

# BIOFAQs

A review of the environmental impacts of marine cage aquaculture, processes of biofiltration relevant to impact mitigation, the biological properties of marine invertebrates relevant to biofiltration and biofouling on artificial structures.

Work Package 1.1, 1.2, 1.3

Deliverable numbers D02, D03

Milestone M01

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## **Chapter 1.**

### **Overview of the report and a review of the relevant pelagic impacts of marine cage aquaculture**

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#### **1. 0 Overview**

In this report the relevant impacts of marine cage culture on benthic and pelagic ecosystems are reviewed. This is followed by a review of important processes and principles relating to the use of biofiltration for the treatment of waste organic material first in a general sense and then focusing on techniques developed for aquaculture. In the third chapter the functional filtration properties of marine invertebrate groups are reviewed in the context of their suitability for providing biofiltration services in a system designed to mitigate impacts of small particulate organic matter originating from marine farms. The fourth chapter reviews the factors affecting the development of biofouling on artificial structures with reference to a variety of biofouling studies.

The first chapter is modified and updated from a review by Pearson and Black (2001) with additional contributions from Angel on impacts in the Mediterranean and Red Sea.

#### **1.1 Introduction**

Culture of fish in cages has the potential to cause both onshore and offshore impacts on the surrounding environment, with a severity scaled to the size and intensity of the farming operation. Such impacts include distortion of the local ecosystem, short and long term impacts and near-field and far-field effects of eutrophication, contamination by xenobiotics, cross transmission of parasites and pathogens and aesthetic deterioration in coastal areas. Such environmental effects must be minimised both to maintain the most favourable conditions for farm stocks in the cages and to preserve environmental amenity for other users.

The most obvious changes caused by intensive marine culture of carnivorous fish in cages are to the local environment. These impacts, predominantly on the benthos, may be long-lived at sites in relatively quiescent waters, persisting for many years after the culture activity has ceased, or, at more dynamic sites, may be relatively short lived. Much of the research activity into impacts has concentrated, understandably, on the immediate local environment and over relatively short time-scales. However, it is likely that with the continued expansion of marine cage farming across many parts of the world, the focus will change to long-term, far-field, systemic interactions. This is particularly true of nutrient discharges where, in essence, nutrients are extracted from the open seas in the form of wild fish that are subsequently converted into meal for consumption by cultured fish followed by excretion into the more valuable and more vulnerable coastal zone.

A goal of environmental research in this area has long been the definition of carrying capacity such that the scale of the aquacultural activity can be matched to the assimilative capacity of the

local environment. While this is relatively straightforward for benthic impacts in temperate environments, great difficulties arise in the pelagic environment. Regulators, therefore, generally require a relatively cautious approach to be taken, based on the precautionary principle, which may be challenged by farmers.

## 1.2 Background

In a bibliographic review, Munday *et al.* (1992) surveyed the existing literature on environmental impacts of aquaculture and found *inter alia* that the majority of such research originated in developed western countries and concentrated on the major cultured species. Gowen and Rosenthal (1993), in attempting to draw conclusions applicable to aquaculture in developing countries, reviewed and discussed some of these results. Wu (1995) reviewed the literature on marine cage culture, essentially reaching similar conclusions to previous reviewers. These suggest that the degree of impact from effluent wastes is dependent on husbandry parameters including species, culture method and feed type and on the nature of the receiving environment in terms of physics, chemistry and biology. The major impacts are on the sea bed, generally within a localised area around the farm and, while chemical treatments or food additives may have a significant local impact, they are unlikely to pose a significant threat to the regional environment at current levels of use. This last view is widely held within the research community. However it begs the question of the ultimate carrying capacity of aquatic systems for fish before significant systemic effects become apparent.

The interactions between aquaculture and biodiversity have been reviewed by Beveridge *et al.* (1994) who argue that aquaculture impacts are usually negative and only rarely positive. These arise from the consumption of a set of resources and their transformation into a desirable product, with the simultaneous production of a waste stream which includes food, faeces, respiratory products, chemicals, microbiota, parasites and escaped fish. They conclude that while fish culture may indeed be a necessary activity in some cases due to over-exploitation of natural stocks, intensive systems which require a large input of fishmeal must exacerbate pressures on wild fisheries in general. These authors regard the output of energy rich wastes from intensive aquaculture, discharges that frequently cause pollution problems, as a poor use of a valuable dwindling resource.

## 1.3 Enrichment of the natural environment

### 1.3.1 Nutrient enrichment

The majority of marine culture of carnivorous species takes place in cages suspended in more or less open water. Cage structures are relatively cheap compared with equivalent land based structures and, by being immersed in the receiving environment, cage culture avoids the need for expensive pumping of water to supply the oxygen requirements of the fish and to remove waste products. This does, however, mean that dissolved components are released directly into the marine environment in a highly biologically active form. The dissolved products include ammonia, phosphorus and dissolved organic carbon (DOC). The DOC component contains fractions rich in nitrogen (DON) and phosphorus (DOP). These waste products have a variety of sources: they may be directly excreted, they may be dissolved from the feed or from faecal particles, or may be released from particles that have been deposited on the seabed around the cages. Lipids released from the diet may form a film on the water surface that is often observed around cages after feeding.

The effect that dissolved wastes may have on the environment will depend on the speed at which these nutrients are diluted before being assimilated by the pelagic ecosystem. Cage structures are often located in areas of partially restricted exchange as such locations generally provide shelter from extreme weather, thus protecting staff and equipment. In restricted exchange environments, it is generally useful to estimate flushing time (i.e. the time taken to exchange all or some part of the local water volume with new coastal water) in order to assess the risks of significantly increasing the nutrient concentrations in the immediate environment (hypertrophication). Strutton *et al.* (1996) have provided a simple expression for estimation of the flushing time of semi-enclosed bays or estuaries with only limited data:

$$T_0 = \frac{h\Delta S}{S_1(E-R) - h \frac{dS_2}{dt}}$$

where  $h$  is the mean depth of the bay.  
 $(E-R)$  is the net evaporation rate,  
 $S_1$  is the salinity of the open ocean  
 $S_2$  is the volume averaged salinity of the bay.

Flushing time can also be calculated using the planar area and volumes of the body of water under investigation. Planar area is the area of the surface of the water body and total volume is determined by summing the volume of smaller sub-volumes (= planar area x depth).

Flushing time ( $T$ ) in days can be determined from the following formula (Edwards and Sharples, 1988):

$$T = \frac{1.05 \text{ lwvolume}}{0.7 \text{ tiderange} (h \text{warea} + l \text{warea})}$$

where  $lwvolume$  and  $lwarea$  are low water volume and planar area at Lowest Astronomical Tide (LAT),  $hwarea$  is planar area of the water body at MHWS (Mean High Water Spring tides) and  $tiderange$  is the tidal range between MLWS (Mean Low water Spring tides) and MHWS.

The equilibrium concentration of Nitrogen originating from the farm can be estimated from the formula (Gowen and Ezzi, 1992):

$$\text{Equilibrium concentration} = \text{Nitrogen released/volume} \times \text{Flushing time}$$

It is assumed that where the flushing time is less than the typical generation time of phytoplankton then the risks of any increase in nutrient concentrations caused by the farm will not lead to measurable increases in the local phytoplankton biomass (eutrophication). However, flushing times are calculated for mean conditions and it is possible that certain events, or combinations of events (e.g. unusually persistent onshore winds combined with neap tides reducing exchange of nutrient rich surface waters), might lead to longer periods of water retention.

Smaller pelagic organisms such as nanoflagellates (micro-zooplankton) and bacteria have much shorter generation times. Heterotrophic bacterio-plankton around fish farms will have access to highly-available organic nutrients but there has been little research on bacterial response and on

any consequences that increased bacterial biomass might have on other compartments of the microzooplankton.

It is generally assumed that, in contrast to freshwaters, nitrogen is likely to be the nutrient limiting phytoplankton growth in marine waters. There have been suggestions, however, that this is not always the case and that alterations in the ratio of nitrogen to phosphorus might cause an effect in the phytoplankton (Arzul *et al.*, 1996). Phosphate limitation resulting from natural alterations in the N:P ratio have been implicated in, e.g. the formation of the toxic *Chrysochromulina polylepis* bloom in the Skaggeiak (Smayda, 1990).

Wildish *et al.* (1993) found that mariculture of salmonids did not significantly affect the concentrations of nitrate, phosphate, and silicate in the Bay of Fundy but there were local increases in the concentration of ammonia. In a more recent study in the Mediterranean, Pitta *et al.* (1998) reported elevated concentrations of phosphate and ammonium near 3 fish farms but no significant effect on chlorophyll.

Only rarely has it been possible to demonstrate any linkage between the nutrients produced from farming and a biological response, although many such linkages have been claimed. Beyond looking at purely local enrichment, it is normally not feasible to attribute wider-scale effects to nutrients from farms. However in the brackish waters of the Finnish archipelago in the northern Baltic Sea increasing levels of eutrophication attributable to nutrients from rainbow trout (*Onchorhynchus mykiss*) farms have resulted in the rapid growth in summer of algal mats on the bottom sediments which have caused bottom water anoxia and strong reductions in local fish and benthic populations (Bonsdorff *et al.*, 1996, 1997). Moreover a dense and catastrophic bloom of *Alexandrium tamarense* in an Italian lagoon in 1993 was linked to local intensive aquaculture activities (Sorokin *et al.*, 1996). The occurrences of nuisance or harmful algal blooms appear to be increasing on a world-wide scale (Anderson, 1997).

### 1.3.2 The N budget of cage farming

Carbon inputs drive sedimentary biogeochemical processes but waste materials from fish farms also contain large amounts of other environmentally relevant elements that influence biological processes in the water column, namely nitrogen, phosphorus and silicon. In one of the few studies that have examined the processing of nitrogen through intensive cage farms in marine waters, Hall *et al.* (1992) found that between 67 and 80% of the nitrogen added to the cage system is lost to the environment. The majority (50 - 60% of total nitrogen) is lost in dissolved form either directly from the fish or by benthic flux from solid waste beneath the cages. Nitrogen (and phosphorus) in feeds has decreased as feed manufacture becomes more closely aligned with the dietary requirements of fish. In particular, modern diets tend to contain more lipid and less protein. This has resulted in a general reduction in feed conversion ratios. These currently approach 1:1 in western Europe, although more efficient feeding methods also play a part in this. The net effect is a reduction in nitrogen released to the environment. Enell (1995) reported a reduction from 132 to 55 kg N t<sup>-1</sup> fish between 1974 and 1994 and estimated that N from aquaculture contributed only 0.5% of the atmospheric input to the Baltic region.

The excretion of nitrogenous compounds by marine fish, and their associated toxicity to fish, have been comprehensively reviewed by Handy and Poxton (1993). Marine fish can assimilate a large proportion of ingested N (up to 95%), but any reduction in assimilation efficiency may lead to significantly elevated levels of faecal nitrogen. Using a wide range of published information, Handy and Poxton (1993) produced worst- and best-case scenarios for loss of N to the environment and concluded that 52-95% of N added in food is ultimately lost through a combination of food wastage and incomplete absorption and retention. Their worst-case scenario

is, however, just that and it is questionable whether any culture operation could perform anywhere near as badly without going out of business.

Fish utilise dietary protein efficiently but a significant proportion is metabolised for energetic purposes, thereby releasing large amounts of nitrogenous wastes, mostly as ammonia but some as urea. Excretion of nitrogenous wastes from sea bass, sea bream, turbot, rainbow trout and brown trout have been compared (Dosdat *et al.*, 1996). Ammonia and urea losses were similar for each species except turbot, which excreted relatively more ammonia and less urea. In addition, nitrogen losses from fish are dependent on temperature and on dietary protein content (Buttle *et al.*, 1996).

The nitrogen budget for the areolated grouper *Epinephelus areolatus* cultured under both laboratory and cage conditions has recently been reported (Leung *et al.*, 1999). These workers attempted to balance the following equation:

$$C=G+M+E+F$$

where each term relates to a mass of nitrogen and C is consumption, G is nitrogen retained for growth, M represents losses from mortality, E is excretory loss and F, loss through faeces. For a fish farm the budget is represented by

$$C= I-W$$

where I is the total input to the farm and W is the food wasted.

By a variety of techniques, Leung *et al.* (1999) were able to quantify each of these terms either by direct measurement or by difference. Excretion of ammonia was the greatest contributor to N loss followed by feed wastage, with faecal N loss being relatively unimportant. Nitrogen loss from this sub-tropical species fed trash fish is around 3 times greater than for temperate species fed formulated diets. Trash diets are inherently wasteful as a consequence of their high N content and their tendency to break up and shed small unconsumed particles during feeding.

Benthic fluxes of ammonia have also received attention (Hargrave *et al.*, 1993). Oxygen uptake and ammonia release from sediments directly beneath cages can be 4 - 27 times higher than at control stations, reaching maximum values of 99 mmol m<sup>-2</sup> d<sup>-1</sup> and 38 mmol m<sup>-2</sup> d<sup>-1</sup> respectively.

### 1.3.3 The P budget of cage farming

Phosphorus in fish farm effluents has been the subject of considerable interest especially with regard to freshwater and brackish systems, where it may be the limiting nutrient for plant growth. See Kelly, chapter 2, this volume, for a review of freshwater culture nutrient impacts. In the marine environment Holby and Hall (1991) showed environmental losses of P to be 19.6 to 22.4 kg t<sup>-1</sup> fish produced, 34 - 41% of which was released in dissolved form with the remainder lost by sedimentation. They estimated that 4 - 8% of the sedimented P was returned to the water column per year.

Karrakassis *et al.* (1999) attributed increases in benthic diatom biomass beneath farms in Greece to the periodic release of phosphate stored in sediments as the sediments oscillated between reduced and oxidised states. Under oxidising conditions, phosphate becomes bound as Iron (III) phosphate which precipitates near the sediment surface. Under reducing conditions, deeper in the sediment, Iron (III) is reduced to Iron (II) the phosphate of which is soluble.



#### 1.3.4 Silicon (Si) budget

Only one comprehensive study of silicon budgets has been published (Holby and Hall, 1994), which is perhaps surprising given the key role of this element in diatom metabolism. Almost all of the Si added in food to the marine trout farm investigated was lost to the environment but this only accounted for around 20% of the total Si budget. The majority of Si was thought to have arisen from diatoms associated with the farm itself, i.e. the farm provided a good niche for organisms utilising Si from sources external to the farm. Fluxes from the sediment to the overlying water were around 2.5 times higher than from local “control” sediments. There is continuing concern that toxic dinoflagellate species may be promoted under conditions of nutrient imbalance (Berry, 1996). It has been proposed, therefore, (Holby and Hall, 1994) that, in order to maintain ratios of Si relative to P and N, cage farms should be sited in areas which are well supplied with fresh sea water and that the deliberate adding of biogenic silica to feed formulations should be considered.

#### 1.3.5 Organic enrichment

Sediments are diverse environments supporting a range of flora and faunas existing in a complex matrix whose defining parameters include particle size, carbon (food) availability, oxygen concentration and redox potential. Biogeochemical processes in marine sediments are dominated by ambient hydrography (deposition, erosion and oxygen supply) and by the net input of carbon, which determines sedimentary oxygen demand and hence redox chemistry.

##### 1.3.5.1 Sampling techniques and strategies

Because of their predominantly sedentary nature, benthic infauna (animals living within the sediments) are the populations most frequently selected for study in assessment of the effects of any environmental disturbance. Quantitative samples of the sediments are taken, using standardised grabs or corers, from disturbed areas and at varying distances from those areas. All animals found in the samples are enumerated and identified and the composition and density of the populations are compared from area to area. Concomitant sediment samples and hydrographic records are taken for the measurement of a range of natural and disturbance related physical and chemical parameters. These would commonly include flow rate through the cages recorded over a full tidal cycle on spring and neap tides, grain size, pH (acidity), Eh (redox potential, TOM (total organic material) and/or TOC (total organic carbon) in the sediments, together with analyses for any chemicals used in cage treatments. Comparisons of the biological and environmental data are made and common trends with distance from the disturbance are sought. Such sampling surveys are repeated at intervals to assess trends over time. Sampling techniques of this type have now been standardised for a range of survey purposes, cf., HelCom (1999); ICES (in press); NS 9423 (1988); OsParCom (1997); SFT (1999). Such standardised guideline manuals have now been issued for use in fish farm surveys in Norway (NS 9410, 2000) and Scotland (SEPA, 1998) and are being compiled for use in other European areas.

The sampling strategies most frequently adopted for fish farm surveys are to establish sampling stations along transects orientated along the axis of the prevailing current flow through the cages and originating beside the cages. Samples are taken at intervals along the transects, e.g. at 0, 25, 50 and 100 m from the cages and at a reference station sited in an area beyond the influence of any cage effects and having similar sedimentary characteristics to those of the transect stations. The intensity of sampling in both time and space is, however, generally site specific and defined in consultation with the regulatory authorities. In Scotland the sampling regime is varied in relation to the estimated carrying capacity of the site and the proposed stocking densities. Small farms in hydrodynamically energetic areas may only be required to undertake a small-scale qualitative visual survey (photo or video) of sedimentary conditions or to take a single set of five replicate samples from under the cages during the time of maximum cage biomass. Large farms

in quiescent areas, on the other hand, may be required to carry out a fully quantitative survey, at the time of peak biomass, of a wide range of physical, chemical and biological factors along up to four transects radiating from the cages. In such cases an annual visual survey is also required. Full technical details for the implementation of the required sampling are given in SEPA (1998).

In Norway a management system (MOM, Modelling Ongrowing fish farms Monitoring) has been adopted which combines simulation modelling of potential environmental impacts with a monitoring programme of increasing elaboration dependent on the model's predicted scale of impacts (Ervik, *et al.*, 1997; NS 9410, 2000). The monitoring has to ensure a farm's compliance with a set of required Environmental Quality Standards (EQS). Three classes of monitoring are defined. Class A for farms predicted to suffer no appreciable environmental impact outside the immediate cage area requires only a simplified assessment of sedimentation rates beneath the cages and does not need to conform to EQSs. Class B will be applied to most farms where some degree of impact is anticipated. It specifies a qualitative assessment of infauna, quantitative measurements of acidity and redox potential and a ranked scoring of a range of visually recorded sedimentary characteristics in samples taken locally around the cages. These measurements have to meet EQSs. Class C will apply to those farms predicted to have a high impact level. These will be required to undertake a long-term survey of benthic faunal changes along transects through the anticipated impact zones. Such surveys will also have to meet set EQSs. The recommended techniques for carrying out each class of survey are set out in NS 9410(2000).

#### 1.3.5.2. Sedimentary microbiological processes.

A variety of terminal electron acceptors are used by different bacterial communities in marine sediments. The oxygen concentration at any point in the sediment is dependent on the rate of its uptake, either to fuel aerobic metabolism, or to re-oxidise reduced products released from deeper in the sediment. When the oxygen demand caused by input of organic matter exceeds the oxygen diffusion rate from overlying waters, sediments become anoxic and anaerobic processes dominate. As sediments become more reducing with increasing distance from the water column interface, a range of microbiological processes become successively dominant in the order:

- aerobic respiration, ammonium oxidation (to nitrite) and nitrite oxidation (to nitrate). These aerobic nitrifying processes are inhibited by sulphide and are, therefore, of limited importance in sediments beneath marine fish farms;
- denitrification (producing dinitrogen from nitrate);
- nitrate reduction (producing ammonium from nitrate) and manganese reduction;
- iron reduction;
- sulphate reduction (producing hydrogen sulphide)
- and lastly, under the most reducing conditions, methanogenesis (producing methane).

To some extent, these processes may overlap spatially. In marine systems, sulphate reduction is the most important terminal anaerobic process for the degradation of organic material (Holmer and Kristensen, 1992) but is much less important in fresh water due to the normally low sulphate concentration.

