously provided the stomach remains partially empty, but the fish probably prefer to feed intermittently (Smith *et al.*, 1989).

Chemical stimulants, particularly L-amino acids, will induce feeding in marine fish (Mackie *et al.*, 1980; Carr, 1982; Mackie, 1982; Mackie and Mitchell, 1983; Knutsen, 1992). For example, Atlantic cod prefer diets containing glycine or alanine, and readily eat food spiked with squid or prawns (Jobling, 1988). Some species prefer chunks of fish rather than formulated foods (e.g. Atlantic cod: Jobling, 1988; Atlantic halibut: Davenport *et al.*, 1990). However, the farmer must consider the availability and cost of any food; it may be more practicable or economical to supply a food of lower preference.

Common sense suggests that it would be wasteful to provide fish with more than they eat in a single meal. However, it is not easy to establish the 'satiation ration' for a particular group of fish as it will depend on their metabolic rate and stomach size (Grove *et al.*, 1985; Hall, 1987; Jobling, 1988), as well as on the relationships between gastric evacuation rate, stomach distension and the return of appetite (Jobling *et al.*, 1977; Grove *et al.*, 1985). Mature Atlantic halibut prefer relatively large, infrequent meals (e.g. 11.7% bw: Davenport *et al.*, 1990), while juvenile turbot will feed on demand to maintain stomach fullness at 85% or more (Grove *et al.*, 1985). The size of the satiation ration will also increase if the energy content of the food is reduced (Grove *et al.*, 1985). The farmer should avoid the satiation ration from an energetic viewpoint, because optimum growth in fish is usually achieved below the maximum ration level (Brett and Groves, 1979). Thus the commonly held view among farmers that more food equals more growth is unrealistic.

The method of food dispersion will depend on practical considerations such as the size of the ponds, whether the farm is land or sea-based, and on fish behaviour. Atlantic salmon fed by automatic feeders may waste 40.5% of the food because the food dispersion is localized, resulting in a few dominant aggressive fish overfeeding close to the dispenser (Thorpe *et al.*, 1990). A similar situation is possible with turbot fed by demand feeders: a few fish will actuate demand feeding, while the remainder will wait for food to drift past before feeding (Grove *et al.*, 1985). Hand feeding minimizes wastage in salmonid culture (Beveridge *et al.*, 1991), but is less practical with large ponds or non-land-based systems.

Differences in the feeding habits of marine fish may also be exploited in duo and polycultures to minimize wastage. Davenport *et al.* (1990) found that Atlantic halibut refused small food items that had settled on the bottom of the tank. The inclusion of a few bottom-feeding lemon sole in each aquarium ensured that all the food was eaten.

Other factors that affect food wastage are not directly related to the nutritional biology of the cultured species, but are a direct consequence of farming practice. Deterioration of water quality by overcrowding, sudden fluctuations in DO as pond aerators are switched on or off, or elevations in ammonia concentrations owing to overfeeding itself, are likely to reduce appetite (Poxton, 1990, 1992). The post-prandial surge in oxygen consumption by fish (e.g. Davenport *et al.*, 1990) may also decrease DO sufficiently to prevent further feeding, even in marine pens (Poxton, 1992). Feeding should also be avoided immediately after stressful treatments such as handling, or the administration of therapeutants (Poxton, 1992; Waring *et al.*, 1992).

*Nitrogen pollution from poor food stability in water*

The requirement of foods to dissolve rapidly in the gut of fish to release nutrients (Storebakken, 1985; Storebakken and Austreng, 1987) also means that some commercial feeds have a tendency to dissolve rapidly in water, a situation at odds with pollution abatement. Two methods may be employed to reduce N loss from feeds. Firstly, the feeding regime should attempt to minimize the time food spends in the water by maximizing appetite and using an efficient dispersion method (see section on food wastage above). Secondly, the stability of the feed may be improved during manufacture (Hilton *et al.*, 1981; Jayaram and Shetty, 1981; Hardy, 1989).

Several types of food are available to feed carnivorous fish, including trash fish, wet pastes, and pelleted diets (Hilton *et al.*, 1981; Hardy, 1989; Beveridge *et al.*, 1991). Trash fish is cheap, but wastage levels can be high in commercial culture (Beveridge *et al.*, 1991). Pastes and silages can utilize locally available protein sources such as offal (Jobling, 1988), but the physical properties of the food are difficult to control. The fish may be presented with a food of variable particle size, which may inappropriately sink or float depending on the batch. More importantly, pastes will rapidly form a fine suspension which pollutes the water as the fish feed.