The redox potential (Eh) profile measured down the sediment column to a depth of 10-15 cm gives a useful guide to the relative degree of carbon enrichment in the sediments (Pearson and Stanley, 1979). Positive Eh values are indicative of aerobic conditions whereas negative values are associated with anaerobic microbial processes. Under normal rates of detrital carbon input to sediments the redox discontinuity level (RDL), i.e. the point at which anaerobic processes become predominant, lies some centimetres below the surface. As carbon inputs increase the RDL approaches ever closer to the surface as the BOD (Biological Oxygen Demand) within the sediments increases. Eventually, under very high detrital inputs, the RDL coincides with the sediment/water interface, where, under low flow conditions, it might even rise into the water column. Since organic degradation rates are lower under anaerobic than in oxygenated conditions (2-3 times lower first order rate constants, Westrich and Berner, 1984) these extreme states are highly undesirable. Not only do they result in the elimination of the benthic infauna which, through bioturbation, play a crucial role in oxygenating the upper sediment layers, but in slowing down carbon recycling carbon accumulation is enhanced, thus perpetuating sedimentary anoxia.

A useful summary of the impact of salmonid cage farming on benthic microbiology is given by Davies *et al.* (1996). A significant disruption to nitrogen cycling in the sediments immediately beneath fish cages, with inhibition of nitrification and denitrification, has recently been reported by McCaig *et al.* (1999). They demonstrate the dominance of a novel subgroup of nitrosomonas bacteria at the cage site which is absent in the normal sediments. This complements the information of Hall *et al.* (1992) that pore water ammonium levels beneath fish cages was greatly enhanced compared to that outside the area (see section 1.3.2 above). However these authors found that the net flux of N from the sediments beneath the cages was only 11 % of the total N input.

A study in the Bay of Fundy, Nova Scotia by Hargrave *et al.* (1997) at sites beneath cage farms and at a comparable number of reference sites showed that total sulphur and Eh in the surface sediment and benthic CO<sub>2</sub> release and O<sub>2</sub> uptake were sensitive indicators of benthic enrichment. However surface sediment water content, grain size, pore water salinity and sulphate were less sensitive indicators. The biomass of deposit feeding organisms was significantly higher at the cage sites but not the total macrofaunal biomass.

#### 1.3.5.3. Benthic macrofaunal response to enrichment.

The gross effects of wastes from intensive cage culture on marine benthic habitats and processes in northern European and other cool-temperate regions are now fairly well established (Brown *et al.*, 1987; Weston, 1990; Holmer and Kristensen, 1992; Hargrave *et al.*, 1993; Wildish *et al.*, 1993; Findlay *et al.*, 1995). Essentially these follow the pattern of impacts from other organic pollutant sources (see Pearson and Rosenberg, 1978) but on a more reduced spatial scale. Recorded effects include reducing sediments, hypoxia in the water overlying the sediment, increased sulphate reduction, and marked changes in benthic faunal and meiofaunal (Duplisea and Hargrave, 1996) assemblages in terms of species number, diversity, abundance and biomass. Benthic macrofaunal populations in sediments receiving normal detrital inputs derived from planktonic production in the overlying water column are species rich, have a relatively low total abundance/species richness ratio and include a wide range of higher taxa, body sizes and functional types, i.e. they are highly diverse communities. As detrital inputs increase diversity also initially increases as the enhanced food supply provides opportunities for the expansion of existing populations and the immigration of additional species. However the concomitant changes in the physical and chemical conditions in the deeper levels of the sediments progressively eliminate the larger and deeper burrowing and longer lived forms and favour smaller, more rapidly growing “opportunistic” species. Eventually, if input levels continue to increase the surface sediments become anoxic and only a small number of specialist taxa can survive, principally

small annelid and nematode worms. However under such conditions populations of these species may reach very high levels. Where the RDL occurs close to the sediment surface, this may become covered in dense mats of sulphide oxidising bacteria *Beggiatoa* sp. Ultimately, increasing levels of sedimentary BOD bring about deoxygenation of the lower levels of the overlying water column leading to the elimination of all macrobenthic fauna. Although the succession is continuous along the enrichment gradient, a number of phases characterised by differing dominant taxa can be distinguished. The successional phases may also be described by reference to the changing relationships along the enrichment gradient of the three most important population parameters, species richness (S), abundance (A) and biomass (B), of benthic communities. Thus in grossly enriched areas, where the immediate bottom water is intermittently or fully anoxic and Eh levels are uniformly negative, no infaunal metazoans survive (zone A). In zone B only a few vermiform taxa can survive, but often in very high numbers and the RDL lies close to the sediment surface. Beyond this zone C is an area where species richness and biomass increase rapidly to a maximum and positive Eh values are found at some centimetres depth in the sediment. In this zone faunal densities are much lower but still well above background levels. Zone D is where levels of detrital input return to normal and the levels of all three parameters fall to their background levels. Here the Eh values are highly positive throughout the sediment column. Four such zones of effect were reported by Brown *et al.*, 1987: an azoic zone immediately under the cages; a highly enriched zone 0 - 8 m from the cage edge with a high biomass dominated by a large number of a few opportunist species; a slightly enriched transitional zone between 8 and around 25 m from the cages and a normal zone beyond that. However, each of these zones may vary in spatial extent (or may be absent) depending on local hydrography, and benthic effects may be measurable at considerably greater distances than 25 m from cages.

The most significant environmental constraint on the development of sedimentary anoxia under conditions of progressive carbon enrichment is the flow rate of bottom water over any particular site. High flow rates bring a continuous supply of oxygen to the sediment water interface that permits the survival of infauna even when sedimentary boundary layers are anoxic. Conversely low rates of bottom water renewal can lead to deoxygenation in the overlying water column as sedimentary BOD increases. Findlay and Watling (1997) examined the relationship between remineralisation rate, bioturbation by macrofauna and oxygen supply from the overlying water. They showed that where sediments suffer oxygen deficit for even relatively short periods of a few hours, e.g. caused by slack water, large sections of the benthic macrofauna are eliminated. Thus the degree of impact at a site can be estimated from knowledge of carbon input and from an examination of the prevailing hydrography.

#### 1.3.5.4. Bioindicators of sedimentary enrichment.

There is a considerable literature detailing species and higher taxa associated with various degrees of carbon enrichment in boreal marine sediments, e.g. Pearson and Rosenberg, 1978; Pearson *et al.*, 1983; Brown *et al.*, 1987; Weston 1990. The majority of such studies and compilations have shown that there are specific organisms or groups of organisms associated with particular levels of enrichment in any one area. However, only at the highest levels of enrichment related sedimentary disturbance is there any ubiquity in the organisms recorded. Thus throughout the world highly polluted marine sediments are dominated by a very few opportunistic macrofaunal species such as *Capitella* sp., often in high abundance. *Capitella* sp. (their taxonomy is not yet well established) are small deposit feeding polychaete worms capable of both benthic and pelagic larval dispersion which thrive in organic-rich sulphidic sediments and have low oxygen requirements (Chareonpanich *et al.*, 1994a). As such, they are well suited to the rapid colonisation of sediments where the original fauna has been impoverished as occurs beneath marine fish cages. Other polychaete taxa that commonly occur under such conditions are the

surface deposit feeding members of the Spionid and Ophryotrochid groups, e.g. in northern European waters *Malacoceros* and *Ophryotrocha*. Large carnivorous nematode worms also frequently predominate in highly enriched areas, but non-vermiform phyla such as the Mollusca and Echinodermata are completely excluded.

### 1.3.6 Carbon (C)

#### 1.3.6.1 Carbon inputs

In open fish culture, fish faeces are lost to the environment. Intensive methods, where fish are fed from an external source, also lead to wastage of uneaten food (processed fishmeal, trash fish). Processed fish food is composed of a highly labile (digestible) mixture of protein, fat, carbohydrate and other minor components such as vitamins and pigments. As it is undigested, uneaten food has a much greater capacity (weight for weight) than faecal material to impact the environment both in terms of energy content and degradation rate. Current estimates of waste pelletised fish food from salmonid cage culture vary between 5 and 15% but in fact this has rarely been objectively measured. There is evidence however that feed losses are being progressively reduced. A sediment-trap study at an Atlantic salmon farm in Scotland in 1999, estimated food loss at between 0 and 5% (Cromeley *et al.*, submitted). This has been forced by declining profits which compel farmers to use more efficient feeding strategies and, perhaps, also by the greater palatability of modern diets. In two sediment trap studies in 1993 and 1994 at a sea bass/bream cage site in Greece, an order of magnitude reduction in food wasted between annual sampling events was found, which was thought to be due in part to the introduction of new feeding strategies in response to the wastage observed during the initial study (Mac Dougall and Black, 1999).

Intensive culture in the developed world has come to rely on the use of pelletised fishmeal from high quality and, therefore, highly digestible sources. This has led to lower feed conversion ratios and less waste. (Enell, 1995) reports that the mean feed coefficient in the Nordic area in 1976 was 2.08 but had fallen to 1.25 in 1994 and was down to 1.0 - 1.1 in 1995 at Danish and Norwegian farms. Intensive culture in many other areas still relies on waste, or “trash”, fish of variable quality (Wu *et al.*, 1994). As mentioned above, such diets tend to cause greater benthic impacts due to lower digestibility and due to wastage during the feeding activity itself.

Several published studies have examined the total amount of particulates released to sediments from fish cages (Hall *et al.*, 1990; Ye *et al.*, 1991; Findlay *et al.*, 1995). Estimates of wastes vary between 29 and 71% (depending on year, Hall *et al.*, 1990) and 78% (Ye *et al.*, 1991) of input carbon. The variation in the sedimentation rate data presented in these studies ( $4.1 - 77.8 \text{ g C m}^{-2} \text{ d}^{-1}$ ) may be attributed to a variety of reasons relating to input parameters. However the difficulty in determining the precise position of sediment traps in relation to (partially mobile) cages also may play a part. A study using precisely positioned sediment traps under cages at Scottish farms gave rates in the range  $11-33 \text{ g solids m}^{-2} \text{ d}^{-1}$  (T.D. Nickell, pers. comm.). To put these input rates in context, typical sedimentation rates near long-sea sewage outfalls around the British coast are less than  $1 \text{ g C m}^{-2} \text{ d}^{-1}$  mainly because of their exposed, dispersive locations (Cromeley *et al.*, 1998).

The isotopic ratio of organic carbon in sediments has been used as a tracer of the extent of dispersion of waste organic material (Ye *et al.*, 1991) as has the presence in sediments of lipids derived from fishmeal (Henderson *et al.*, 1998). In both of these studies the influence of the farm was measurable at considerable distance from the cages.



#### 1.3.6.2. Carbon recycling and benthic productivity in enriched sediments.

Various studies have shown that microbiological metabolism in sediments is stimulated by organic wastes from fish farms. In a shallow marine cage-farm in Kolding fjord, Denmark, microbiological metabolism in the sediments was measured at around 10 times greater ( $525 - 619 \text{ mmol CO}_2 \text{ m}^{-2} \text{ day}^{-1}$ ) than at a reference site, most of which could be accounted for by sulphate reduction (Holmer and Kristensen, 1992).

Studies on the production of macrobenthic populations in the vicinity of cage farms in the west of Scotland (Pearson *et al.*, 1995) have suggested that the production of infaunal benthos close to the cages is between 4-6 times the background levels. This supports a greatly increased population of epibenthic predators, principally demersal fish and malacoceran crustacea whose productivity is some 50% higher than that of similar predator populations on normal sediments. Thus the cage farms make a significant contribution to the production of surrounding native populations.

#### 1.3.7. Seasonality in benthic response to sedimentary enrichment.

A number of studies have shown that the micro- and macrobiological changes associated with sedimentary enrichment are influenced by the seasonal cycle. Holmer and Kristensen (1992; 1996) found that sulphate reduction rate in the surface sediments at a marine fish farm in shallow Danish waters varied from low levels in the early spring and late summer to peaks in early summer and in winter when pools of organic matter decreased. Methane production occurred concurrently with sulphate reduction in the late summer. Peaks in pore water solutes appeared in late summer but diminished as water temperatures fell in the autumn. Karakassis *et al.* (1998) also investigated seasonal changes in geochemical processes in the sediments around farm cages in Cephalonia Bay in the eastern Mediterranean and reported increased accumulation of organic matter in summer followed by increased carbon mineralisation in the cooler winter months.

In contrast to these case histories, Johnsen (1996) reported no seasonal effects on the concentration of fatty acids, which act as markers for microbiological sedimentary activity, in the sediments adjacent to a fish cage in western Norway.

Hargrave *et al.* (1993: 1997) found that maximum ammonium release from the sediments coincided with highest water temperatures in July around and beneath salmon cages in the Bay of Fundy, Nova Scotia. Peak oxygen uptake and sulphide accumulation in the sediments occurred in September. The latter was in excess of 100 mM S in the pore water in that month which could have been toxic to infaunal benthos and coincided with a reduction in the population of *Capitella* spp. In a similar study in coastal waters in Maine, Findlay *et al.* (1995) reported low levels of sedimentary organic matter beneath cages in spring and early summer followed by increases which reached a peak in November accompanied by the development of surface bacterial mats and a switch in the benthic communities to those associated with high levels of enrichment. Subsequent storm-related resuspension reversed this development. In the warmer waters of an embayment in southern Japan with a 22 year history of cage aquaculture Tsutsumi (1995) found extremely reducing conditions developed in the bottom water throughout the bay in the summer months resulting in the elimination of all bottom fauna. Recolonisation took place during the autumn and spring but only by an opportunist polychaete fauna. Molluscs, which had formerly dominated the benthos, were entirely absent and the total biomass of benthos had decreased markedly.

#### 1.3.8. Benthic recovery

The rate at which sedimentary ecosystems recover following the removal of cages or the cessation of farming is of considerable interest, particularly as the fallowing of sites and rotation of cages has now become recommended practice in many areas where hypertrophic sedimentary

conditions are a problem. Up to the present there have only been a few detailed studies of the time taken for sedimentary conditions to return to an undisturbed state following the fallowing of a cage site. Karakassis *et al.* (1999) report on one such study undertaken over two years following the removal of cages at an intensive farm in Cephalonia Bay, Greece. They found that most geochemical variables in the sediment 10 m from the edge of the cage site had values similar to those found at the reference station 1.2 km from the site 11 mo. after cage removal. However values at a station in the centre of the site were still showing large fluctuations indicative of continuing enrichment at the end of the study after 23 months. At this time the benthic populations at the centre station were still dominated by small opportunist polychaetes typical of high levels of enrichment, although the presence of some small bivalves and infaunal brittle stars suggested the recovery process was continuing. At the 10 m station, the fauna showed a strong recovery at the end of the first year, but a regression to hypertrophic characteristics occurred during the second year when the communities were again dominated by small polychaetes, although the bivalves, crustacea and echinoderms, which had recolonised that area during the first year, retained their presence. This secondary regression was attributed to increased carbon input from benthic algal production stimulated by nutrient regeneration from the enriched sediments during the recovery process in the summer months. Lu and Wu (1998) carried out an experimental study on the macrobenthic recolonisation of trays of defaunated organically enriched sediment collected from beneath a fish farm in Hong Kong. The trays were exposed to the sub-tidal area of a clean site with similar hydrographic characteristics. Recolonisation was rapid, with 144 individuals from 26 species per tray recorded within the first month. Molluscs made up half the species present but polychaetes comprised 80% of the total abundance. Maximum abundance in the trays was recorded after 3 months and species richness peaked after 4 months, followed in both cases by a decline to putative background levels. It was suggested that, because of such rapid recolonisation, cage farming in the area would be unlikely to have any long-term effects.

These various studies suggest that recovery rates are considerably higher in the warmer waters of the eastern Mediterranean and the South China Sea than in the boreal North Atlantic. However it should be noted that local hydrographic conditions have a considerable influence on recovery rates in all areas. In quiescent areas benthic community normalisation might be expected to take considerably longer than in more hydrodynamically energetic areas.

#### **1.4 Impacts in differing environments**

Although most research has concentrated on marine culture in temperate zones much of the major expansion in aquaculture is occurring in sub-tropical and tropical zones. It is relatively easy therefore to pick out those few research areas that have been studied and identify those where further work is urgently required.

##### *1.4.1 Mediterranean*

The Mediterranean is a semi-enclosed warm sea with mean summertime temperature of 25°C and a narrow tidal range (<50 cm) (Karakassis 2001 A). The Eastern Basin of the Mediterranean is generally oligotrophic, characterized by low nutrient and phytoplankton biomass levels (Azov 1986). Tidal flows are weak in many areas but current speeds and therefore flushing can be of a similar order to fjordic Atlantic sites (Black and Mac Dougall, in press).

During the past 10 years mariculture activities in the Eastern Mediterranean have expanded rapidly, focusing mainly on sea bass *Dicentrarchus labrax* and sea bream *Sparus aurata*

production (Deniz et al. 1997, White 1999, Kararassis 2000). Most of the Greek production is focused in coastal bays, whereas in Turkey the generally small farms are located in sheltered sites along the southern Aegean Sea while larger farms (100 to 300 tons year<sup>-1</sup>) are usually set in more exposed locations. Despite the large production of marine fish in the Eastern Mediterranean, relatively little is known regarding the environmental impacts of this industry (Munday et al. 1994) outside of the few environmental studies of Greek fish farms.

As is the case in many other areas, most of the mariculture environmental research and monitoring has focused on benthic impacts. A number of workers examined the impact of fish farms on the seabed in Greece and found that it was local and did not exceed 25 m from the farm perimeter (Lamy and Guerlorget 1995, Karakassis 1998, Karakassis et al. 2000). Karakassis (1998) found that the top layer of the silty sediments under a farm situated in Cephalonia Bay contained high levels of organic matter, phaeopigments, total phosphorus, yet the water content and the redox potential values were very low. While comparing three different fish farm sites in Greece, Karakassis et al. (2000) found that the redox potential in the sediments under and in the vicinity of all fish farms studied was lower compared to the control sites, however only at the site located over a silty sediment (at Cephalonia) were the redox values negative. Moreover, organic carbon and nitrogen and ATP content (proxy for microbial biomass) were all higher under the fish cages as compared to the control sites. However, neither Papaoutsoglou et al. (1996) nor McDougall and Black (1999) found accumulation of organic matter on the sediment under fish farms in the western Saronikos Gulf, despite the low current speeds and the large amounts of fish farm waste collected in sediment traps placed under the fish cages.

Lamy and Guerlorget (1995) found a pronounced decrease in species diversity under floating-net cages as compared to a control site in Kalloni Bay, Lesbos, Greece. Karakassis et al. (2000) recorded an increase in species diversity along a transect from the cages and up to 25 m from the Cephalonia and Ithaki farms, while at Sounion there was hardly any difference between the farm and control sites. The abundances and biomasses of macrofauna in the coarse sediments under the Ithaki and Sounion fish farms were significantly higher than at the control sites, whereas in the silty sediments at Cephalonia no such difference was found (Karakassis et al. 2000). At all three sites: Cephalonia, Ithaki and Sounion, the macrofauna community formed three distinct clusters. Based on the different environmental impacts of the fish farms located at these sites Karakassis et al. (2000) concluded that the impact of the fish farms on the benthos is site-specific.

The recovery of the sediments after the removal of a fish farm at Cephalonia Bay was a long-term process (Karakassis et al. 1999). Two years after the removal of the farm the nitrogen, phosphorus, chl *a* and phaeopigments content were still higher than at a nearby reference site. However, the water content of the sediment at the farm and at the control sites was the same. Opportunistic macrofauna continued to dominate the benthos at the farm site, and species diversity and overall abundances were lower than at the control site. A benthic algal bloom was observed during summer, probably caused by the release of phosphate from the enriched sediments.

In addition to benthic impacts, the fish farms also exerted measureable effects on water quality. Increases (above ambient) in ammonia concentration around fish cages located in the western Saronikos Gulf, Greece were related to enhanced feeding during summer and to reduced current speeds prevailing during this season (Papaoutsoglou et al. 1996). Paraskevi et al. (1999) measured high concentrations of ammonia between the cages of the Ithaki fish farm, however no increases were detected at the Cephalonia and Sounion farms. Karakassis et al (2001 B) found that concentrations of NH<sub>4</sub>, PO<sub>4</sub> and Si within the fish cages of the Cephalonia farm increased during



the day, reaching maximal concentration at noon and dropped to background levels thereafter. Moreover, there was a consistent decrease in the levels of all nutrients with depth.