Pelleted foods are relatively stable in water (Hilton *et al.*, 1981; Jayaram and Shetty, 1981) allowing the fish time to ingest the food before it 'dissolves'. The density of the food may be controlled during manufacture so that animals are presented with either a floating (e.g. extruded pellets) or sinking (e.g. compressed pellets) diet (Hardy, 1989) appropriate to their feeding behaviour. The disintegration of pellets may also be delayed by coating or encapsulating the food in agar, alginates, or synthetic materials (Hardy, 1989). Another approach to N pollution control would be to reduce the N content of the food, but this could also compromise the nutritional value of the diet.

*Nitrogen pollution from ingested food*

Ingested food can cause pollution by the direct excretion of undigested N in the faeces (Table 6), or N may be absorbed across the gut, only to be lost via the gills, skin or urine. Thus two processes are important in minimizing N pollution from ingested food: (1) adequate N absorption by the gut and (2) retention of any absorbed N by the tissues.

Nitrogen uptake by the gut can be expressed as a N assimilation efficiency, which is the ratio of absorbed N (ingested N minus faecal N) divided by ingested N. An efficiency of 100% indicates complete N uptake and therefore no N pollution from excreted faecal material. In laboratory studies N assimilation efficiencies are often greater than 80% (Table 7). Assimilation efficiencies may fall to less than 70% if the diet contains high levels of raw starch, or other materials with a low digestibility and negligible N content

**Table 7.** Nitrogen assimilation and retention efficiencies of fish

| Common name | Seawater (SW) or freshwater (FW) | Efficiency (%) | Notes | Source |
|---|---|---|---|---|
| **Assimilation efficiency** | | | | |
| Turbot | SW | 97.98 | 1% bw ration | Grove *et al.* (1985) |
| | | 96.59 | 2% bw ration | |
| | | 97.61 | 4% bw ration | |
| | | 95.67 | Multiple feeds | |
| Atlantic salmon | SW | 87.44 | Restricted ration | Usher *et al.* (1990) |
| | FW | 74.60 | Unrestricted | |
| | | 96.30 | Restricted | |
| | | 86.14 | Unrestricted | |
| Oxeye tarpon | FW | 97.5–94.0 | Calculated from author's data: ration size 2.1–4.8% bw $day^{-1}$ | Pandian (1967b) |
| Cape anchovy | SW | 73.75–94.35 | Zooplankton diet | James *et al.* (1989) |
| Turbot | SW | 81 | Control diet | Jobling (1986) |
| | | 88 | +20% casein | |
| | | 63 | +20% albumen | |
| | | 61 | +20% raw starch | |
| Plaice | SW | 82 | Control diet | Jobling (1986) |
| | | 93 | +20% casein | |
| | | 77 | +20% albumen | |
| | | 68 | +20% raw starch | |
| Sea bream | SW | | Calculated from author's data | Porter *et al.* (1987) |
| | | 88.98 | 3 g fish | |
| | | 94.34 | 40 g fish | |
| | | 92.2 | 90 g fish | |
| Oxeye tarpon | FW | | Calculated from author's data | Pandian (1967a) |
| | | 97.7 | 1.38 g fish | |
| | | 99.1 | 12.62 g fish | |
| | | 94.6 | 100 g fish | |
| | | 96.1 | 149.6 g fish | |
| White steenbras | SW | 83.2 | 15 °C | Cockcroft and Du Preez (1989) |
| | | 83.3 | 20 °C | |
| | | 88.2 | 25 °C | |
| Sea bass | SW | 82.5–94.2 | Various methods of faecal collection | Spyridakis *et al.* (1989) |
| **Nitrogen retention efficiency** | | | | |
| Plaice | SW | 18.07 | Fed *Arenicola*, *Mytilus*, *Tubifex* sp. | Jobling (1981) |
| Various teleost fish | | 21–48* | Range of values | Bowen (1987) |
| | | 31* | Median | |

**Table 7.** continued.

| Common name | Seawater (SW) or freshwater (FW) | Efficiency (%) | Notes | Source |
|---|---|---|---|---|
| Plaice | SW | 27.5–41.7 | Mean live weight 21.42–1.11 g | Birkett (1969) |
| Sole | SW | 39.1–49.0 | Mean live weight 23.0–0.62 g | Birkett (1969) |
| Perch | FW | 41.3 | Mean live weight 114 g | Birkett (1969) |
| Atlantic salmon | SW | 25.0 | Fish farm | Carter *et al.* (1992) |
| | FW | 27.4–23.2 | Ration size 0.5–1.5% bw $day^{-1}$ | |
| Oxeye tarpon | FW | 20.6–33.1 | Ration size 2.1–4.8% bw $day^{-1}$ | Pandian (1967b) |
| Atlantic cod | SW | 13–42* | 0.25–2.0% growth per day | Houlihan *et al.* (1988) |
| Oxeye tarpon | FW | | Calculated from author's data | Pandian (1967a) |
| | | 33.4 | 1.38 g fish | |
| | | 26.8 | 12.62 g fish | |
| | | 21.2 | 100 g fish | |
| | | 18.7 | 149.6 g fish | |
| Bluegill | FW | 43.9 | 13.9 g fish | Gerking (1971) |
| Sunfish | | 14.1 | 85.2 g fish | |

*Protein retention efficiency.

(Jobling, 1986; Table 7). Overfeeding may reduce assimilation efficiency by 10% (Usher *et al.*, 1990), while changes in ration size between 1 and 4% bw $day^{-1}$ may have a negligible (Grove *et al.*, 1985) or minimal effect (Pandian, 1967b; Table 7). Fish size may cause marginal changes (± 4%) in assimilation efficiency depending on the species (Pandian, 1967a; Porter *et al.*, 1987), while increases in acclimation temperature may elevate N uptake by a few percent (Cockcroft and Du Preez, 1989). The effects of ration size, fish weight and acclimation temperature on N assimilation efficiency may be considered insignificant in a nutritional context (Pandian and Marian, 1985). Nevertheless, if pollution from faecal waste is considered, a 4% decrease in assimilation efficiency may result in a fivefold elevation in faecal N output (Table 6). Thus apparently marginal changes in N uptake could have significant effects on pollution associated with feeding.

Nitrogen retention is an important aspect of fish growth, because any N retained will ultimately be utilized in protein synthesis (Brett and Groves, 1979; Houlihan *et al.*, 1988, 1989). Given the importance of N retention in nutrition, there are surprisingly few data available (Table 7; reviews, Brett and Groves, 1979; Bowen, 1987) and some confusion over terminology. Some authors refer to 'protein retention efficiency' when in fact they have measured 'N retention efficiency' (e.g. Pandian, 1967a, b). More recent studies