Although elevated nutrient concentrations were measured, there were no parallel increases in chl *a* concentrations in the vicinity of the Ithaki, Cephalonia and Sounion fish farms (Paraskevi et al. 1999). Karakassis et al (2001 B) also reported that the diurnal changes in nutrient concentrations at Cephalonia fish farm had little effect on chl *a* and phaeopigments concentrations, except at the late afternoon when the concentrations of chl *a* at the deeper layer doubled. Paraskevi et al. (1999) concluded that seasonality was the major factor controlling the abundance of all plankton groups. Karakassis (1998) found that the concentrations of phosphorus in the sediments beneath Cephalonia fish farm increased with time and thus it was not readily available for phytoplankton growth. This may partially explain the minor changes in chl *a* concentrations observed around fish farms in Greece.

It has been reported that large numbers of wild fish (e.g. mullets) are present around Greek fish farms (Papaoutsoglou et al. 1996, McDougall and Black 1999). In comparing the relatively unimpacted sediments below the Greek farms to those in temperate regions, it was suggested that the wild fish populations may play a major role by feeding on the farm wastes and preventing these from reaching the seafloor (McDougall and Black 1999).

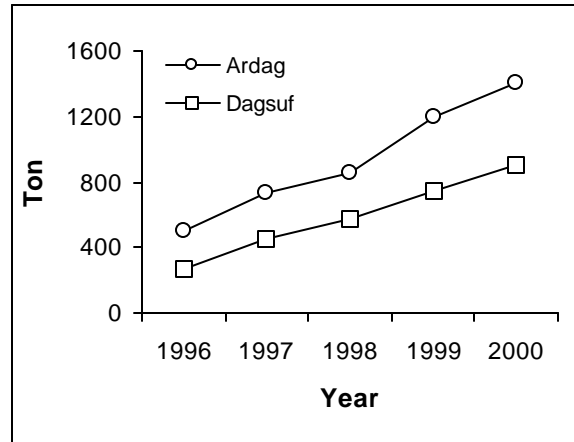
The growing need of the mariculture industry for juveniles and the shortage in the supply from hatcheries has increased the fishing pressure on wild fry of sea bass and sea bream. In Turkey, between 3-4 million wild sea bass and 140-156 million sea bream fry were collected from 1995 to 1999. However, the Turkish government has decided to prohibit the collection of wild juveniles from the end of 2000 onwards (White 1999, Sadek and Mires 2000). Moreover, Sadek and Mires (2000) suggested that developing more fish hatcheries would supply the growing demand for juveniles and could prevent “waste” due to the high mortalities of wild fry during transport to the fish farms. It has also been argued that the transfer of genetic stocks of wild fish between regions may impact the gene pool of the endemic populations (Smith 1999), as is currently claimed regarding salmon in Scotland and Canada.

The environmental impacts of mariculture also include various pathobiological phenomena. Papaoutsoglou et al. (1996) could not find any distinct relations between the number of parasites found on sea bass and sea bream and the water quality parameters measured at a fish farm in Saronikos Gulf. Zlotkin et al. (1998) reported that farmed seabass and seabream in net cages on the Mediterranean coast of Israel, as well as wild populations of rabbitfish *Siganus rivulatus* that were shoaling around the nets, were infected by a single clone of *Streptococcus iniae*. Since the wild rabbitfish populations were highly susceptible to *S. iniae* it was suggested that the source of infection was the farmed rather than the wild fish populations.

Meadows of the seagrass *Posidonia oceanica* cover vast areas in shallow regions of the Mediterranean. They are regarded as the cornerstone of the littoral ecosystem providing a wide variety of niches, accounting for the high diversity of these areas. A recent study (Pergent, *et al.*, 1999) examined the impact of cage farming on this protected species. This concluded that while the nutrient input from the farms studied resulted in an increase in leaf length and increases in the biomass of epiphytes and ichthyofauna, there was evidence of decreased meadow density and total disappearance beneath cages. Because of its ability to record environmental alterations including nutrients, light and trace metals (by examination of dead leaf sheaths), it is proposed that *Posidonia* is a useful bioindicator for monitoring fish farm impacts in these environments.

#### 1.4.2 The Red Sea

Two commercial net pen fish farms, Ardag and Dagsuf, operate at the northern end of the Gulf of Eilat. The farms are located 300-500 m offshore close to the Jordanian border. The main fish produced in the floating sea cages is gilthead seabream *Sparus aurata*. The production of *Sparus aurata* (ton/year) in the Gulf of Eilat have increased considerably between 1996-2000 (Figure 1).



**Figure 1:** Annual increase in the production of gilthead sea bream *Sparus aurata* in the Gulf of Eilat between 1996-2000. Ardag and Dagsuf are the 2 commercial net-cage fish farms operating in the Gulf of Eilat (adapted from Snovsky and Shapiro 2000).

The influence of the fish farms on the marine environment is largely related to the materials released from the cages to the surrounding waters. In 1999 the fish feed in both farms was changed to an extruded pellet high-energy diet. Between 1996 and 1999, tank-based nutritional studies showed that 1.79 ton of feed were required to produce 1 ton of fish (mean weight 400 g) (Lupatch and Kissil 1998), however the actual feed conversion ratio was higher than that. The nutrient budget calculated from these studies indicated that 68.7% of the nitrogen (N), 29% of the phosphorus (P) and 56% of the carbon provided in the feed was released to the environment as dissolved compounds, while 9.3% of the N, 42% of the P and 15% of the C in the feed descended to the seafloor as particulate matter. In 1999 the fish farms started using an extruded, high-energy feed which was more expensive than the previous formulation, but required less feed input (1.39 ton feed were required to produce 1 ton of fish). Tank-based measurements indicated that the extruded formula should also be more environmentally-friendly, releasing only 64.7% N, 21% P and 46% C of the feed as dissolved matter, and 7.3% N, 42% P and 9% C as particulates (Lupatch personal communication).

In an attempt to get a general notion regarding the dispersal of dissolved compounds from the fish farms to the surrounding waters, a hydrodynamic model (Princeton Ocean Model) was employed with a passive tracer, using data from the Gulf of Eilat. This model yielded worst-case scenarios since it focused on dissolved nitrogen which is not an inert tracer at all (Angel et al. 1998). The model predicted very limited local impact during the winter months due to high background nitrogen levels in this season (deep vertical mixing) yet up to a fourfold increase in local N levels during summer, when the water column is stratified and N levels are barely measurable. The model also showed that the impact decreases with distance from the fish farms.

The flux of particulate organic carbon (POC) to the sediment, as measured under the ARDAG farm, varied between 4.5-12.7 g C M<sup>2</sup> d<sup>-1</sup> (Angel et al. 1995, Katz 1999). The input of particulate organic matter (POM) to the sediment (measured by loss-on-ignition (LOI) varies seasonally (Lupatch and Kissil 1998) with higher input in summer than in winter months (Table 1). Unpublished data indicate that despite increased fish production, there was a decrease in summer LOI levels between 1990-1999, possibly resulting from improvements in feed quality and feeding strategies.

The studies conducted below the ARDAG fish farm indicated that farm-impacted sediments are restricted to the immediate vicinity of the farm (Angel et al. 1995, Angel et al. 1998, Eden et al. in prep.). Decomposition rates of the organic matter in the enriched sediments under the ARDAG fish cages based on oxygen demand were 2.7±0.5, 5.8±3.1 and 5.4±1.3 gC m<sup>-2</sup> d<sup>-1</sup> for July, August and September 1998, respectively (Katz 1999), very similar to the mean rate (5.3 g C m<sup>-2</sup> d<sup>-1</sup>) previously determined by Angel et al. (1995) based on ammonia flux data. Although sedimentation rates were higher than decomposition rates, Angel et al. (1995) did not find accumulation of organic matter in the sediments under the fish farm and they suggested that occasional strong bottom currents and bioturbation may be responsible for lateral transport and additional OM decomposition.

Table 1: Organic content of the sediment, as measured by loss-on-ignition (LOI) beneath the Eilat fish farms ARDAG and DAGSUF as measured during several studies conducted between 1990 to 1998.

Location	Year	Season	LOI %	Reference
ARDAG	1990-1992	summer	6-12	Angel et al. (1995)
ARDAG	“ “	winter	4-6	
ARDAG	1993	summer	13	Angel et al. (2000)
150m from ARDAG	“ “		5	
ARDAG	1994	winter	6-8	
ARDAG	1997	summer	3-8	Angel et al. (1997)
DAGSUF			3-5	
>50m from ARDAG			1.5-2	
ARDAG	1998	summer	5-6	Katz (1999)
ARDAG	1998, 1999	summer	5-7	Eden et al. (in prep.)
ARDAG	1998, 1999	winter	3-5	
100-800m west of ARDAG			1.4-2	

Due to the organic enrichment the sediments under the fish cages contain high concentrations of dissolved nitrogen, phosphorus and hydrogen sulfide and low concentrations of dissolved oxygen (DO) (Table 2). Concentrations of dissolved nitrogen, phosphorus and hydrogen sulfide in the sediment porewater decreased while the concentrations of DO at the sediment surface increased with increasing distance from the farm (Angel et al. 1995, Eden et al. in prep.). In summer (May-October) the porewater nutrient levels in the sediment below the farms were higher than the winter concentrations (November-March). Undisturbed sediments did not contain measurable H<sub>2</sub>S in the top 3 cm.

Table 2 Concentration of hydrogen sulfide, phosphate, ammonia in the top 3cm of the sediment) and dissolved oxygen at the sediment surface under the ARDAG fish farm and at reference stations.

Location	Year	Month	H <sub>2</sub> S (mM)	Phosphate (μM)	Ammonia (μM)	DO ( M)	Reference
ARDAG	1990-1992		1-2.3	40-140	400-1200		Angel et al. (1995)
50m west of ARDAG	same			2.1-8.7	36-76		same
ARDAG	1993	Oct		250	1300		Angel et al. (2000)
50m west of ARDAG	1993			0	100		same
ARDAG	1994	Jan.		50	150		same
ARDAG	1998	July	0.672			4.1	Katz (1999)
ARDAG	1998	Aug.	1.90			1.5	same
ARDAG	1998	Sep.	1.44			1.2	same
ARDAG	1998-1999	April	0.67			2.0	Eden et al. (in prep.)
ARDAG	same	July	1.43			0	same
ARDAG	same	Oct.	3.66			0	same
ARDAG	same	Feb.	2.14			32	same
100-800m west of ARDAG	same	April	0			80	same
100-800m west of ARDAG	same	July	0			69	same
100-800m west of ARDAG	same	Oct.	0			39	same
100-800m west of ARDAG	same	Feb.	0			150	same

Ammonia, nitrate, nitrite and phosphate concentrations in the water column near the fish farms were generally under detection limit (Angel et al. 1998). The ammonia concentrations recorded on the Jordanian side of the northern shore of the Gulf of Eilat (nearshore) were consistently higher than the concentrations measured at an offshore reference station during 1994-1995 (Badran and Foster 1998). Ammonia concentrations at this station reached a peak of 0.12-0.25 μM between March and June 1995; whereas nitrite and nitrate peaked at 0.25-0.38 μM and 1.2μM, respectively. Angel et al. (1998) measured 0.40 nM (0 - 0.04μM) phosphate in the vicinity of the fish farms, which was not significantly higher than that recorded at an offshore reference station. The phosphate concentrations recorded at a nearby sampling station on the Jordanian side of the north shore were somewhat higher (100 nM) in spring and lower again in summer (30 nM) (Badran and Foster 1998).

Chl *a* levels were 2-4 times higher around the fish cages (0.35-0.55 μg/l) as compared with an open water reference station (0.15-0.35 μg/l) and may have contributed to the higher turbidity occasionally observed near the fish farms (Angel et al. 1998). Badran and Foster (1998) observed high chl *a* concentrations (>0.60 μg l<sup>-1</sup>) towards the end of winter-early spring and low concentrations during summer at the northern tip of the Gulf of Aqaba near the Israeli fish farms. Similarly high levels of chlorophyll were not detected at any of the other stations sampled, including the port of Aqaba, the industrial area, an offshore station and a distant coral reef. Long

term monitoring in the middle of the Gulf of Eilat (this station is located several km south of the north shore where the fish farms are situated) revealed a gradual increase in chl *a* concentrations, from 0.1  $\mu\text{g l}^{-1}$  in 1995 to 0.4  $\mu\text{g l}^{-1}$  in 2000 (Genin and Zakai 2000). It was argued that this increase correlated well with the increase in commercial fish production from @1000 ton year<sup>-1</sup> in 1995 to about 2000 ton year<sup>-1</sup> in 2000, but the expansion of the towns of Eilat and Aqaba, and all related activities, during this period were ignored.

The enriched sediments under ARDAG fish farm are usually covered by *Beggiatoa* (bacterial) mats while the sediments up to 100m away from the farm are covered by pigmented mats comprised of a complex microbial community, including *Beggiatoa* spp., filamentous cyanobacteria, euglenoids, pennate diatoms and ciliates (Angel et al. 1992, 1995). The mats undergo seasonal changes wherein the filamentous cyanobacteria dominate in summer and fall and *Beggiatoa* spp. and *Euglena* spp. dominate during winter and spring. Occasionally during winter strong bottom currents erode the mats, strongly reducing the organic content of the surface sediments, however the mat communities generally reestablish and recover at the beginning of spring.

Live benthic foraminifera (>45 $\mu\text{m}$ ) were found under the ARDAG fish farm in the early 1990's and peak abundances were recorded near (but not below) the farm (Angel et al. 2000). The most abundant species were *Assilina ammonoides*, *Borelis schlumbergeri*, *Hauerina diversa* and *Peneroplis planatus*. The abundance of live foraminifera showed negative correlation with sediment porewater ammonia values but no correlation was found with any of the other geochemical variables.

Strauss (2000) found that meiofaunal assemblages under the ARDAG farm were dominated by Nematoda, although Ciliophora and Turbellaria were also occasionally abundant. In the unenriched sediments, Nematoda, Harpacticoid Copepoda and Gastrotricha were the major taxa. The over-all meiofauna density, taxonomic richness and taxonomic diversity increased with increasing distance from the fish cages. In this study, consistently larger abundances of benthic copepods were found with increasing distance from the farm, suggesting that overall copepod abundance (as opposed to the traditional nematode/copepod ratio) might serve as a reliable indicator for sediment organic enrichment.

Increased abundances of the opportunistic mud snail *Nassarius sinusigerus* were observed in the vicinity of the ARDAG fish farm since 1995 (Eden et al. in prep.). A peak in abundance was found some distance from the farm and its position was apparently related to the geochemical conditions in the sediment. Since the peak in abundance appears at the boundary between moderately to slightly impacted conditions it may serve as a means to assess the extent of the fish farm impact on the local benthic communities.

The Eilat net-cage fish farms attract many pelagic and reef fishes by virtue of the shelter and nutritional opportunities they provide. Angel et al. (1995) observed large groups of goatfish (*Parupeneus forsskalii*) and rabbitfish (*Siganus rivulatus*) feeding from the sediment in the highly impacted sediments below the fish cages. Gut content analysis of some of the benthos-feeding fishes in the area (including *S. rivulatus*) revealed high numbers of the mud snail *N. sinusigerus* (unpublished data).

The fish reared in the cages occasionally experience outbreaks of parasitic diseases and there is concern that these may spread to the wild fish living just outside the net cages. Diamant et al. (1999) found significantly lower numbers of heteroxenous macroparasites (digenea and other gut helminths) in the local rabbitfish, *S. rivulatus* collected around the ARDAG fish cages as

compared with specimens collected at a coral reef habitat 10 km away. However, there was no significant difference in the prevalence of microparasites in *S. rivulatus* (mainly monoxenous protozoa) between the two sites. Moreover, total (both monoxenous and heteroxenous) parasite species richness and infection loads were considerably higher at the coral reef site as compared to the mariculture site. Thus, in habitats such as the mariculture site where the full range of parasite hosts does not occur, the number of heteroxenous parasites decreases.

Net cage mariculture may also expose wild fish populations to new diseases and may amplify existing diseases. The pathogenic *Mycobacterium* was not detected among *S. rivulatus* during studies conducted in the 1970's and 1980's (Paperna et al. 1984, Diamant and Paperna 1986). However, since 1990 when it was first detected in farmed sea bass, *Dicentrarchus labrax* (Colorni 1992) the prevalence of the disease increased dramatically in both farmed fish and in wild rabbitfish (Diamant et al. 2000) and since 1995 it has been identified in 20 different species of native Red Sea wild fish (Diamant in press). The pathogen was identified as *Mycobacterium marinum* (Knibb et al. 1993) and may be a local strain (Ucko and Kvitt 2000). Another pathogen, *Pasteurella piscicida* (*Photobacterium damsela* spp.) was recently isolated from the farmed fish (Colorni and Diamant 2000). Nucleic acid analyses of isolates of *P. damsela* taken from infected fish in Israel, Europe and Japan revealed that the Israeli isolates form a separate cluster (Kvitt et al. submitted) and may therefore also be a local strain.

The pathogenic bacterium *Streptococcus iniae* was detected in two cage-cultured species reared in Eilat: red drum (*Sciaenops ocellatus*, in 1996) and sea bass (*Dicentrarchus labrax*, in 2000), and was recently isolated from wild fish captured from around the sea cages (Colorni et al., unpubl. data). Biochemical and molecular similarities of the isolates from cultured fish to those from the wild specimens strongly suggest that amplification and dispersal of this pathogen from captive to feral fish have occurred (Colorni et al., unpubl. data).

#### 1.4.3 Tropical culture

Much less work has been published on impacts in warmer climates. Wu *et al.* (1994) studied four small, shallow farms around Hong Kong and reported broadly similar results to Brown *et al.* (1987) but found that benthic impacts extended up to 1 - 1.5 km from the site. This covers a considerably larger area than that described by Brown *et al.* (1987) which may be due to the use of trash fish as feed in the Hong Kong study. Particles of waste fish may have a much lower sinking velocity than pellets and, therefore, may be dispersed across a greater area. Unfortunately, Wu *et al.* (1994) give no data on the positioning of their sampling stations relative to the cages and their method of determining the affected area is not clear. In their study of nitrogen budgets, Leung *et al.* (1999) predicted that from an annual production of only 3000 tonnes, 962 tonnes of nitrogen are released into the Hong Kong marine environment.

### 1.5 Minimisation of impacts

The use of filter-feeding shellfish species to reduce impacts of intensive culture while also producing a secondary product has also been examined. Oysters *Crassostrea gigas* grow up to three times faster, have greater condition factors and faster post-spawn recovery when grown near marine Chinook salmon cage farms compared to control sites as a consequence of the greater availability of particulate organic matter (Jones and Iwama, 1991). However, these results were not repeated with mussels *Mytilus edulis* where no increase in performance with proximity to the farm was found (Taylor *et al.*, 1992).



In several areas of the enclosed coastal seas of Japan where intensive cage culture has been practised for many years, sediments around fish farms may become anoxic and azoic during the summer months. There is the potential for the rapid degradation of the accumulated organic material by seeding the sea-bed with large numbers of cultured *Capitella* Sp. (Chareonpanich *et al.*, 1993). It was calculated that abundances of 59 000 individuals  $\text{m}^{-2}$  could treat organic material arriving at the sediment at the rate of  $0.58 \text{ kg m}^{-2} \text{ year}^{-1}$ . This represents a considerably lower sedimentation rate than is common at many farms in W. Europe (up to  $15 \text{ kg solids m}^{-2} \text{ year}^{-1}$ ) where *Capitella* sp. abundances are typically up to 90 000 individuals  $\text{m}^{-2}$  (T. Nickell, personal communication). Thus, assuming the calculations of Chareonpanich *et al.* (1994b), *Capitella* only process directly a fraction of the total organic input to these sites. However, the working of the sediments by these animals will render organic material more available to microbiota.

Various methods of reducing the discharge of feed from farms have been examined, including using an acoustic feed detector on marine cage sites to reduce the loss of medicated pellets (Ervik *et al.*, 1994); various sensors to detect when fish reduce feeding activity linked to feed input controllers; and cages which are completely enclosed by a tarpaulin supplied with water by a pump and wastes can be recovered for processing. None of these systems are in very widespread use at the moment although it is feasible that a regulator might require their use in certain circumstances.

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## Chapter 2

### A review of biofiltration processes as used in waste management

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#### 2.1. Biological sewage treatment

The following review considers a variety of systems designed to treat wastewater generated by human activities. In all of the treatment systems reviewed, there is an element of biofiltration which plays a key role in transforming or absorbing the undesirable waste compounds.

Most wastewater treatment systems have been designed to address similar biochemical processes; namely, the mineralization of organic matter and the uptake/incorporation of inorganic compounds liberated by this. The most abundant and biologically-active organisms involved in these processes are the bacteria. They play a central role in all of the major nutrient cycles, including the carbon, phosphorus, oxygen, nitrogen and sulfur cycles.

The most common biological treatment process for domestic and industrial wastewaters is “activated sludge”. In this process the wastewater is mixed, under aerobic conditions, with a dense culture of microbes, resulting in rapid microbial growth and respiration/breakdown of the biodegradable organic matter to  $\text{CO}_2$ ,  $\text{NO}_3$ ,  $\text{SO}_4$  and  $\text{PO}_4$ . Following this, the particulate matter is removed to a settling basin (clarifier) where, following a period of sedimentation, most of the settled material (detritus and bacterial biomass) is removed for disposal while the remainder of the bacteria-rich slurry is returned to the aerobic treatment area to inoculate a fresh batch of sewage water. There are several advantages to the activated sludge process, in comparison to other treatment methods, including high efficiency in removal of a variety of pollutants, cost-efficiency, size-versatility, it is controllable (i.e. possible to determine and vary the effluent quality) and resilience (i.e. ability to function at widely variable loads).

More modern activated sludge systems (the modified *Bardenpho* process) target the excess phosphorus that characterizes domestic sewage and is not removed by the simple aerobic activated sludge process described above. It is desirable to eliminate this phosphorus from the treated wastewater to avoid eutrophication problems following discharge of the clean water. In the modified Bardenpho process, the sewage is taken through a series of anaerobic – aerobic sequences, which release the phosphate from a bound state in the sludge, enabling the microbes to take up and incorporate a lot of the otherwise unavailable phosphate (Barnard 1976). The treatment process typically includes: 1) a primary anoxic zone, where sewage enriched in nitrate and nitrite undergoes denitrification as well as removal of soluble and colloidal organic matter. In addition, there may also be some release of phosphate. 2) a primary aerobic zone, where organic matter is oxidized; ammonia is oxidized to nitrite and nitrite to nitrate. Moreover, this is the main zone where phosphate released in the previous stage and orthophosphate that arrived with the untreated sewage are incorporated by the microbes. 3) secondary anoxic zone, which serves as a denitrification polishing stage to eliminate excess nitrates from the sewage. 4) secondary aerobic zone, where residual phosphates and ammonia are further removed via microbial uptake and nitrification, respectively. 5) clarifier, which further removes suspended solids prior to recycling of this material for partial reinoculation at the start of the process.

Treatment of wastewater by the activated sludge method relies on the physiology of the microorganisms therein. Suspended solids, colloidal material and dissolved organic matter become absorbed onto the surface of the sludge flocs and the microbes use the organic matter as a source for cellular carbon and for energy. Moreover, part of the wastewater organic material is converted into reserve food in the microbes. In order to maintain a rapid rate of organic matter removal, it is essential to provide the proper balance of available nitrogen (required for microbial energy transfer systems) and phosphorus (for microbial biosynthesis) in the activated sludge. If there is an imbalance in the levels of nitrogen and phosphorus, this may lead to increased abundances of filamentous microbes in the sludge. Large abundances of filamentous microorganisms are undesirable mainly because they may cause bulking which interferes with the process of separating between sewage sludge solids and liquid effluent (Blackall 1993). On the other hand, excessively low abundances of filamentous microbes may lead to foaming and different separation problems (Eikelboom 1993).

Removal of colloidal, suspended and dissolved materials from the wastewater occurs mainly on the surfaces of bacterial aggregates (flocs) in the aeration tank phase. The flocs are the one of the most important elements in the water treatment system because they are the main site of biological removal activity and because the treatment systems are designed to select for floc-forming groups of microorganisms. It is noteworthy that the flocs include a small percentage of filamentous microbes (Jenkins et al. 1986). In the aerobic phases of wastewater treatment, organic nitrogen is mineralized by ammonifying bacteria to ammonia and the ammonia is subsequently oxidized by nitrifying bacteria to nitrite and to nitrate. In the anoxic phases of the treatment, nitrate is reduced to atmospheric nitrogen and then released to the environment. Organic phosphorus in the wastewater is rapidly oxidized and converted to orthophosphate. Orthophosphate is removed from the wastewater by many different types of microbes, but the most efficient removal is by those bacteria that accumulate polyphosphates inside the cells. The composition of the microbial community in the activated sludge is determined by the conditions in the various components of the wastewater treatment system (Buchan 1984) and these may be quite variable in different systems. Most of the bacteria in sewage treatment systems are heterotrophs and the absence of the necessary growth media has generally limited our ability to identify the members of these complex communities. Nonetheless, the genus *Zooglea* is recognized as the major bacterium responsible for floc formation in activated sludge. Although many other bacterial species have been isolated from activated sludge, the relative abundances and roles are still not clear. With the aid of new molecular techniques that do not rely on cultivation and growth it should be increasingly possible to quantitatively describe the bacterial communities in activated sludge and improve our understanding of these systems. Activated sludge consists not only of complex bacterial communities but also fungi, algae and protista (Muyima et al. 1997). Many of the protista are bacterivores and algivores and they play an important role in the sewage treatment process by: a) packaging some of the bacterial biomass generated by the sewage decomposition process, thereby facilitating its removal and b) mineralizing the bacterial prey, thereby assisting in the general oxidation process.

In addition to the classical forms of wastewater treatment using large volume reactors and relying on floc formation and organic matter degradation in the suspended phase, there is increasing interest in the use of biofilm technology in the treatment of wastewater. In this approach, the natural growth of aquatic bacteria on surfaces is utilized. The advantage of biofilm reactors is that these may be designed with large surface areas that support a dynamic, yet fairly stable bacterial communities. Due to the complex 3-dimensional structure and nature of the biofilm communities, it is essential to understand how the biofilm organisms process the materials that we want to eliminate or decompose in the wastewater. Initially, the compounds of interest must travel from the liquid wastewater medium to the surface of the biofilm. Next, they must diffuse into the



biofilm and finally, they must reach the microbes within the biofilm community. Unlike the removal processes that take place in activated sludge flocs, microbial biofilms cannot process suspended or colloidal organic materials since these are too large to diffuse into the biofilm. These large compounds must first be broken down to lower molecular weight entities that can diffuse across the biofilm-water interface. The thickness of the biofilm is influenced by many factors, but perhaps foremost among these is the diffusion rate of the limiting nutrient(s) in the wastewater stream.

Within the biofilm, it is accepted that the microbial community is structured such that slow-growing bacteria (e.g. nitrifiers) are found deeper within the biofilm, whereas fast-growing microbes (heterotrophs) occur closer to the biofilm surface (van Loosdrecht et al. 1994). Biofilm wastewater reactors are generally designed on the basis of either fixed-substrate or suspended-particle processes. Fixed substrate reactors include trickling filters, rotating biological contactors and submerged biofilters (either upflow or downflow). Suspended particle systems include fluidized-bed reactors or airlift reactors; both based on a large biologically-active surface area wherein the particulate substrate is suspended either by the wastewater stream or by air which stimulates the necessary removal of senescent biofilms without eroding the living microbial community.

The non-intensive treatment of wastewater in many rural areas, or small neighborhoods that are not linked to major municipal wastewater treatment plants, is by means of wastewater treatment ponds. The ponds are generally artificial depressions where wastewater is stored or accumulated while natural microbial decomposition processes purify the water. Aerobic ponds are very shallow (<0.5m) and enable algae and heterotrophic bacteria to develop on the nutrient rich wastewater and remove up to 95% of the BOD. Facultative ponds are slightly deeper and are stratified: the upper layer consists of algae and is aerobic, while the bottom is generally anaerobic. The combination of aerobic and anaerobic processes allows for more complete decomposition of the organic matter and nutrient stripping. Very deep ponds enable formation of anaerobic conditions which gradually (after they become covered by a surface scum which prevents light penetration and algal growth) extend throughout the water column. These enable decomposition of some of the more refractory organics during lengthy wastewater treatment durations. In order to overcome some of the problems associated with facultative and anaerobic ponds, and to reduce the area of the treatment ponds, it is possible to aerate the wastewater, thereby stimulating aerobic processes.

In addition to the aerobic decomposition of organic matter, it is also possible to digest OM in wastewater by anaerobic pathways. Although the OM is not completely mineralized to water and carbon dioxide, this process may generate such endproducts as methane (biogas) which has economic value and can be used as a source of energy (Pfeffer 1979). When not designed for biogas production, anaerobic digestors may be used to stabilize sewage sludge, i.e. help decompose the refractory compounds not generally targeted by aerobic microbes. Most anaerobic digestors do not apply to treatment of wastewater but rather to sewage sludge which is a by-product of the wastewater treatment process and the anaerobic sludge treatment process is generally much slower than aerobic wastewater treatment.

## 2.2. Wetlands

One of the largest examples of biofilters, both natural and artificial, are Wetlands. *Natural wetlands* are very difficult to define accurately because there is a wide variety in such systems in terms of scale, location, composition, etc. Nevertheless, an acceptable general definition is:

“wetlands are lands transitional between terrestrial and aquatic systems where the water table is usually at or near the surface or the land is covered by shallow water... Wetlands have one or more of the following three attributes: (1) at least periodically, the land supports predominantly hydrophytes; (2) the substrate is predominantly undrained hydric soil; and (3) the substrate is nonsoil and is saturated with water or covered by shallow water at some time during the growing season of each year.” (Cowardin and Golet 1995). Natural wetlands include freshwater and salt marshes, sloughs, swamps, bogs and fens. It is accepted that wetlands provide unique habitats for wildlife and reduce erosion, but perhaps their most important function is in improving water quality.

In addition to natural wetlands, there are also *treatment wetlands* which have been used and developed primarily to improve water quality. Because wetlands are natural sinks for chemicals, they have been used in many applications where wastewater requiring treatment could be introduced and the clean water flowing out of the treatment wetlands could safely return to the environment (Mitsch and Gosselink 2000). In such examples, natural wetlands are purposely used for water treatment. However, in many cases it is not possible to use natural wetlands as water purification systems and the alternative is to create *constructed wetlands* (CW) that are operated as either *surface-flow* or *sub-surface-flow constructed wetlands*.

Surface flow CW are similar to natural wetlands in that they have standing water throughout most of the year and provide a good habitat for many wetland species. Subsurface flow CW consist of a porous medium, such as sand, that allows water to seep underground so that there is no standing water, and these wetlands generally support only a narrow range of wetland plant species. These systems are specifically designed for treatment below the surface to avoid the development of odors and other nuisance problems. Both types of treatment systems are usually constructed in channels with a natural or constructed subsurface barrier to limit seepage.

Some of these systems have been designed with the sole purpose of treating wastewater, while others have been planned with additional objectives in mind, such as using treated wastewater effluent as a water source for the restoration of wetland habitat for wildlife use and environmental enhancement (US-EPA 1993). Constructed wetlands treatment systems utilize the natural processes involving wetland vegetation, soils, and the associated microbial assemblages in treating wastewater.

Biological decomposition of particulate, colloidal and dissolved organic matter in wastewater is carried out by bacteria, fungi, and actinomycetes. These microbes occur on the surfaces of aquatic plants and soils and the decomposition produces effluents with a characteristic low dissolved oxygen level, low pH and low BOD. Aquatic plants play a complex and diverse role in the removal of nutrients and organic matter. There are wetland plants that inject oxygen into submerged stems, roots, and tubers, thereby oxygenating the hypoxic microenvironment and influencing the composition and physiological activity of the aquatic microbial community. Wetlands plants may also actively incorporate nitrogen, phosphorus, and other nutrients from the wastewater and may release nutrients when decaying plant material is shed.

Wetland design is determined primarily by the location and the objectives in mind and one of the most important variables that needs to be considered in effective design is the hydrology of the wetland. Both biotic and abiotic processes are influenced by the period of time that the water remains within the wetland basin and this “retention time” is determined by the hydrology of the system. There are numerous factors that affect the hydrology of wetlands, including water depth, hydroperiod (temporal pattern of water depth), seasonal pulses, hydraulic loading rates (flux of water through the wetland) and retention times (primarily affected by the characteristics of the wetland substrate).

In addition to their function as water purification systems, constructed wetlands may also provide an area for wildlife refuges or parks, for public education and recreation in the form of birding, hiking, camping, hunting, etc. An analogy to this, in the marine environment, is the use of artificial reefs or benthic biofilters around fish farms for nutrient uptake and mineralization, for coral-reef conservation, underwater eco-tourism, etc.

### 2.3. Recirculating Aquaculture Systems

Recirculation aquaculture systems (RAS) is a very broad term, yet it is generally used to specify intensive aquaculture in virtual “greenhouses” that can be operated practically anywhere, regardless of the local climate or season, since the rearing is done indoors, within well-controlled, closed systems (Losordo et al. 2001). The systems are closed, or practically-closed, since they include various filtration steps that clean the water for recycling back through the central culture tanks. New water is added to the tanks only to compensate for evaporation and for the small volume of water used to flush out waste compounds. The size range of RAS varies from small family-size systems (<25 tons/year) to large-scale production systems (>500 tons/year). RAS are relatively expensive systems to construct and maintain as constant supervision and skilled technical support are required to operate the circulation, aeration, and biofilter systems, and to conduct water quality analysis.

The functional components of a RAS include: a tank for rearing of the desired species, a sedimentation tank for removal of particulate matter, a biofilter, oxygen injection system and water circulation pump(s). Depending on the water temperature and fish species selected, a water heating/cooling system may be necessary. Ozone and ultraviolet sterilization are also used to reduce organic and bacteria loads in the system. It is also possible to reduce the loads of crude and fine particulate matter by mechanical filters, foam fractionators or protein skimmers.

A good supply of high quality water is essential to a successful fish farming enterprise. However, because the quality of the recirculated water changes with time, RAS are more suitable for warmwater fish such as channel catfish, hybrid striped bass, and tilapia that can tolerate lower water quality conditions and higher temperatures than trout. As a general rule, 8-40 liters of water are needed for every kilogram of fish reared.

Fish can be grown in tanks of nearly every shape and size. Circular tanks with central drains are somewhat easier to clean and circulate water through than rectangular ones. Tanks can be constructed of any material that will hold water, but will not injure the fish. The choice of tank size depends on: stocking rates, species selected, water supply, water quality and economic considerations. The rearing tank volume must correspond to the volume of the other components of the system; in particular - the size of the biofilter and the sedimentation unit (or the particulate matter removal step) so that all parts of the system are synchronized.

The biological filter (biofilter) is the heart of the RAS and is essentially a living filter composed of solid substrate (e.g. plastic sheets, beads or sand grains) upon which a film of bacteria grows. The biofilter bacteria provide the waste treatment by removing pollutants from the water. The two primary pollutants that need to be removed from the system are: dissolved fish wastes and uneaten fish feed pellets.

Among the dissolved fish wastes the potentially toxic compounds are ammonia and nitrite. The toxic form of ammonia is free (unionized) ammonia ( $\text{NH}_3$ ) and it may cause fish kills at 0.05

mg/l. Nitrite at levels above 0.5 mg/l may cause brown blood disease (methemoglobinemia) and this may be lethal. It is clear, therefore, that these two forms of nitrogen must be eliminated in fish culture systems. Elimination of ammonia may be performed by *air-stripping*, but this is a complicated process that involves two drastic pH adjustments. Another possibility is *ion exchange*, but this is expensive and requires frequent stripping of the ammonia from the ion-exchange resin to maintain efficient ammonia removal rates from the recirculated water. The method that is most commonly used to remove ammonia and nitrite from recirculating systems is *biological filtration*. Ammonia is oxidized by ammonia-oxidizing bacteria to nitrite and the nitrite is converted to nitrate by nitrite-oxidizing bacteria. This two-stage process of ammonia oxidation to nitrate is collectively known as *nitrification*.

Nitrification is an aerobic process and approximately 5 mg of oxygen are required to convert 5 mg ammonia to nitrate. Moreover, nitrifying bacteria remove large amounts of carbon dioxide from the water and as a result, the pH of the water drops. However, if pH decreases below 6.5, nitrification is inhibited. Therefore, the biofilters in recirculating systems require careful regulation of the pH, carbon dioxide and dissolved oxygen levels.

A biofilter is basically a tank or a container that is filled with media that provides a large surface area on which nitrifying bacteria can grow. The biofilter container can be constructed of any nontoxic substance. The size of the biofilter directly determines the carrying capacity of fish in the system. Larger biofilters have a great ammonia assimilation capacity and can support greater fish production. It is necessary for the water flowing through the biofilter to come into direct contact with the bacterial biofilm in order to allow the bacteria to oxidize  $\text{NH}_3$  and  $\text{NO}_2$  to  $\text{NO}_3$ . There are various ways in which biofilters may be inoculated by nitrifying bacteria so that they fulfill their role. Nitrifiers are present in all aquatic systems and even if the biofilters in recirculating aquaculture systems are not purposely inoculated with them, they will appear after several months, provided the prevailing conditions in the aquaculture systems are suitable. The conditions preferred by aquatic nitrifying bacteria include high aeration, large surface area, low-light levels, and fairly high ammonia and  $\text{CO}_2$  levels. Alternatively, it is possible to inoculate biofilters by adding commercial cocktails of nitrifiers and other “good” bacteria, specifically prepared for this purpose.

Bacterial biofilters are either submerged (i.e. constantly under-water) or emerged (i.e. in contact with a thin layer of water or periodically submerged). Fluidized bed biofilters are among the more common forms of submerged filters and these consist of a substrate with generally large surface area (sand, beads or other particles that allow nitrifying bacteria to attach) that is constantly suspended by a stream of water and air. Emerged biofilters are either trickling filters, wherein the water trickles down over a thin biofilm of nitrifiers (attached to the non-moving filter medium) in a highly aerobic environment, or rotating biological contactors (RBC) where the biofilter with attached microflora is slowly rotated (like a paddle-wheel) in the nutrient-rich water.

#### **2.4. Integrated Land-Based Mariculture Systems**

One of the main problems of land-based aquaculture systems is maintaining good water quality for the cultivated species. When there is an abundant supply of high quality freshwater, this appears to be less of a problem for the cultivated animals, as the production units may be flushed clean at high frequency. However the constant release of wastes into the receiving waters will eventually lead to environmental problems that may also backfire by reducing the quality of the water supply to the aquaculture production facility. One of the simple solutions to this is to couple the aquaculture system to a reservoir or a treatment pond. The prerequisite for the

treatment unit is that it must be capable of metabolizing the particulate, organic and nutrient loads such that the quality of the water returning to the aquaculture unit remains high. There are examples of such systems that have operated with varying degrees of success (Liao and Chen 1983, Mires et al. 1990, Chin et al. 1993).

The only-partial success of such coupled systems is related to stability of the water quality. The water quality was generally unpredictable because it relies heavily on the microalgal community that generates oxygen (photosynthesis) and removes nutrients. When the algal community was stable, water quality was high. However, fluctuations in abundances and species composition of the phytoplankton may have rapid and dire effects on water quality (oxygen supersaturation, hypoxia, high ammonia levels, etc.) and on the cultured species (gas bubble disease, general stress and susceptibility to disease, etc.) (Krom and van Rijn 1989, Neori et al. 1996, van Rijn 1996). One of the modern alternatives to ensure high water quality in intensive aquaculture is to employ mechanical and biological filters in sophisticated recirculating aquaculture systems (see review of RAS). In such systems, there is only one crop and all waste products are discarded. Whereas this is relatively simple from an engineering point of view, it is not the most efficient use of the protein-rich feed that is under-utilized by the cultivated species. One approach that emphasizes a more efficient use of the aquaculture inputs is that of integrated aquaculture systems.