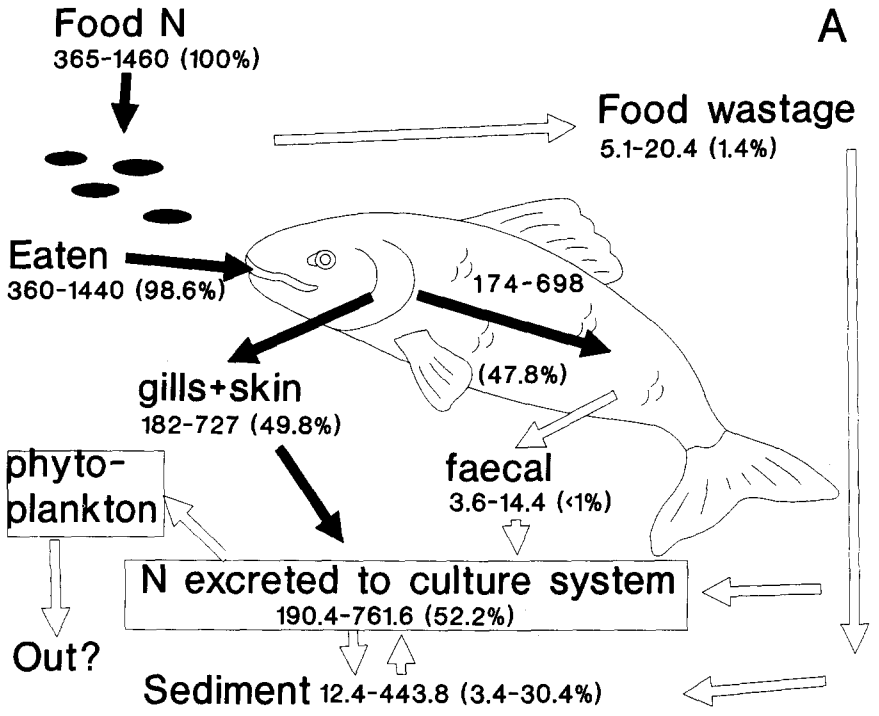
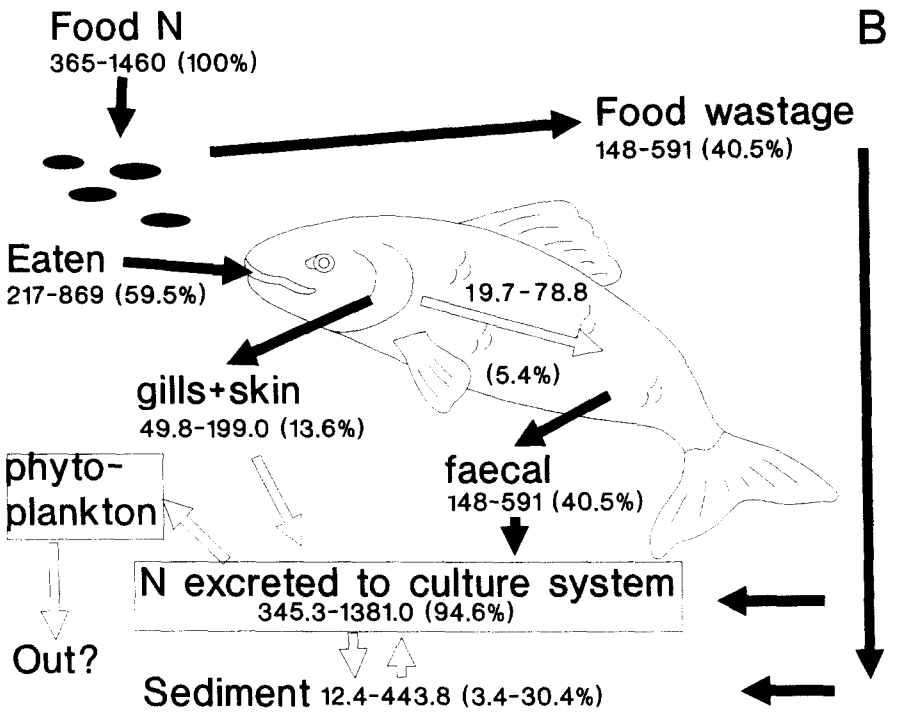



**Fig. 4.** Routes of nitrogen pollution in mariculture. (a) Minimum pollution scenario where food wastage is low (1.4%) and N assimilation (99% of ingested N) and retention (49% of ingested N) are high. (b) Maximum pollution scenario where high food wastage (40.5%) is coupled with poor N assimilation (68% of ingested N) and retention (13.4% of ingested N). Wastage levels are taken

measuring changes in internal amino acid pools may produce more direct values of protein retention (e.g. Houlihan *et al.*, 1988).

The available N retention data suggest that fish are likely to excrete about two-thirds of any N absorbed across the gut (Table 7). Thus the post-prandial excretion of N across the gills and skin of marine fish is probably the primary cause of N pollution associated with ingested food (unless assimilation efficiency is low). Nitrogen retention varies considerably with the size of the fish (Pandian, 1967a; Birkett, 1969; Gerking, 1971), or more accurately, with the growth rate (e.g. Bowen, 1987; Houlihan *et al.*, 1988). Adult fish with low growth rates may retain 15–20% of the absorbed N, compared with 40% in rapidly growing fish (Table 7). Thus the greatest risk of N pollution from ingested food is associated with mature fish stocks. This problem may be minimized by reducing the N content of the feed as growth slows and by feeding adult fish with feeds containing a lower proportion of protein.

If the sum effects of N assimilation and retention are considered, fish will excrete about 51% of N added to the culture system as food when conditions are optimal (i.e. 99% assimilation, 49% retention, Table 7). However in a 'worse case scenario' (68% assimilation, 13% retention, Table 7), 91% of the N will be lost rather than retained by the fish. If the additional effect of food wastage is considered, 52–95% of N added as




from Thorpe *et al.* (1990) and Beveridge *et al.* (1991). Assimilation and retention efficiencies are high and low values recorded from the literature (Table 7). Values are in kg N $t^{-1}$ of fish production and show a range for a 1–4% bw $day^{-1}$ ration. Numbers in parentheses are the percentage of the food N added to the culture system.

food will be lost (Fig. 4). Under average farm conditions food wastage may be about 10% (Beveridge *et al.*, 1991), while N assimilation and retention efficiencies may be about 95% and 31% respectively. Under such conditions fish stocks may only retain 26.5% of N added as food. The farmer is thus losing substantial quantities of dietary N, even when conditions for N accumulation by the fish are optimal (Fig. 4).