There are several motivations to carrying out aquaculture in integrated systems that involve the production of more than a single commercial crop. These include such rationales as a need (or requirement/legislation) to capture and remove some of the nutrient-rich effluents produced by fish or shellfish in order to prevent pollution or enrichment of the receiving water body, and a desire (from an economic standpoint) to make more efficient use of the costly, protein-rich feed offered to fish by producing a second (or more) crop which can utilize the effluents (many fish release >70% of the ingested protein nitrogen) released by the fish. There are numerous examples of such integrated freshwater or brackish water systems (Naegel 1977, Zweig 1986, Ng et al. 1992, Porath and Pollock 1992, etc.). In comparison, there is very little literature on either recirculating or integrated marine aquaculture systems.

The development of integrated mariculture systems is a relatively new field since land-based mariculture (cultivation of marine animals and plants in ponds or tanks) was only initiated, mostly in research systems and in small-scale production facilities, during the past 2 decades. In the 1970's Ryther et al. (1972, 1975) and Goldman (1974) examined the cultivation of bivalves and algae on sewage water as a means to both purify this water and make a profit. Although the concept was successful, the product was not due to the problems associated with the use of sewage water for human food. Not long thereafter, integrated mariculture was proposed for the treatment of fish pond effluents (Gordin et al. 1981, Gordin 1982) and in the early 1990's several groups demonstrated the potential for its success (Vandermulen and Gordin 1990, Wang et al. 1990, Cohen and Neori 1991, De-Pauw and Salomoni 1991, Rosenthal 1991, Gordin et al. 1990, Shpigel et al. 1993, Neori and Shpigel 1999, Evans and Langdon 2000).

The system proposed by Shpigel et al. (1993) consisted of trapping large organic particles from the fishpond effluent in a sedimentation pond which would also enable the buildup of microalgal populations that would then feed suspension-feeding bivalves (clams or oysters) situated either in the pond sediment or in a separate particle filtration unit thereafter (Shpigel and Friedman 1991). The bivalve effluent would then be polished by a macroalgal biofilter (Neori et al. 1996) before being returned (recycled) to the fishponds. A large-scale integrated system was tested in 1993 for two years to examine the concept, though it was only operated in an open or semi-closed configuration (i.e. mainly operated using fresh seawater) because it was not sufficiently stable and reliable to allow complete seawater recirculation (Mozes and Gordin 1996). In addition to



studying the operational aspects of the integrated system, the economic feasibility was also examined and an economic assessment of each of the components was carried out. This assessment indicated that although the concept had great potential, it was not operational from either an environmental or an economic perspective.

The fish-alga integrated systems rely on the high affinity of the macroalgae for the dissolved inorganic nutrients (mainly N, P) released in the finfish effluent and solar irradiance to energize the nutrient uptake. These systems require pretreatment of the effluents to eliminate dissolved organics which can lead to biofouling and failure of the macroalgal biofilters. The macroalgae must be grown in shallow tanks or ponds to maximize exposure of their thalli to solar irradiance and they must be continuously resuspended and aerated to avoid sinking to the bottom, where suboptimal conditions may cause disease and death of the algae. Care must also be taken to continuously clean all macroalgal tank or pond surfaces since these will otherwise be colonized by nitrifying bacteria that will compete with the macroalgae over the ammonia and will lead to accumulation of nitrite and nitrate in the recirculating systems, which may affect finfish health. These and other problems that require attention and solutions mean that the integration of macroalgae and finfish cultivation can be as intensive an undertaking as the RAS. One of the more recent developments and sophistications of these integrated systems is the addition of abalone; a profitable macroalgal consumer that can profit from the abundant production of macroalgae and provide the mariculturist with a slow-growing, but economically-lucrative supplementary crop (Neori and Shpigel 1999).

The other alternative to produce marine fish in recirculating seawater systems is to employ the RAS technology in tanks or ponds and to focus on hyperintensification in order to enhance profitability. This has been a focus of intensive research at the National Center for Mariculture Research, IOLR in Eilat, Israel during the past decade, and especially in the past few years (Mozes et al. 1998, 2000). Such systems are heterotrophic by nature and do not rely on micro or macroalgae to remove inorganic nutrients. These systems provide high quality seawater to very high stocking densities (up to 100 kg/m<sup>3</sup>) of marine fish by employing a combination of: mechanical particle-removing filters, nitrifying biofilters, protein skimmers, and liquid oxygen (use of UV oxidation and ozone are still in the experimental phase). There are currently no large-scale commercial fish farms that employ this technology, however it is expected that such technology will be available during the next few years, as the final technical obstacles are solved and mastered.

## **2.5. Integrated Finfish Aquaculture Systems At Sea**

At the present time, marine finfish aquaculture takes place, almost exclusively, in net pens at sea. Whereas net-pen production is the most cost-effective practice that also ensures high quality water and good growth conditions for the fish, it has a non-negligible impact on the surrounding waters and seafloor. Although there are physical and chemical means by which some of the farm effluents might be captured, these are generally technically impractical, environmentally unsound and/or extremely costly. On the other hand, various biological solutions have been suggested for trapping particulate and dissolved effluents released by the fish farms. These solutions have generally been derived from integrated, land-based aquaculture systems (see review of this topic). Suspension-feeding bivalves can efficiently remove particles from fish tank or pond effluents and provide a second aquaculture crop (e.g. Shpigel and Friedman 1990, Wang et al. 1990, Shpigel and Blaylock 1991, Couteau and Sorgeloos 1993, Kwei Lin et al. 1993, etc.). If planned properly, dissolved inorganic nutrients may be taken up by macroalgae, as shown by Goldman et al. (1974), Lignell et al. (1987), Vandermulen and Gordon (1990), Cohen and Neori (1991), Indergaarden

and Jensen (1991), Haglund and Pedersen 1993, Buschmann et al. (1994), 1996, Jimenez del Rio et al. (1994), etc. and might serve as a profitable supplementary biomass.

Although technically challenging, the potential use of macroalgae, bivalves and other macroinvertebrates to manage the wastes derived from open-water, net-pen aquaculture has been considered by various researchers in the endeavor to develop both sustainable fish farms and viable polyculture.

Folke and Kautsky (1989) compared between salmonid and mussel production in Scandinavia and concluded that salmon farming was not a sustainable activity. They suggested that production of mussels on long-lines situated around the salmon farms was the first step toward sustainability, and that incorporation of the mussels in the salmon feed would greatly reduce the global impacts of salmon farms on the marine environment.

In another study, Bodvin (1992; cited in Bodvin et al. (1996)) concluded that the only real way to economically and efficiently control water quality in salmon farms was by constructing enclosed floating production units that include two types of treatment units (bivalves and macroalgae), in addition to the finfish-production units. Bodvin et al. (1996) provided a numerical model to demonstrate the potential of this concept, based on data gathered during 4 years from a full-scale enclosed salmon production facility in Norway. In this model, a farm producing 300 metric tons of salmon in twelve 500m<sup>3</sup> units requires a standing stock of 112.5 metric tons of mussels (situated in another twelve 500m<sup>3</sup> units) to capture all of the particles that do not fall into a particle trap. The dissolved nutrients (mostly N and P) released by the salmon and the mussels will be captured by a standing stock of 45 metric tons of seaweeds distributed in twelve 1000m<sup>3</sup> units. One of the shortcomings of this model is that the values for mussel biofiltration are based on data taken from other authors and it is not clear how the mussels will perform in capturing salmon farm effluent particles. Moreover, it is not clear what sort of water quality conditions (dissolved oxygen, ammonia, etc.) the mussels will experience if they are grown in salmon effluents. Another “unknown” is how the macroalgae will perform as nutrient biofilters when these are grown in large, deep enclosures. The values for macrophyte biofiltration and production in this model were adopted from shallow tanks on land that provided sufficient light energy and large contact with fish pond effluents (nutrients) for rapid uptake and growth (Shpigel et al. 1993, Buschmann et al. 1994). Commercial polyculture along the lines of this theoretical model will only be realistic after the problems outlined above, and others, are carefully considered and solved.

#### *Finfish - bivalve polyculture*

Jones and Iwama (1991) found that the oyster *Crassostrea gigas* grew up to three times faster and had greater condition factors when grown near salmon cages as compared to nearby control sites. In another study, Taylor *et al.* (1992) compared between mussels (*Mytilus edulis*) grown near fish cages and at a control site and they found no significant site-related differences between the growth rates or condition factors of the mussels.

Stirling and Okumus (1995) measured growth and production rates of mussels growing below salmon net pens, below mussel rafts and on long lines on the west coast of Scotland. Particulate organic matter and chlorophyll-a levels were higher at salmon farms than at adjacent mussel farms. Overall, there were no major differences between mussel growth and production at the 3 study sites, however it appeared that mussels at salmon farms did not deplete their reserves during the winter as much as those at mussel farms. The differences in mussel performance between salmon and shellfish farms probably resulted from the utilization of higher organic matter concentrations at salmon farms.

Buschmann et al. (1996) reviewed the general environmental impacts and concerns related to salmon, mollusc and macroalgal aquaculture. They concluded that mollusc farming causes biodeposition, faunal changes and potential problems related to introduction of new species, pathogens and other unforeseen species and, owing to these risks, this group of researchers would recommend that policy makers in Chile not promote integrated aquaculture to reduce salmon farm impacts.

Troell and Norberg (1998) modelled the output of particulate salmon farm wastes and the capture of particles by mussels cultivated near the farm in order to evaluate efficacy and practicality of the integrated farming approach. They concluded that: (1) current speeds are critical to the success of this concept since rapid water flow will dilute the particle load that reaches the bivalves and affect their filtration efficiency and growth rates. (2) fish farm wastes are released in pulses, yet the feeding of mussels is continuous; thus the “long-term” seston concentration (suspended living and nonliving particulate matter) will be the main determinant of mussel growth/production. In other words, mussel biofilters may serve as an efficient means to capture particulate fish farm effluents, but only at certain sites and in given hydrographic conditions.

Soto and Mena (1999) examined the use of the freshwater mussel, *Diplodon chilensis* (Hyriidae), which is naturally abundant in many of the southern Chilean lakes where salmon are raised, to mitigate some of the impacts of salmon farming. Despite the hesitation of Buschmann et al. (1996) regarding polyculture, co-cultivation experiments with salmon and mussels indicated that the mussels could rapidly and efficiently reduce chlorophyll a, ammonia and phosphate levels in the tanks. Considering their high clearance rates and large abundances in the lakes, these mussels could be employed to reduce both particulate and dissolved nutrient loads around fish farms.

Lefebvre et al. (2000) pointed out that we do not know enough about the relative importance of living microalgae vs detrital matter (fish-faeces and uneaten feed) in the diet of bivalves grown around fish cages. This study compared the feeding responses of the Pacific oyster (*Crassostrea gigas*) to a fish-farm effluent (mainly *Dicentrarchus labrax* feces) vs those obtained with a cultured diatom (*Skeletonema costatum*) and showed that food quality (nature of particulate organic matter, organic content, etc.) had no effect on clearance rates but that the most important variable was the life-stage of the oysters.

In a more recent study, Mazolla and Sara (2001) addressed a similar question regarding the utilization of organic matter by the clams and bivalves situated around fish farms in Italy. They divided the particulate and suspended material to “organic waste” (uneaten food and feces) and living organic material (phytoplankton) and by using stable isotope techniques, they found that organic waste appears to be the dominant food in the clam (benthic) diet, whereas mussels (suspended) prefer phytoplankton. By consuming “organic wastes” the clams take up detritus not only from the cultivated fish, but also from the cultivated mussels (feces and pseudofeces). They conclude by saying that bivalve cultivation around fish farms may reduce environmental impacts caused by organic waste and increase the profitability of the fish farm.

#### *Finfish-macroalgae polyculture*

Fish farms release large quantities of dissolved nutrients and it has been estimated that as much as 80% of the nutrients are readily available to plants (Hakanson et al. 1988, Persson 1991). Indeed, there have been many anecdotal observations (e.g. Angel et al. 1998) as well as a few studies that have shown enhanced growth of macroalgae around fish farms (Ruokolahti 1988, Ronnberg et al. 1992). Although there has been a recent surge in studies examining the use of macroalgae to strip nutrients (biofilters) from fish pond effluent in land-based mariculture (see review of this topic),



this has not been the case in net pen mariculture. In open culture systems the continuous movement of water makes the capture of nutrients more complicated (Troell et al. 1997) and only a few studies have examined the production of seaweeds around fish farms (Hirata and Kohirata 1993, Hirata et al. 1994, Petrell et al. 1993, Troell et al. 1997). During a 2-month trial, Troell et al. (1997) followed the growth of *Gracilaria chilensis* on ropes suspended near a salmon farm at different depths and distances from the farm. They found 20-40% higher algal growth rates next to the farm and best growth at the shallow depths; as anticipated, algae exposed to high fluxes of nutrients and light will grow fastest. The algae that grew adjacent to the fish farm had higher tissue nitrogen and lower agar content than the algae at the control stations. Troell et al. (1997) did not measure the reduction in nutrients as a function of the macroalgal growth adjacent to the salmon cages, however they extrapolated from the rates recorded in tank cultivation of *G. chilensis* and estimated that a harvest of 34 metric tons (dry weight) of the macroalga would essentially remove 6.5% and 27% of the dissolved N and P, respectively released in the fish farm effluents. Some of the biggest practical problems associated with seaweed cultivation “in the open”, namely epiphytes and grazers, were apparently not a great problem in these Chilean waters.

Ahn et al. (1998) examined the ammonia and nitrate uptake rates of 2 local seaweeds (*Laminaria saccharina* and *Nereocystis luetkeana*) that were incubated in British Columbian salmon farm effluents. Both macroalgae were able to absorb both forms of dissolved nitrogen and are considered good candidates as biofilters for salmon farm effluents.

Chopin et al. (1999) examined the potential for cultivation of the endemic red alga *Porphyra* (seven native north-west Atlantic *Porphyra* species were under consideration) at sea, adjacent to salmon net pens off the coast of Maine, USA. They pointed out that this alga has commercial value and requires high levels of nutrients for rapid growth and pigmentation, especially during summer, when the waters in this region become nutrient-poor. They indicated the economical and environmental benefits of the proposed co-cultivation.

#### *Polyculture using echinoderms and holothurians*

In a study designed to examine the possibility of co-cultivating the red sea cucumber, *Parastichopus californicus* inside salmon net pens in Alaska, Ahlgren (1998) found that the holothurians consumed fouling debris and cleared a significant amount of surface area on the nets. Moreover *P. californicus* assimilated amino acids and other organic matter from the net pens much more efficiently than from unenriched sediments and showed enhanced muscle development as compared to the control sites. This work indicates that polyculture of the red sea cucumber with salmon is promising in both environmental and economic aspects.

Although their studies were not oriented toward polyculture, Cook et al. (2000) found that the sea urchin *Psammechinus miliaris* grown under salmon net pens, and in aquaria (fed commercial salmon-food pellets), had significantly higher docosahexaenoic acid (DHA; fatty acid) levels, yet substantially lower stearidonic and arachidonic acid levels, than a comparable group of sea urchins collected from intertidal sea loch sites and fed macroalgal diets (*Ulva lactuca* and *Laminaria saccharina*) in aquaria. Cook et al. (1998) also showed that *P. miliaris* had higher growth rates and gonadal indices when reared on salmon food as compared to the macroalgal diets. Similar observations and measurements were also made by Angel et al. (unpublished) with regard to growth rates and gonadal indices of the sea urchin *Tripneustes gracilla* on hard substrates below a commercial fish farm in the Gulf of Aqaba, Red Sea, as compared to control sites. These data and observations suggest that there is indeed potential for the polyculture of commercially-valuable sea urchins and marine finfish at sea.

*Deploying artificial substrates to promote “natural” biofiltration of FF effluents*

Although organic matter (OM) does not accumulate under all fish farms, it will do so when the rate at which it descends to the seafloor exceeds the rate of its decomposition (Hall et al., 1990). Accumulation of OM on the seafloor will eventually lead to anoxia, buildup of hydrogen sulfide in the sediments and ultimately substantial alteration in the composition of the benthic and epibenthic biota below the fish farms (Gowen and Bradbury 1987, Weston 1990). Various solutions have been proposed to reduce organic enrichment of the sediments below the net cages, e.g. collection of the particles falling from the cages, collection of detritus from the seafloor using submersible pumps, harrowing the sediments, etc. (reviewed in Beveridge, 1996), however, most of these are not practical. An alternative option is to construct biofilters or artificial reefs below fish farms in order to absorb and mineralize some of the organic and inorganic matter released from the cages and thereby reduce environmental enrichment. Laihonon et al. (1996) described the use of various types of artificial reefs as a possible means of nutrient removal in the Baltic Sea.

By providing a large surface area for microbial colonization and activity in the oxygenated water above the seafloor, the artificial reef structures could facilitate aerobic microbial breakdown of the OM released from the farm. OM decomposition is mostly a function of microbial processes and it appears that aerobic microorganisms are more efficient at OM decomposition than anaerobes (Cowie and Hedges, 1992). Thus a substantial part of the particulate and dissolved OM absorbed by the reef organisms will probably be metabolized (respired) to CO<sub>2</sub> and H<sub>2</sub>O and thereby naturally removed from the system. Moreover, by reducing the flux of organic matter from the fish cages to the benthos, the artificial reef should enable macrofauna to recolonize the surrounding sediments, and eventually enable demersal fish and other invertebrates to return to the region as well. This sort of recovery has been observed at this site in the past (see Porter et al., 1996 and Angel et al., 1998).

Two pyramid-shaped artificial reefs (reef volume 8.2m<sup>3</sup>) constructed from porous durable polyethylene were deployed at 20m; one below a commercial fish farm and the other 500m west of this farm in order to monitor the colonization of these reefs by the local fauna and to determine whether the reef community can remove fish farm effluents from the water. Artificial reefs with a crosshatch design were chosen in order to provide both large surface area for settlement of sessile organisms and ample flow of oxygenated water through the holes and openings in the structure. Both reefs became rapidly colonized by a wide variety of organisms with potential for the removal of compounds released from the farms. Fish abundances and the number of species reached 518 - 1185 individuals per reef and 25 - 42 species per reef. Moreover, numerous benthic algae; small sessile invertebrates (bryozoa, tunicates, bivalves, polychaetes, sponges, anemones) and large motile macrofauna (crustaceans, sea urchins, gastropods) settled on the reef surfaces. Depletion of chlorophyll *a* (chl *a*) was measured in the water traversing the artificial reefs in order to assess the biofiltration capacity of the associated fauna. Chlorophyll *a* was significantly reduced to a level 15 – 35% lower than ambient chl *a* concentrations. This reduction was greatest at intermediate current speeds (3 - 10cm s<sup>-1</sup>), but was not influenced by current direction. The reef structures served as a successful base for colonization by natural fauna and flora, thereby boosting the local benthic biodiversity, and also served as effective biofilters of phytoplankton.

*Use of grey mullets to ameliorate organically-enriched sediments below a commercial fish farm*

A field study was carried out to assess the use of the bottom-feeding grey mullet (*Mugil cephalus*) within benthic enclosures as a means to reduce the benthic impacts of fish farms (Katz et al. in press). The enclosures had no bottom so that mullets could feed from and bioturbate the sediment. Seventy days after the beginning of the field trial, a comparison between sediments inside the mullet enclosures vs those in bare and enclosed control sites indicated that those had only 14%

and 19% of the TDS and 69% and 44% of the sediment oxygen demand, respectively. These changes in the sediment geochemistry were accompanied by a steep increase in abundance of opportunistic mud snails (*Nassarius sinusigerus*) in the mullet enclosures. Essentially no snails or other macrofauna were found in the other treatments. One of the most dramatic changes observed in the mullet enclosures, as compared with the bare and enclosed controls, was the reduction in thickness of the organically enriched sediment layer by 5cm. The “missing” sediment was equivalent to 2.6 kg organic carbon, and corresponded to a mean carbon removal rate of 20.6g m<sup>-2</sup> day<sup>-1</sup>. While foraging for food and swimming near the sediment surface, mullets within the benthic enclosures resuspended detritus, increased the oxygen supply to the benthos and oxygenated buried organic matter, thereby dramatically improving the status of organically-enriched, reduced sediments within a relatively short period of time. Therefore, deployment of detritivores in enclosures under active net cage fish farms may be a viable means to alleviate some of the environmental impacts of intensive mariculture.

*Use of capitellid polychaetes to decompose organic matter in enriched sediments below fish farms*

Tsutsumi et al (1993) and Chareonpanich et al. (1993, 1994) examined the possibility of employing the deposit-feeding capitellid polychaete, *Capitella* sp. I to stimulate decomposition of the organic matter on the seafloor below fish farms. Their study involved a laboratory simulation of the field situation wherein natural marine sediments were organically-enriched by mixing these with fish-feed pellets and comparing the sediment geochemistry in treatments with and without *Capitella*. They found that there was a substantial increase in abundance of *Capitella* in the organically-enriched sediments and the polychaete activities (e.g. feeding, sediment mixing, etc.) decomposed the added organic matter and prevented development of reduced conditions in the sediment. The authors concluded that it might be possible to inoculate the sediment below fish culture sites with dense cultures of *Capitella* sp. I during the fallow season (autumn/winter in Japan), thereby enabling rapid breakdown of the buried organic matter and improvement of sediment quality.

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## Chapter 3

### A review of biological filtration by marine invertebrates

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#### 3.1. General Introduction

##### *3.1.1 Purpose and structure of chapter*

The BIOFAQS project seeks to investigate and test the feasibility of biofiltration as a means of mitigating the effects of organic discharges from mariculture sites. The chapter does not seek to present a comprehensive review of filtration by marine organisms, but instead concentrates on those aspects of the phenomenon that are directly relevant to the needs and objectives of BIOFAQS. In broad terms, the scope of the chapter is to summarize:

- Filtration rates of known biofilters (ie. quantification of active pumping/passive filtration rates).
- Estimation of biofiltration potential per unit area based on information on known biofouling communities and published filtration rates.

The detailed structure of the chapter is as follows:

1. A brief general summary of the suspension-feeding process and an explanation of the terminology used in the published literature and in this chapter.
2. For the major groups of marine suspension-feeding organisms in turn, the chapter will briefly summarize (with guidance to sources of more detailed information):
  - The mechanism of particle filtration.
  - The nature of the predominant food source, and the size range of particles retained and rejected.
  - Individual-level filtration rates, either in laboratory or field, with information on variability in relation to major environmental parameters where such data exist.
  - Population-level filtration rates, either in laboratory or field, ie. examples where the collective filtration capacity of monospecific aggregations of marine suspension-feeders has been measured.
3. Summary of studies in which the filtration capacity of mixed populations of marine suspension-feeders has been measured in the field.

4. A summary of the relative usefulness of different suspension-feeding taxa (with respect to the objectives of BIOFAQS) as indicated by the published literature.

### *3.1.2 Aspects not covered in this chapter*

This chapter focuses on particulate filtration by the major groups of marine organisms which constitute typical 'biofouling' communities on hard substrata in European seas, since these are likely to include the taxa most relevant to BIOFAQS. The following aspects of biofiltration are not discussed here:

- Suspension-feeding by pelagic organisms, either adult or larval (eg. copepods, larvaceans, salps, fish).
- Suspension-feeding by taxa living mainly or exclusively as infauna in soft substrata (eg. upogebiid mud-shrimps, some polychaetes and bivalves).
- Sessile, epifaunal suspension-feeders belonging to groups which form a very minor component of most marine hard-substratum communities (eg. brachiopods, phoronids, pterobranchs).
- Uptake of dissolved organic matter by marine invertebrates or plants.

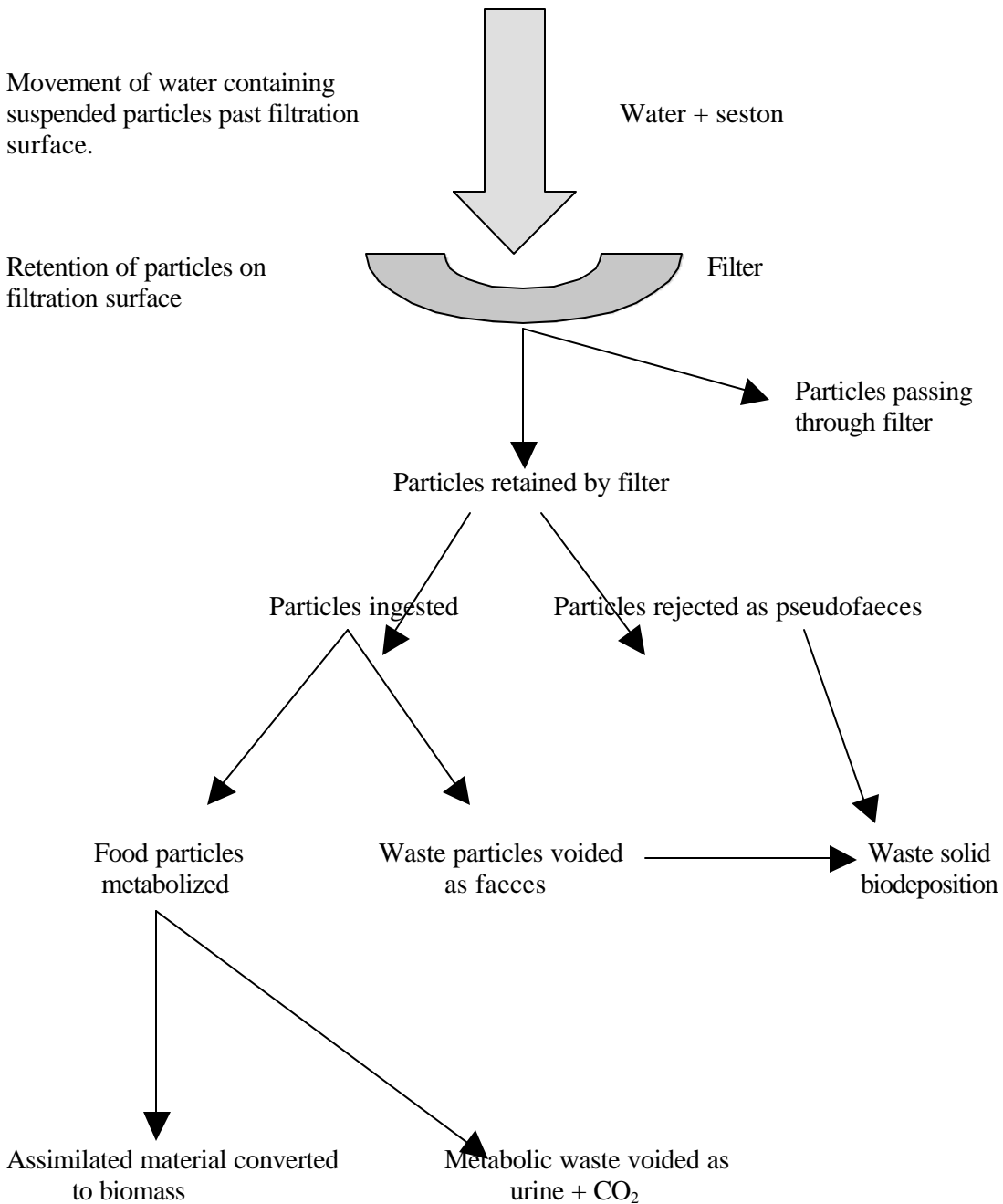
## **3.2. Introduction To Suspension-Feeding**

### *3.2.1. Definitions and terminology*

Suspension-feeding is a trophic mode independently evolved by a wide variety of marine and freshwater animal groups, in which nutrition is obtained by removing suspended food particles from the water column. By implication, suspension-feeders are microphagous, ie. the food particles are very small relative to the body size of the organism ingesting them. The suspended matter may be either living (eg. bacteria, phyto- or zooplankton) or non-living (eg. particulate organic detritus), both components being covered by the term seston. Suspension-feeding is often used interchangeably with filter-feeding, but some authors restrict the use of the latter term to describe a process in which water is passed through an array of structures that retain particles according to size and shape. By this definition, not all suspension-feeders are filter-feeders. To avoid confusion, only the term suspension-feeding/feeder will be used in this chapter. This allows consideration of the broadest possible range of organisms which remove seston from suspension (the process of interest to BIOFAQS), irrespective of the mechanism by which this is achieved.

The literature on suspension-feeding is replete with terms such as 'pumping rate', 'clearance rate', 'filtration rate' etc., which may be used in different ways by different authors, and may have subtly different meanings dependent on the experimental techniques used or the type of organism under consideration. It is therefore necessary to briefly summarize the successive steps involved in suspension-feeding, from the initial contact with suspended particles to the metabolic assimilation of a proportion of that material by the suspension-feeder, and to define the terms used to represent each step. This will facilitate comparison of process rates measured and published by different authors. A breakdown of suspension-feeding into successive steps may also help in the mathematical modelling of seston uptake rates which may be required under BIOFAQS.

The successive stages of the suspension-feeding process can be visualized as shown below:



Most process-rate orientated studies of suspension-feeding are concerned with the key elements of the particle retention process defined below. Terminology is based on that used by Wildish and Kristmanson (1997, pp. 47-48). At the individual level, these rates can be expressed per animal, or per unit body mass (fresh or dry).

The parameter likely to be of greatest importance to BIOFAQS is:

- Seston Uptake Rate (S): the mass of seston removed from the water column per unit time by an individual suspension-feeder (or unit body mass).

The Seston Uptake Rate (S) will be determined by the concentration of seston in the water column and rate at which water is cleared of particles by the animal, hence:

$$\text{Seston Uptake Rate} = (\text{Seston concentration}) \times (\text{Clearance Rate})$$

where:

- Clearance Rate (C): the volume of sea water filtered per unit time, assuming 100% capture of sestonic particles, by an individual suspension-feeder (or unit body mass).

Because the filtration surface of a suspension-feeder may not capture suspended particles with 100% efficiency, it is necessary to break down the Clearance Rate (C) into two further components:

$$\text{Clearance Rate (C)} = (\text{Pumping Rate}) \times (\text{Retention Efficiency})$$

where:

- Pumping Rate (P): the volume of sea water that passes across the filtration surface, or through the fluid transport system, per individual suspension-feeder (or per unit body mass) per unit time, irrespective of the efficiency with which particles are captured.
- Retention Efficiency (R): the proportion of seston particles captured by the filtration surface in relation to the total number which encounter it.

It therefore follows that the Clearance Rate is equal to the Pumping Rate only if Retention Efficiency is 100%, ie. if  $R = 1$ . It is also the case that Seston Uptake Rate does not necessarily equal the amount of seston ingested, since some suspension-feeding taxa (notably bivalves) may reject unwanted particles as pseudofaeces before ingestion. An additional parameter, Feeding Rate (F) can therefore also be defined:

- Feeding Rate (F): the mass of seston ingested per unit time by an individual suspension-feeder (or per unit body mass).

Use of a consistent terminology is essential if confusion is to be avoided when comparing the results of different studies in the literature. In this chapter, published data on rates of suspension-feeding by individual taxa will be discussed using the parameters defined above, even if different terms were used by the original authors.

### *3.2.2. Measurement of suspension-feeding rate by individuals and populations*

The techniques used to measure the various parameters defined above have an important bearing on the degree to which published rates can be taken as representative of the activity of suspension-feeders under field conditions. In the bivalve literature in particular, controversy still persists concerning the 'natural' rates of suspension-feeding to be expected in the field (Jørgensen,



1996; Bayne, 1998; Riisgård, 2001). This stems partly from differences of opinion concerning the reliability of various laboratory measurements of bivalve clearance rates.

Wildish and Kristmanson (1997, pp. 48-53) provide a summary of the methods used to measure rates of suspension-feeding processes. Historically, suspension-feeding rate has been most often measured in the laboratory using indirect methods, which involve placing one or more individual animals in a known volume of water containing suspended particles and allowing them to feed for a set period of time. The difference between the initial and final concentrations of seston in the ambient water is used to calculate Seston Uptake Rate (S) or Clearance Rate (C). The indirect method suffers from a number of drawbacks (Wildish and Kristmanson, 1997, p. 49) and this has led to the development of more sophisticated direct methods, in which particle concentrations in the inhalent and exhalent currents of the suspension-feeder are sampled using optical or microprobe techniques.

When considering the filtration capacity of natural populations of suspension-feeders (either monospecific or mixed), the important distinction to be drawn is that between studies in which clearance is estimated using data obtained from the laboratory, and those in which it is measured directly. In the former case, rates measured on individual animals in the laboratory are scaled-up using population density estimates from the site of interest. The accuracy of such extrapolations obviously depends on the extent to which laboratory measurements are representative of activity under natural conditions. In consequence, an increasing number of studies now involve direct measurement of changes in seston concentration over beds of suspension-feeders in the field or in aquarium flumes. In the following chapter sections dealing with individual suspension-feeding taxa, it will be made clear whether population-level Seston Uptake or Clearance Rate data were obtained by estimation or direct measurement.

### 3.2.3. *Functional classification of suspension-feeders*

Owing to the diverse phylogenetic origins of the invertebrate groups that have adopted a suspension-feeding lifestyle, there are wide differences in the physical structures used to capture suspended particles. However, in spite of this diversity, two major functional categories of benthic suspension-feeders can be defined by the extent to which the filtration process is dependent on external water flow (Wildish and Kristmanson, 1997).

1. Passive suspension-feeders are entirely dependent on external ambient flow to bring seston to the filtration surface. Major groups in this category are hydroids, suspension-feeding anthozoans (octocorals, sea pens, some anemones), crinoids (feather stars), and ophiuroids (brittlestars).
2. Active suspension-feeders expend energy to drive ciliary or muscular pumps which actively transport sea water and suspended seston across the filtration surface. Major examples include bivalve molluscs, bryozoans, ascidians and suspension-feeding polychaetes.

Three further categories can be defined:

3. Facultative active suspension-feeders are able to switch between passive and active filtering depending on the ambient flow conditions. These animals behave as passive suspension-feeders at high flow velocities but filter actively in still or slowly-moving water. Barnacles are the main examples in this category.

4. Combined passive-active suspension-feeders employ two parallel filtering modes, actively pumping water by ciliary means but also taking advantage of ambient water movement to create a feeding current through the body. Both active and passive processes occur simultaneously and there is no switching from one mode to another at critical flow velocities. Sponges are known to use this feeding strategy, and some brachiopods and ascidians may possibly also do so.
5. Deposit-suspension-feeders ingest already-deposited particles from the sediment surface at low flow velocities, but switch to suspension-feeding at higher speeds. The known examples, which include some spionid polychaetes and bivalves, are found among the benthic infauna of soft sediments and are therefore not considered further in this chapter.

#### 3.2.4. Sources of information

Suspension-feeding is one of the most intensively-researched trophic processes in the marine ecosystem. Several reviews published during the past few decades provide entry points to the huge primary literature on the subject. Jørgensen (1966) provides an overview of the biology of suspension-feeding and summarizes much of the older literature. The physical mechanisms of particle capture are discussed by Rubenstein and Koehl (1977), LaBarbera (1984) and Shimeta and Jumars (1991). The ecophysiology of water pumping by suspension-feeders is reviewed by Riisgård and Larsen (1995, 2000). The book by Wildish and Kristmanson (1997) focuses on the interactions between ambient water movement and the suspension-feeding process. Reviews of suspension-feeding by particular major taxonomic groups are mentioned in the corresponding sections of this chapter.

### 3.3. Suspension-Feeding Capacity Of Major Invertebrate Taxa

This section will review the activity rates of the major functional and taxonomic groups of suspension-feeders listed in Section 2.3. For each major group, information will be presented in the following sequence:

- General biology and mode of suspension-feeding
- Predominant food source and size range of particles retained
- Individual suspension-feeding rates
- Population suspension-feeding rates

The terminology that will be used in the following sections has been outlined above. The variety of units in which activity rates have been expressed by various authors is another factor that can cause difficulty in comparing the results of different studies. In the account below, literature data have been converted to a uniform scale wherever possible. In a few cases, authors did not provide enough information to allow this, or exact equivalence may be impossible owing to the differing body plans of major suspension-feeding taxa. Pumping and Clearance Rates are expressed on a common volumetric scale of  $\text{ml h}^{-1}$ . Activity rates are expressed either per individual animal, and/or per gramme dry mass. Where the original authors provided fresh (ie. wet) mass measurements but not dry masses, the latter were estimated using the fresh-dry mass conversion factors for major invertebrate taxa given by Ricciardi and Bourget (1998).

It is important to remember that activity rates of poikilothermic animals such as marine invertebrates will vary as a function of ambient temperature. In almost all cases, the authors of the studies reviewed in this section of the chapter recorded the temperature (and other relevant environmental conditions) at which their measurements were made, but for the sake of brevity most of this information has been omitted here. Unless otherwise stated (eg. the few studies relating to tropical or polar species), it should be assumed that data represent measurements made at normal summer temperatures for temperate seas, ie. mostly 15-20° C. The original papers should be consulted if additional details of experimental conditions are required.

### 3.3.1. Hydroids (*Phylum Cnidaria, Class Hydrozoa*) *General biology*

Hydroids are sessile cnidarians, with most species occurring as colonies of small polyps (hydranths) on hard substrata (a few larger, solitary species also exist). They are abundant and diverse in coastal seas. Particle capture is achieved by means of nematocysts ('stinging cells') on the polyp tentacles. Suspension-feeding is entirely passive. A comprehensive review of hydroid biology is given by Gili and Hughes (1995).

#### *Food source and particle size*

Most hydroids are believed to be largely carnivorous, feeding on a variety of small zooplankton including crustacean nauplii, juvenile and adult copepods, cladocerans and invertebrate eggs (Barangé, 1988; Gili and Hughes, 1995, Gili et al., 1996). However, significant ingestion of non-living material has been recorded in two hydroid species. Coma et al. (1995) found that zooplankton made up only 12% of the digestive cavity contents of *Campanularia everta*, the remaining 88% being non-living particulate organic matter (POM). Orejas et al. (2000) recorded copepod faecal pellets as a major component of the diet of *Obelia geniculata*.

Zooplanktivorous hydroids are able to capture a broad size range of prey items. Recorded size spectra are 1-5000 µm for *Tubularia larynx* (Gili and Hughes, 1995) and 30-1300 µm for *Eudendrium racemosum* (Barangé, 1988). Detrital particles found in the gut of *Campanularia everta* ranged from 10-80 µm (Coma et al., 1995).

#### *Individual suspension-feeding rates*

Hydroids are not truly microphagous, instead capturing prey items that are often of a similar size to the tentacle-bearing hydranths. Measurements of Feeding Rate are therefore typically made by counting (by microscopy) the number of prey items ingested by individual hydranths over a period of time, rather than by measuring the clearance of suspensions. Gili et al. (1996) found that each hydranth of *Tubularia larynx* ingested 36 prey items day<sup>-1</sup> in September. A lower mean rate of 4.3 items hydranth<sup>-1</sup> day<sup>-1</sup> was measured in *Eudendrium racemosum* (Barangé and Gili, 1988), equivalent to 26% of hydroid biomass ingested day<sup>-1</sup> (Barangé et al., 1989).

A very similar proportional ingestion rate of 19% of its own biomass day<sup>-1</sup> was calculated for *Campanularia everta* by Coma et al. (1995). This represents a Seston Uptake Rate (in this case synonymous with Feeding Rate) of 69.6 µgC µgC polyp<sup>-1</sup> year<sup>-1</sup>, with non-living POM accounting for most of the ingested material.

#### *Population suspension-feeding rates*

The population-level Seston Uptake Rate has been estimated for a few hydroid species by multiplying uptake rates per hydranth by the estimated number of hydranths per unit area on

natural substrata. At a local density of 66 colonies  $\text{m}^{-2}$ , *Eudendrium racemosum* was estimated to capture  $> 10^4$  prey items  $\text{m}^{-2} \text{day}^{-1}$  (Barangé and Gili, 1988). A much higher uptake rate of  $632 \times 10^3 - 10393 \times 10^3$  prey  $\text{m}^{-2} \text{day}^{-1}$  was calculated for the epiphytic hydroid *Obelia geniculata* in Chile (Orejas et al., 2000). Coma et al. (1995) estimated that their population of *Campanularia everta* consumed  $\sim 4000$  items  $\text{m}^{-2} \text{day}^{-1}$  in summer and  $\sim 800000$  items  $\text{m}^{-2} \text{day}^{-1}$  in winter. Averaged over the year, this amounted to a Seston Uptake Rate of  $\sim 1925 \mu\text{gC POM m}^{-2} \text{day}^{-1}$  and  $\sim 2260 \mu\text{gC zooplankton m}^{-2} \text{day}^{-1}$ .