The percentages of N lost/excreted to the culture system may be used to estimate the N pollution arising from feeding in kg N $t^{-1}$ fish production (Fig. 4). If cultured fish are fed a ration of 1–4% bw $day^{-1}$, and the food contains about 10% N (Pandian and Marian, 1985), then the N input to the culture system will be 1–4 g N $kg^{-1}$ fish (equal to 365–1460 kg N $t^{-1}$ production, Fig. 4). When optimum N retention and assimilation are coupled with low food wastage, 190–762 kg N $t^{-1}$ (1–4% bw ration) may theoretically be lost to the culture system (Fig. 4(a)). Conversely, when food wastage is high and N retention plus assimilation are poor, 95% of the N added to the culture system as food may ultimately pollute the environment. This corresponds to 345–1381 kg N $t^{-1}$ of production (ration 1–4% bw, Fig. 4(b)). However, much of the N will be utilized by phytoplankton (Krom *et al.*, 1989) or deposited in the culture system as sediment (30.4%, Philips and Beveridge, 1986; 3.4%, Gowen *et al.*, 1988; 15.74%, Ackefors and Enell, 1990). Alternatively, laboratory measurements of N assimilation and retention

efficiencies may not be reflective of those for animals held in aquaculture systems, or food wastage could be over-estimated on commercial farms.

## Conclusions

1. Assessment of the N discharged from marine fish farms is difficult as few culture systems are land-based with point sources of effluent. Further complications arise owing to the incomplete reporting of fish biomass, effluent quality, and dilution in receiving waters.

2. Ammonia is acutely toxic to marine fish in the range 0.09–3.35 mg $l^{-1}$ $NH_3$-N (96 h $LC_{50}$ or less). Insufficient chronic toxicity data exist, but the threshold for no growth is about 0.1 mg $l^{-1}$ $NH_3$-N. Marine fish will be protected from $NH_3$ toxicity by high salinity and DO levels. The pH effect on toxicity in seawater is currently unclear.

3. Data for nitrite toxicity to marine fish are sparse. The 24 h $LC_{50}$ is between 675 and 4000 mg $l^{-1}$ $NO_2^-$-N for the few species studied. Methaemoglobinaemia and hypoxia may occur at 12 mg $l^{-1}$ $NO_2^-$-N. Nitrite levels should therefore not exceed about 1–2 mg $l^{-1}$ $NO_2^-$-N.

4. Marine teleosts have basal N excretion rates of 1.35–34.93 mg N $kg^{-1}$ $h^{-1}$. Feeding may increase N excretion to 600 mg N $kg^{-1}$ $h^{-1}$ in some fish. The rates of N excretion for marine fish suggest that they do not have the metabolic capacity to exceed the suggested N loading limits for discharges from aquaculture in the UK. Thus any failure in consent compliance is more likely to arise from poor farming practice.

5. Marine teleosts can produce ammonia and urea, but many species are predominantly ammoniotelic. Edible species tend to excrete relatively low amounts of urea-N compared with nonedible fish. In unfed fish N is excreted via the gills and body surface, while fed fish excrete a third of ingested N as faeces.

6. Marine fish can assimilate 95% and retain 31% of any ingested N under controlled conditions. Small changes in N assimilation efficiency have a marked effect on faecal N excretion. The post-prandial surge in N excretion is the primary cause of contamination from ingested food.

7. Wastage of uneaten food and the poor stability of some fish feeds in water will contribute to N pollution.

8. The sum effects of food wastage and incomplete N absorption or retention imply that 52–95% of any N added as food will ultimately pollute the environment.

## Summary

The toxicological and environmental significance of N-containing effluents discharged to seawater from fish farms is difficult to establish. Environmental quality standards for N compounds in seawater are hard to derive in the context of aquaculture because the toxicity of $NH_3$ and $NO_2^-$ to marine fish is poorly understood. Furthermore, details of aquacultural effluents are not routinely reported. Marine teleosts excrete N via the gills, skin and faeces, but do not have the metabolic capacity to cause breaches in discharge consent conditions. The most likely cause of discharge consent breaches will be poor farming practice. Nitrogen pollution will arise from food wastage, poor N absorption, and N retention. It is estimated that 52–95% of any N added to the culture system as food will ultimately pollute the environment.