Although relatively few data are available, these results have led to the suggestion that in dense populations, hydroid feeding may be a significant pathway for the transfer of organic matter between the pelagic and benthic ecosystems (Coma et al., 1995).

### 3.3.2. Octocorals (*Phylum Cnidaria, Class Anthozoa*)

#### *General biology*

'Octocoral' is a general term covering several orders of colonial anthozoans whose polyps carry eight pinnate tentacles. Familiar examples include the soft corals (Order Alcyonacea), horny corals (Order Scleractinia) and sea pens (Order Pennatulacea). The best-studied octocorals are probably the 'dead-men's fingers' (*Alcyonium* spp.) of temperate seas. As with the hydroids, prey capture is effected by means of nematocysts, and the animals are totally dependent on ambient water flow to bring food particles into contact with the polyp tentacles. The feeding ecology of octocorals has been reviewed by Lewis (1982).

#### *Food source and particle size*

Alcyonaceans are believed to feed largely on zooplankton (Lewis, 1982), although an ability to capture diatoms has also been demonstrated in the laboratory (Roushdy and Hansen, 1961). Sebens and Koehl (1984) compared the digestive cavity contents of *Alcyonium siderium* with the prey items available in the surrounding water and demonstrated a strong positive electivity for ascidian larvae and foraminifera, and a strong negative electivity for most planktonic crustaceans. Prey in the size range 256-345  $\mu\text{m}$  were taken.

#### *Individual suspension-feeding rates*

There are few data on particle capture rates by octocorals. Roushdy and Hansen (1961) studied colonies of *Alcyonium digitatum* in diatom suspensions at different concentrations. One colony captured 23% of the available cells in 23 hours at high concentration, another captured 93% in 6.5 hours at low concentration.

Patterson (1984, 1991a, b) studied prey capture by polyps of *Alcyonium siderium* in relation to location on the colony and ambient flow regime. Prey capture rate was shown to be greater in small colonies and at lower flow speeds. Retention Efficiency of individual polyps was very low (8% or less).

#### *Population suspension-feeding rates*

There appear to be no published measurements of octocoral suspension-feeding rates in the field, either at the individual or population level.

### 3.3.3. Sea anemones (*Phylum Cnidaria, Class Anthozoa*)

#### *General biology*

Sea anemones (Order Actiniaria) are large, usually solitary, benthic anthozoan polyps. Many species are macrophagous carnivores, while some others obtain nutrition with the aid of

symbiotic photosynthetic algae. However, several genera are predominantly microphagous and can be regarded as passive suspension-feeders (Van-Praët, 1985). Of these, the plumose anemone *Metridium senile* is a common member of fouling communities in temperate seas and is the only one to have been studied in any detail.

#### *Food source and particle size*

Gut content analyses show that *Metridium senile* feeds mainly on zooplankton (Purcell, 1977; Sebens, 1981). Specimens from the New England subtidal were found to show a strong positive electivity for barnacle cyprids, ascidian larvae and amphipods, and a strong negative electivity for invertebrate eggs, foraminifera, copepods and ostracods (Sebens and Koehl, 1984). Prey in the size range 200-6000  $\mu\text{m}$  were captured, with the main prey items (cyprids) measuring  $\sim 1500 \mu\text{m}$  (Sebens, 1981).

#### *Individual suspension-feeding rates*

Sebens (1981) studied the Feeding Rate of *Metridium* in the field by releasing suspensions of brine shrimp over clumps of anemones, then counting the numbers of shrimp (and natural prey) in the digestive cavities of collected specimens. Allometric equations relating numbers of prey captured to anemone body mass were calculated. This study did not consider Retention Efficiency, as the total numbers of brine shrimp contacting the anemone tentacles were not measurable.

Experiments in a laboratory flume at different flow velocities showed that the Feeding Rate of *Metridium* (nauplii captured  $\text{cm}^{-2}$  tentacle crown  $\text{min}^{-1}$ ) varied inversely with anemone size (Anthony, 1997). Small anemones were able to capture up to 26% of *Artemia* nauplii passing over the projected tentacle crown at optimal flow speed ( $20 \text{ cm sec}^{-1}$ ).

#### *Population suspension-feeding rates*

There are no published estimates of Seston Uptake Rates by natural populations of suspension-feeding anemones. Anthony (1997) measured the effects of neighbouring conspecifics on prey capture by *Metridium* in the laboratory. Prey captured  $\text{cm}^{-2}$  tentacle crown declined significantly with increasing numbers of upstream conspecifics up to a threshold of seven anemones. Further increases up to 16 did not cause any further reduction in area-specific Feeding Rate.

### *3.4. Crinoids (Phylum Echinodermata, Class Crinoidea)*

#### *General biology*

Crinoids, or feather stars, are suspension-feeding echinoderms common in many shallow-water hard-substratum communities, both in the temperate zone and on tropical reefs. All shallow-water species can move across the substratum on their basal cirri and can swim or drift through the water column, so are not restricted to one post-settlement feeding site. Crinoid suspension-feeding is entirely passive, with food particles captured using a basket of finely pinnate arms. Functional descriptions of the feeding mechanism are given by La Touche (1978), Byrne and Fontaine (1981), Meyer (1982), Holland et al. (1986) and Leonard (1989).

#### *Food source and particle size*

La Touche and West (1980) analyzed the gut contents of *Antedon bifida* from the coasts of Ireland. The diet consisted of non-living POM (detrital aggregates and faecal pellets) and phytoplankton, with a negligible zooplankton component. The phytoplankton contribution to the diet varied from 4% (February) to 36% (August). Detrital particles from 7-100  $\mu\text{m}$  size were ingested. Observations in aquaria showed that 300-1000  $\mu\text{m}$  particles were conveyed to the

mouth in still water, but that retention of this larger fraction was noticeably impaired in flowing water.

In contrast, the Red Sea crinoid *Lamprometra klunzingeri* was found to rely on living foods, with proportions of 10% phytoplankton, 50% protozoa (mostly tintinnid ciliates) and 40% planktonic crustaceans and molluscs (Rutman and Fishelson, 1969).

#### *Individual suspension-feeding rates*

Leonard et al. (1988) measured the capture rate of 90  $\mu\text{m}$  diameter particles by the tropical crinoid *Oligometra serripinna* at a range of flow velocities. Optimum flow speed for particle capture was 6.4  $\text{cm sec}^{-1}$ . However, there appear to be no data on absolute Seston Uptake or Clearance Rates either in the field or laboratory.

#### *Population suspension-feeding rates*

Seston uptake by crinoid populations in the field has not been measured or estimated.

### *3.3.5. Brittlestars (Phylum Echinodermata, Class Ophiuroidea)*

#### *General biology*

Brittlestars are a class of echinoderms found in virtually all benthic environments from the intertidal zone to the deep sea. Many species are carnivores or deposit-feeders but some are passive suspension-feeders which extend arms into the current and capture seston on rows of mucus-covered tube feet (Warner and Woodley, 1975). In some temperate seas, and in particular around the British Isles, the suspension-feeding brittlestar *Ophiothrix fragilis* occurs in dense beds with up to several hundred individuals  $\text{m}^2$  (Hughes, 1998). These aggregations represent significant concentrations of suspension-feeding biomass on the sea floor and may form an important route for the flow of carbon from the pelagic to the benthic environment (Davoult and Gounin, 1995; Allen, 1998).

#### *Food source and particle size*

There is little detailed information on the food sources exploited by suspension-feeding brittlestars. In Torbay, Devon, Warner and Woodley (1975) found that food boluses on the arms of *Ophiothrix fragilis* consisted of 'detritus of unidentifiable origin and large numbers of silt particles', with lower proportions of diatoms, coccoliths, foraminifera and faecal pellets. In contrast, diatoms were common in the gut of *Ophiothrix fragilis* from the Isle of Man (Brun, 1969). It is likely that this brittlestar is an unselective feeder, able to exploit the predominant source of seston in the local water column.

#### *Individual suspension-feeding rates*

Allen (1998) studied the Retention Efficiency of *Ophiothrix fragilis* filtering polystyrene microspheres in a laboratory flume. Retention of small spheres (80-140  $\mu\text{m}$ ) was ~90% in both high and low current speeds. Larger particles (240-500  $\mu\text{m}$ ) were more efficiently retained at lower current speeds (~80% as opposed to ~60%). It was observed that large naturally-occurring nutritive particles (eg. small zooplankton) were actively enveloped by the tube feet on contact with the arms, a response not seen with artificial particles of similar size.

There appear to be no other individual-level quantitative measurements of brittlestar suspension-feeding.

#### *Population suspension-feeding rates*

Davoult and Gounin (1995) described the cycle of suspension-feeding activity by beds of *Ophiothrix fragilis* in the English Channel in relation to current speed and seston availability. The



optimal flow velocity for feeding was found to be  $20 \text{ cm sec}^{-1}$ , but no absolute measurements of Seston Uptake Rate were made.

### 3.3.6. Polychaete worms (Phylum Annelida, Class Polychaeta)

#### General biology

Suspension-feeding has evolved independently in several polychaete families, typically associated with a sessile, tube-dwelling lifestyle (Fauchald and Jumars, 1979). There are two quite different major suspension-feeding modes among the Polychaeta (Riisgård and Larsen, 2000). Fan worms of the families Sabellidae, Serpulidae and Spirorbidae (and several smaller families) actively filter seston using an elaborate crown of ciliated cephalic tentacles which is extended from the open end of the dwelling tube (Nicol 1931; Mayer, 1994). In contrast, the families Chaetopteridae and Nereidae include species which secrete a mucus filter-net to trap particles and use muscular pumping movements of the body to generate a feeding current through the tube or burrow (Wells and Dales, 1951; Jørgensen et al., 1984). The best-studied mucus-net feeders are the chaetopterid *Chaetopterus variopedatus* (Brown, 1977; Flood and Fiala-Médioni, 1982; Riisgård, 1989) and the nereid *Nereis diversicolor* (Riisgård, 1991, 1994; Riisgård et al., 1992). Although both species are typically associated with sedimentary habitats, the tubes of *Chaetopterus* spp. can also be found on hard substrata. They are discussed here owing to the paucity of detailed information on most other suspension-feeding polychaetes.

#### Food source and particle size

Dales (1957) found that fan worms could retain particles in the 1-2  $\mu\text{m}$  size range. For *Sabella penicillus*, the optimal particle size for retention is 38  $\mu\text{m}$  (Riisgård and Ivarsson, 1990), but particles as small as 1.5  $\mu\text{m}$  can also be captured with 50% Retention Efficiency (Jørgensen et al., 1984). The serpulid *Ficopomatus enigmaticus* shows maximum Retention Efficiency at a similar size range of 2-12  $\mu\text{m}$  (Davies et al., 1989).

The mucus net of *Chaetopterus variopedatus* has a Retention Efficiency of ~90% for particles 1  $\mu\text{m}$  in diameter and can retain material as small as 0.5  $\mu\text{m}$  (Flood and Fiala-Médioni, 1982; Jørgensen et al., 1984; Riisgård, 1989). The net of *Nereis diversicolor* shows a Retention Efficiency of ~100% for particles > 7.5  $\mu\text{m}$ , and can retain particles down to 2-3  $\mu\text{m}$  (Riisgård, 1991; Riisgård et al., 1992).

There is much less information on the nature of the seston that suspension-feeding polychaetes ingest under field conditions, but the animals will clear suspensions of phytoplankton in the laboratory. Vedel et al. (1994) found that the presence of phytoplankton (at levels of 1-3  $\mu\text{g}$  chlorophyll a litre<sup>-1</sup>) triggered suspension-feeding activity of *Nereis diversicolor*. This species has a highly flexible trophic strategy: the worm is able to meet its nutritional requirements entirely by suspension-feeding (Riisgård, 1991) but will also graze benthic diatoms and ingest macroalgal fragments or animal flesh if opportunity arises (Vedel et al., 1994).

#### Individual suspension-feeding rates

Several authors have measured the filtering activity of suspension-feeding polychaetes in the laboratory, with results expressed either as Clearance Rate or Pumping Rate. Since these are not necessarily equivalent (see Section 2.1), some caution is required when comparing data obtained in different studies.

Dales (1957) measured Pumping Rates of several species of fan worms. Predictably, larger species (eg. the sabellid *Sabella pavonina*) had much higher volumetric Pumping Rates per individual than the much smaller serpulids and spirorbids. Dales also calculated mass-specific

Pumping Rates. As would be expected, Pumping Rate per unit mass declined with body size. Data from species potentially relevant to BIOFAQS are given below:

Family	Species	Mean Pumping Rate	
		ml ind <sup>-1</sup> h <sup>-1</sup>	ml g dry mass <sup>-1</sup> h <sup>-1</sup>
Sabellidae	<i>Sabella pavonina</i>	286	1960
Serpulidae	<i>Pomatoceros triqueter</i>	73	7035
Serpulidae	<i>Hydroides norvegica</i>	27	4523
Spirorbidae	<i>Spirorbis borealis</i>	0.23	4774

Clearance Rates of 1700 and 4000 ml g dry mass<sup>-1</sup> h<sup>-1</sup> at 17°C and 22°C were reported for the sabellid *Sabella spallanzanii* in Australia (Lemmens et al., 1996). Clearance Rate of *Sabella penicillus* was found to be highest at low algal concentrations, declining at higher levels due to overcrowding of the gut (Riisgård and Ivarsson, 1990). The relationship between Clearance Rate and body mass in this species was expressed by the following equation:

$$\text{Clearance Rate (ml ind}^{-1}\text{ h}^{-1}\text{)} = 13620 W^{0.24}, \text{ where } W = \text{g dry mass}$$

A Clearance Rate of 8590 ml g dry mass<sup>-1</sup> h<sup>-1</sup> was recorded for the serpulid *Ficopomatus enigmaticus* in South Africa (Davies et al., 1989).

For the mucus-net suspension-feeder *Chaetopterus variopedatus*, a Pumping Rate of 300 ml ind<sup>-1</sup> h<sup>-1</sup> was recorded by Dales (1957) and a mean Clearance Rate of 853 ml ind<sup>-1</sup> h<sup>-1</sup> by Riisgård (1989). For large individuals of *Nereis diversicolor*, Clearance Rates of 480 ml ind<sup>-1</sup> h<sup>-1</sup> (Riisgård et al., 1992) and 997 ind<sup>-1</sup> h<sup>-1</sup> (Vedel et al., 1994) have been recorded. The relationship between Clearance Rate (of 6.3 µm algal cells) and body size in *Nereis diversicolor* was determined by Riisgård (1991) to be:

$$\text{Clearance Rate (ml ind}^{-1}\text{ h}^{-1}\text{)} = 3.6 (3.52 + 2.46 W), \text{ where } W = \text{mg dry mass}$$

#### *Population suspension-feeding rates*

Using the individual-level data listed above, a population of *Ficopomatus enigmaticus* in a South African marina was estimated to have a total Clearance Rate of 5.93 x 10<sup>8</sup> litres day<sup>-1</sup>, equivalent to a filtering of the entire marina water volume in ~26 hours (Davies et al., 1989).

The only other population-level filtration data for polychaetes refer to the mucus-net feeder *Nereis diversicolor*. Riisgård (1991) used individual laboratory Clearance Rate to estimate the filtration capacity of a population in a Danish bay as 9.8 m<sup>3</sup> m<sup>-2</sup> day<sup>-1</sup>. This estimated value was later supplemented by field measurements of changes in seston concentration over dense beds of the worms. In Odense Fjord, Vedel et al. (1994) measured Clearance Rates of 5600 (May) and 7000 (June) litres m<sup>-2</sup> day<sup>-1</sup>. The May value represents a water volume 11-55 times greater (depending on tidal state) than the overlying volume of the fjord. In Kertinge Nor Bay, Denmark, Riisgård et al. (1996a) measured a population-level Clearance Rate of 13800 litres m<sup>-2</sup> day<sup>-1</sup>. On calm days, when wind-driven mixing was at a minimum, filtration of this intensity was shown to create a phytoplankton-depleted layer of water extending 5-10 cm above the sea bed.

#### 3.3.7. *Bryozoans (Phylum Bryozoa or Ectoprocta)*

##### *General biology*

Bryozoans (or 'moss animals') are active suspension-feeders occurring as colonies of individual feeding-units, or zooids. Although the individual zooids are tiny, the colonies may be quite large,

taking the form of encrusting sheets, branching tufts or flattened-leaf like growths according to species. Individual zooids capture particles using a crown of ciliated tentacles (lophophore). Winston (1977, 1978) and McKinney (1990) give general reviews of the feeding biology of bryozoans, while the mechanics of particle capture by the lophophore have been studied in detail using modern techniques by Riisgård and Manríquez (1997) and Nielsen and Riisgård (1998).

#### *Food source and particle size*

All studies of bryozoan feeding indicate that small algal cells are the principal food source (Winston, 1977). Zooid mouth size sets a limit on the size of particles that can be ingested, to those < 50 µm diameter in most species. In a minority of bryozoan species the zooids are equipped with a gizzard which allows them to process diatoms or other armoured cells, but in the majority of cases naked flagellates are the main food source. Non-photosynthetic protists may also form part of the diet of some bryozoans (Winston, 1978).

Best and Thorpe (1994) analyzed the seston available to the intertidal bryozoan *Flustrellidra hispida* and concluded that in addition to flagellate microplankton, the spores of intertidal macroalgae and very small particles of macroalgal detritus made up a high proportion of the material in the size range accessible to the bryozoan. It is not known whether non-living detritus forms a significant part of the natural diet of any bryozoan species, although logic suggests that it may do so in the case of deep-sea bryozoans. Winston (1976) found that the estuarine species *Conopeum tenuissimum* could not be cultured on detritus from laboratory oyster tanks.

Studies of Retention Efficiency in bryozoans show that particles < 5 µm pass through the ciliary filter, whereas those in the 6-14 µm range are retained with close to 100% efficiency (Riisgård and Goldson, 1997; Riisgård and Manríquez, 1997).

#### *Individual suspension-feeding rates*

The capture of inert latex microspheres by bryozoan colonies 'feeding' in a range of flow conditions has been studied intensively by Okamura (1984, 1985, 1987, 1988, 1990, 1992) but it is doubtful whether these data can be taken to represent Clearance Rates of natural algal suspensions (Riisgård and Manríquez, 1997).

Two main methods have been used to calculate rates of bryozoan suspension-feeding on natural foods:

- Pumping Rates have been estimated indirectly using microscopic observations of the dimensions of the lophophore and the velocities of particles passing through it.
- Clearance Rates have been calculated using measured declines in the concentrations of algal suspensions containing feeding bryozoan colonies.

In both types of study, authors typically express activity rate per individual zooid ( $\text{time}^{-1}$ ), which creates difficulties in comparing results with data from other suspension-feeding taxa with different body plans (expressing activity rates per bryozoan colony would be of limited use as colonies of most species are of indeterminate size, and few authors have measured mass-specific suspension-feeding rates in bryozoans).

A brief summary of bryozoan Pumping Rates calculated using the 'particle velocity' method is given below. With the exception of *Himantozoum antarcticum*, all species are from temperate

coastal waters of Northern Europe or North America. Some authors measured variation in Pumping Rate in relation to ambient temperature or particle concentration. In these cases, rates at optimum conditions (ie. those supporting maximum suspension-feeding activity) have been given.