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Professor Marco Saroglia of Potenza University, Italy, is thanked for providing the field data on sea bass farms in Figs 1 and 2. This work was supported by an EEC grant under the 'FAR' programme (No. AQ.2.580) awarded to MGP.

## Appendix

**Table 1A.** Fish names cited in the manuscript

| *Family* | *Species name* | *Common name* |
|---|---|---|
| Agonidae | *Agonus cataphractus* | Pogge |
| Anguillidae | *Anguilla anguilla* | European eel |
| Anguillidae | *Anguilla rostrata* | American eel |
| Antherinidae | *Menidia beryllina* | Inland silverside |
| Batrachoididae | *Opsanus beta* | Gulf toadfish |
| Blenniidae | *Blennius pholis* | Blenny |
| Centrarchidae | *Lepomis macrochirus* | Bluegill sunfish |
| Centrarchidae | *Micropterus salmoides* | Largemouth bass |
| Ceratodontidae | *Neoceratodus forsteri* | Australian lungfish |
| Chanidae | *Chanos chanos* | Milkfish |
| Cichlidae | *Oreochromis mossambicus* | Tilapia |
| Cichlidae | *Oreochromis alcalicus grahami* | Lake Magadi tilapia |
| Cottidae | *Leptocottus armatus* | Sculpin |
| Cyprinidae | *Chalcalburnus tarichi* | No common name |
| Cyprinodontidae | *Cyprinodon variegatus* | Sheepshead minnow |
| Engraulidae | *Engraulis capensis* | Cape anchovy |
| Engraulidae | *Engraulis rigens* | Peruvian anchovy |
| Gadidae | *Gadus morhua* | Atlantic cod |
| Gadidae | *Gaidropsarus capensis* | Cape rockling |
| Gadidae | *Melanogrammus aeglefinus* | Haddock |
| Gadidae | *Theragra chaliogramma* | Walleye pollock |
| Gasterosteidae | *Gasterosteus aculeatus* | Threespine Stickleback |
| Holconoti | *Taeniotoca lateralis* | Sea perch |
| Icelidae | *Taurulus bubalis* | Sea scorpion |
| Labridae | *Crenilabrus melops* | Corkwing wrasse |
| Lophiidae | *Lophius americanus* | Goosefish |
| Megalopidae | *Megalops cyprinoides* | Oxeye tarpon |
| Moronidae | *Morone saxatilis* | Striped bass |
| Mugilidae | *Mugil cephalus* | Grey mullet |
| Otolithidae | *Cynoscion nebulosus* | Spotted seatrout |
| Paralichthyidae | *Paralichthys lethostigma* | Southern flounder |
| Paralichthyidae | *Paralichthys olivaceous* | Japanese flounder |
| Percidae | *Perca fluviatilis* | Perch |
| Periophthalmidae | *Periophthalmus gracilis* | Mudskipper |
| Pleuronectidae | *Hippoglossus hippoglossus* | Atlantic halibut |
| Pleuronectidae | *Limanda limanda* | Common dab |
| Pleuronectidae | *Microstomus kitt* | Lemon sole |
| Pleuronectidae | *Platichthys stellatus* | Starry flounder |

**Table 1A.** continued.

| | | |
|---|---|---|
| Pleuronectidae | *Pleuronectes platessa* | Plaice |
| Salmonidae | *Oncorhynchus kisutch* | Coho salmon |
| Salmonidae | *Oncorhynchus mykiss (Salmo gairdneri)* | Rainbow trout |
| Salmonidae | *Oncorhynchus tshawytscha* | Chinook salmon |
| Salmonidae | *Salmo salar* | Atlantic salmon |
| Salmonidae | *Salvelinus alpinus* | Arctic charr |
| Scophthalmidae | *Scophthalmus maximus* | Turbot |
| Serranidae | *Dicentrarchus labrax* | European sea bass |
| Soleidae | *Solea solea (Solea vulgaris)* | Dover sole or Sole |
| Sparidae | *Diplodus sargus* | White sea bream |
| Sparidae | *Lithognathus lithognathus* | White Steenbras |
| Sparidae | *Sparus aurata* | Sea bream |
| Squalidae | *Squalus acanthias* | Dogfish pup |

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