Author	Species	Pumping Rate ml zooid <sup>-1</sup> h <sup>-1</sup>
Menon, 1974	<i>Conopeum tenuissimum</i>	0.12 - 0.46
	<i>Electra pilosa</i>	0.15 - 0.39
Winston, 1977 (includes data from Strathmann, 1973)	Data for 13 spp. given	10 spp. in range 0.21 - 1.60 Highest rate of ~ 4.0 for <i>Flustrellidra hispida</i>
Best and Thorpe, 1983	<i>Flustrellidra hispida</i>	9.28 (maximum observed)
Best and Thorpe, 1986	<i>Flustrellidra hispida</i>	3.95 (mean rate)
	<i>Alcyonidium gelatinosum</i>	1.47
	<i>Alcyonidium hirsutum</i>	1.75
	<i>Electra pilosa</i>	0.77
	<i>Membranipora membranacea</i>	0.88
Sanderson et al., 1994	<i>Himantozoum antarcticum</i>	1.2

Zooid-specific pumping rates determined by this method mostly fall in the general range 0.12 - 1.2 ml h<sup>-1</sup>. The higher rates found in the genera *Alcyonidium* and (especially) *Flustrellidra* can be explained by the large size of the lophophores in the ctenostomate bryozoans, the group to which these genera belong (Winston, 1977).

Some of the older studies using the 'particle velocity' method have been criticized recently (Riisgård and Goldson, 1997; Riisgård and Manríquez, 1997) for failing to take into account variations in flow velocity in different regions of the lophophore, and in some cases for exposing the experimental animals to unnaturally high concentrations of algal cells. It is therefore likely that rates based either on measured clearance of algal suspensions (at concentrations similar to those experienced in nature), or by a more sophisticated 'particle velocity' model which allows for a flow gradient within the lophophore will give a more accurate picture of bryozoan suspension-feeding capacity. A summary of rates obtained using these methods are given below (all bryozoans studied are temperate-water coastal species):

Author	Species	Pumping Rate ml zooid <sup>-1</sup> h <sup>-1</sup>
Riisgård and Manríquez, 1997	Data for 15 spp. given	12 spp. in range 0.14 - 1.72
		<i>Alcyonidium gelatinosum</i> 2.48
		<i>Bowerbankia imbricata</i> 1.93
		<i>Flustrellidra hispida</i> 7.49
		Clearance Rate ml zooid <sup>-1</sup> h <sup>-1</sup>
Bullivant, 1968	<i>Zoobotryon verticillatum</i>	0.37
Riisgård	<i>Celleporella hyalina</i>	0.17

and Manríquez, 1997

Riisgård and Goldson, 1997	<i>Electra pilosa</i>	0.28
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Lisbjerg and Petersen, 2000	<i>Electra bellula</i>	0.09
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According to conversion factors given by Lisbjerg and Petersen (2000), the maximum Clearance Rate recorded for *Electra bellula* is equivalent to 115 ml cm<sup>-2</sup> colony area h<sup>-1</sup> or 22.3 litres g dry mass<sup>-1</sup> h<sup>-1</sup>.

#### *Population suspension-feeding rates*

There is only one published estimate of the filtration capacity of a bryozoan population in the field. Using data from colonies in the laboratory and the observed biomass of the species, Lisbjerg and Petersen (2000) estimated Clearance Rates of 80 and 195 litres m<sup>2</sup> day<sup>-1</sup> for populations of *Electra bellula* in two seagrass beds in Western Australia. However, the authors noted that extrapolation of laboratory measurements to population Clearance Rate was problematic owing to variability in numbers of actively-feeding zooids per colony. There are no measurements of absolute Seston Uptake Rate by bryozoan populations.

### 3.3.8. *Ascidians (Phylum Chordata, Class Ascidiacea)*

#### *General biology*

Ascidians are sessile animals distantly related to vertebrates. The simple body plan is built around the filtering system, in which water entering through an inhalent siphon is passed through a finely perforate pharynx or branchial sac before exiting via an exhalent siphon. Water is actively pumped through the body by ciliary action and particles are trapped on a mucus net covering the branchial sac. Some ascidian species occur as solitary individuals, others as colonies of asexually-budded zooids. Millar (1971) gives an overview of ascidian biology, while the functional characteristics of the water-pumping system are reviewed by Riisgård (1988b).

#### *Food source and particle size*

The ability of the ascidian filtering system to retain particles (with Retention Efficiencies > 90%) down to 1 µm diameter has been demonstrated in several studies (Jørgensen, 1949; Jørgensen and Goldberg, 1953; Randløv and Riisgård, 1979; Jørgensen et al., 1984; Klumpp, 1984). Klumpp (1984) found that *Pyura stolonifera* could also retain kelp particles up to 100 µm with 100% efficiency.

The ascidian filter is capable of retaining a wide range of seston types, including bacteria, diatoms and other phytoplankton, and non-living detritus. Detailed individual case studies suggest that the predominant food source varies according to species, season and environmental setting. *Pyura stolonifera* retains phytoplankton and kelp detritus at equal rates and efficiencies (Klumpp, 1984). However, most of the ingested diatoms and detritus pass through the gut undigested, with small phytoplankton cells 3-5 µm making up most of the assimilated material (Seiderer and Newell, 1988). In contrast, stable isotope measurements were used to demonstrate a significant assimilation of kelp detrital carbon by the arctic species *Molgula griffithsi* (Dunton and Schell, 1987). Ribes et al. (1998) showed that *Halocynthia papillosa* fed on particles in the size range 0.6 - 70 µm, including detritus, prokaryotic cells, protozoa and phytoplankton. Detrital carbon accounted for 92% of the total carbon ingested, but living plankton was still important as a source of nitrogen. In antarctic ascidians, maximum Retention Efficiencies were found for particles in

the bacterial-protozoan (rather than phytoplanktonic) size range (Kowalke, 1999). Consumption of a variety of invertebrate larvae (including conspecifics in some cases) has also been demonstrated in ascidians (Young, 1988; Bingham and Walters, 1989)

#### *Individual suspension-feeding rates*

There have been many laboratory studies of rates of suspension-feeding by individual ascidians, mostly involving measurement of Clearance Rate of algal or inorganic suspensions. Existing data relate mostly to the larger species of solitary ascidians, with relatively little information on the colonial forms. Compilations of rates determined in different studies have recently been published by Ribes et al. (1998) and Kowalke (1999). A simplified version of Kowalke's table is given below to illustrate the range of values recorded. With the exception of the antarctic species at the foot of the table, most rates were measured at temperate-zone summer water temperatures (ie. 10-20°C).

Species	Clearance Rate, ml g dry mass <sup>-1</sup> h <sup>-1</sup>	Source
<i>Ciona intestinalis</i>	5880	Fiala-Médioni (1978b)
	3540	Robbins (1983)
	7080	Petersen and Riisgård (1992)
	2760	Randløv and Riisgård (1979)
<i>Phallusia mammillata</i>	6300	Fiala-Médioni (1978b)
<i>Styela plicata</i>	10680	Fiala-Médioni (1978b)
<i>Styela clava</i>	4680	Holmes (1973)
<i>Ascidiella aspersa</i>	3180	Holmes (1973)
	3240	Randløv and Riisgård (1979)
<i>Ascidia mentula</i>	2500	Robbins (1984)
	3422	Fiala-Médioni (1978a)
<i>Pyura stolonifera</i>	480-1260	Klumpp (1984)
4 Antarctic species	108-230	Kowalke (1999)

It can be seen that high Clearance Rates can be attained by ascidians, amounting to several litres g dry mass<sup>-1</sup> h<sup>-1</sup>. The low values for the antarctic species are partly attributable to the very low ambient temperature (1°C) at which they were measured.

Aspects of ascidian suspension-feeding that have received attention include the effects of major environmental variables on activity rates. Factors studied include temperature (Fiala-Médioni, 1978c; Petersen and Riisgård, 1992; Ribes et al., 1998), oxygen tension (Fiala-Médioni, 1979a) and seston concentration. With respect to the last factor, inhibition of suspension-feeding at very high seston concentrations has been described (Fiala-Médioni, 1979b; Robbins, 1984). In unfavourable conditions, ascidians can use 'back-squirting' to expel unwanted material through the inhalent siphon (Shumway, 1978). In *Pyura stolonifera*, this occurs at a silt load of 25 mg



litre<sup>-1</sup> or at high densities of particles > 65 µm (Klumpp, 1984). However, the current opinion is that at seston levels below those required to induce back-squirting, suspension-feeding proceeds at a constant rate without rhythmicity or active regulation by the animal (Fiala-Médioni, 1978b; Randløv and Riisgård, 1979; Klumpp, 1984)

#### *Population suspension-feeding rates*

Population-level filtration has been investigated only in the common temperate-zone ascidian *Ciona intestinalis*. Petersen and Riisgård (1992) used laboratory Clearance Rate data and field measurements of population density to estimate the grazing impact of *Ciona* in a Danish fjord. The estimated volumetric turnover of water by the ascidians varied throughout the year, with a maximum value in September, when the animals processed the equivalent of the total volume of the fjord each day. The grazing impact of the *Ciona* population was subsequently modelled in more detail, with algal concentration related to Clearance Rate, current velocity and mixed-layer depth (Riisgård et al., 1996b). The model suggested that in calm conditions filtration by *Ciona* would deplete the phytoplankton in a 20-30 cm deep layer of near-bottom water. Measurable declines in chlorophyll a concentrations in water passing over the ascidian bed were subsequently detected in the field at this site (Riisgård et al., 1998).

*Ciona intestinalis* is one of the most widespread and abundant ascidians in fouling communities and is probably the most intensively-studied species in the group. Detailed studies have been made of distribution and habitat choice (Dybern, 1963, 1967), life cycle (Dybern, 1965) and growth and energetics (Petersen et al. 1995).

#### *3.3.9. Bivalves (Phylum Mollusca, Class Bivalvia)*

##### *General biology*

The Bivalvia includes many suspension-feeding species with modes of life ranging from completely sessile (many oysters) to highly mobile (scallops). Suspension-feeding is an active process, with food particles captured from the current generated by the beating of cilia on greatly enlarged filamentous gills (ctenidia). Particle sorting takes place on the gills, with unwanted material rejected as pseudofaeces.

Because the Bivalvia includes species of great ecological and economic importance, suspension-feeding has been intensively researched and frequently reviewed, with a volume of literature which probably exceeds that for all other suspension-feeding groups combined. Consequently, only a very brief summary of the subject, focusing on issues relevant to BIOFAQS, can be presented here, together with a guide to the main sources of more detailed information.

A general review of bivalve suspension-feeding is given by Jørgensen (1990). Jørgensen (1996) provides an update on the continuing disagreements over methodology and interpretation of feeding rates that persist in the bivalve literature. A contrasting viewpoint is provided by Bayne (1998) in an introduction to a volume (J. Exp. Mar. Biol. Ecol, 1998) devoted to bivalve suspension-feeding. Mussels (especially *Mytilus* and *Modiolus* spp.) are the most intensively-studied bivalves, and their feeding biology has been reviewed by Bayne et al. (1976) and Hawkins and Bayne (1992). The volume edited by Dame (1992) deals with the wider ecological role of suspension-feeding bivalves in the coastal environment.

##### *Food source and particle size*

Mussels (*Mytilus edulis*) are able to retain suspended particles down to the bacterial size range (Hawkins and Bayne, 1992). Retention Efficiencies for particles < 1 µm are in the range 20-30%, rising to 100% for particles > 4 µm (Riisgård, 1988). Scallops and oysters are also able to retain



L = Shell length, mm

Species	Allometric equation	Original source
<i>Mytilus edulis</i>	$C = 7450 W^{0.66}$	Møhlenberg and Riisgård (1979)
	$C = 7370 W^{0.72}$	Riisgård and Møhlenberg (1979)
	$C = 1.2 L^{2.14}$	Kiørboe and Møhlenberg (1981)
<i>Modiolus modiolus</i>	$C = 6000 W^{0.75}$	Møhlenberg and Riisgård (1979)
<i>Perna perna</i>	$C = 8850 W^{0.66}$	Berry and Schleyer (1983)
	$C = 27 L^{1.86}$	
<i>Geukensia demissa</i>	$C = 6150 W^{0.83}$	Riisgård (1988a)
<i>Chlamys hastata</i>	$C = 8700 W^{0.94}$	Meyhöfer (1985)

The good agreement between the dry mass-specific allometric equations for different species suggests that these relationships can be taken as indicative of the Clearance Rates achievable by suspension-feeding bivalves under optimal conditions.

#### Population suspension-feeding rates

It has often been proposed that the collective suspension-feeding activity of dense bivalve populations can significantly reduce phytoplankton concentrations and thus potentially act as a natural control on eutrophication (Cloern, 1982; Officer et al., 1982; Nichols, 1985; Dame, 1993; Helfrich et al., 1995; Wilkinson et al., 1996). Consequently, much attention has been paid to measuring and modelling the suspension-feeding capacity of bivalve aggregations, in most cases beds of the common mussel *Mytilus edulis* (Fréchette et al., 1989). It is believed that laboratory data on Pumping or Clearance Rates of individual mussels may be of only limited value for estimation of population-level suspension-feeding capacity, owing to the need to consider additional processes such as particle resuspension and interactions between the individual bivalves (Doering and Oviatt, 1986; Prins et al., 1996). Many authors have therefore attempted to directly measure changes in seston load in the water passing through flumes placed over intertidal mussel beds. The table below summarizes the results from several studies using this methodology (all data refer to *Mytilus edulis*). Data have been expressed in a number of ways by the various authors, usually either as percentage removal of phytoplankton biomass or as Clearance Rate per unit of mussel dry mass.

Study	Result
Wright et al. (1982)	Clearance Rate 2400 ml g dry mass <sup>-1</sup> h <sup>-1</sup>
Dame and Dankers (1988)	Seston Uptake 5.4 - 8.8 mg g dry mass <sup>-1</sup> h <sup>-1</sup>
Asmus and Asmus (1991)	37 ± 20% phytoplankton removal
Muschenheim and Newell (1992)	~ 20% phytoplankton removal
	Clearance Rate 9800 ml g dry mass <sup>-1</sup> h <sup>-1</sup>
Prins et al. (1994)	Clearance Rate 290 - 1980 ml g dry mass <sup>-1</sup> h <sup>-1</sup>

Prins et al. (1996) Clearance Rate 700 - 5300 ml g dry mass<sup>-1</sup> h<sup>-1</sup>

Measured field Clearance Rates are quite variable but very high in some cases. In addition to measuring the total uptake rate, several authors have examined how seston composition is changed by passage over a bed of actively suspension-feeding mussels. The *Mytilus edulis* bed studied by Wright et al. (1982) showed a substantial uptake of phytoplankton but had no effect on bacterial numbers in the overlying water. The capacity of *Mytilus* beds to act as a selective filter for phytoplankton was also shown by Wildish and Kristmanson (1984) and Prins et al. (1996). In contrast, beds of *Modiolus* showed a significant uptake of both phytoplankton and bacteria (Wildish and Kristmanson, 1984).

The mussel bed studies discussed above all refer to bivalve aggregations extending in two dimensions across the substratum. The biofilter design currently proposed for use in BIOFAQS consists of three-dimensional substratum units suspended vertically in the water column near or below a cage site. Suspension-feeding rate data obtained from mussel aquaculture are therefore highly relevant to the interests of the project, since these relate to bivalve aggregations growing in mid-water on ropes or other artificial supports. There are fewer published measurements made in these circumstances. Cabanas et al. (1979) measured filtration and biodeposition of raft-grown mussels in Spain. The mussels were found to retain 30% of the particulate carbon, 42% of the nitrogen and 60% of the chlorophyll a in water flowing through the raft. The higher retention of chlorophyll a indicates a selective uptake of phytoplankton. Clearance rate was estimated as 5300 ml ind<sup>-1</sup> h<sup>-1</sup>. The raft population of ~ 5.5 million mussels was estimated to biodeposit 190 kg dry sediment d<sup>-1</sup>. In another Spanish mussel farm, Navarro et al. (1991) measured individual Clearance Rates in relation to the position of mussels on the raft. Mussels from outer locations cleared 2690 ml ind<sup>-1</sup> h<sup>-1</sup>, whereas those from close to the raft centre (which presumably received water that had already been processed by mussels on the periphery) managed only 1630 ml ind<sup>-1</sup> h<sup>-1</sup>. This result demonstrates the occurrence of interactions between individual suspension-feeders and reinforces the conclusion that data obtained from isolated animals in the laboratory cannot be simply extrapolated to estimate the suspension-feeding capacity of dense aggregations.

### 3.3.10. Barnacles (*Phylum Arthropoda, Class Crustacea*)

#### *General biology*

Barnacles are sessile suspension-feeding crustaceans which occur at high densities on rocky shores and shallow subtidal hard substrata. Seston is filtered from the water using a basket of modified legs or cirri. Crisp and Southward (1961) described two distinct suspension-feeding methods: the cirri may be held outstretched to trap larger particles carried into them by the prevailing current (raptorial feeding), or may be moved actively to 'comb' the water for smaller particles (microphagy). The behavioural transition between feeding modes in *Semibalanus balanoides* was studied more recently by Trager et al. (1990). A switch from active cirral beating to passive filtering occurred at flow velocities above 3.1 cm sec<sup>-1</sup>. This behavioural plasticity requires barnacles to be classed as facultative active-passive suspension-feeders.

#### *Food source and particle size*

The flexible suspension-feeding strategy of barnacles means that a wide variety of food items can be exploited (Crisp and Southward, 1961; Glasstetter and Senn, 1986). *Balanus balanoides* can be reared in the laboratory on mixed cultures of diatoms (Barnes and Barnes, 1982). Capture of zooplankton by barnacles has been documented by Young and Cameron (1989), Hunt and Alexander (1991) and Trager et al. (1994). Barnes (1959) found that 74% (by dry mass) of the gut contents of *Balanus cariosus* was composed of particles (largely crustacean remains) in the size

range 4 - 8  $\mu\text{m}$ . In contrast, animal remains were infrequent in the guts of *Balanus rostratus*, which contained large quantities of diatoms.

Zardus et al. (1991) compared the gut contents of *Balanus nubilus* with the seston available in the local water column. By mass, the ingested material consisted of organic detritus > zooplankton > phytoplankton > inorganic particles. Zooplankton was the most preferred food, followed by organic detritus. Phytoplankton and inorganic particles were ingested in lower proportions relative to their availability.

The varied composition of the barnacle diet is reflected in the wide size range of particles that can be ingested. Particulate matter as small as < 2  $\mu\text{m}$  was ingested by both barnacle species studied by Barnes (1959). In contrast, zooplankters and fragments of chopped mussel > 1 mm in size can also be eaten (Crisp and Southward, 1961). Olson (1979) measured the selectivity of *Semibalanus balanoides* for four particle size classes in the 5 - 49  $\mu\text{m}$  range and found that the largest particles were preferentially captured.

#### *Individual suspension-feeding rates*

Although there is a large literature on many aspects of barnacle biology, there is very little quantitative information on suspension-feeding rates. For animals feeding passively, the volume of water filtered will be a function of current velocity and the surface area of the extended cirral basket. Crisp and Southward (1961) estimated the Pumping Rate of three barnacle species when feeding actively:

*Balanus perforatus*    2.0 - 8.8 ml ind<sup>-1</sup> h<sup>-1</sup>  
*Semibalanus balanoides* < 0.5 - 10.0 ml ind<sup>-1</sup> h<sup>-1</sup>  
*Elminius modestus*    11.4 ml ind<sup>-1</sup> h<sup>-1</sup>

The authors noted that many seston particles passed through the cirral filter, so that Pumping Rate is not equal to Clearance Rate in these animals.

#### *Population suspension-feeding rates*

There appear to be no data on population-level suspension-feeding by barnacles. The seasonality of feeding activity was investigated by Ritz and Crisp (1970) in *Semibalanus balanoides*. Peaks of feeding activity were seen in the March-May period and in October, followed by a sharp decline in November coincident with the onset of breeding. Food intake essentially ceased in late November and December.

### 3.3.11. Sponges (Phylum Porifera)

#### *General biology*

Sponges are sessile animals in which the body tissue is permeated by a system of water-carrying passageways and cavities (varying in complexity with the species), connecting a large number of small inhalent pores (ostia) with a few larger exhalent openings (oscula) (Reiswig, 1975a). Flow of water through the sponge is created or enhanced by the flagellar beating of specialized 'collar cells' (choanocytes) which occur in the lining of the aquiferous system. The choanocytes also intercept and engulf food particles. Digestion is entirely intracellular and there are no specialized digestive organs. Because ambient currents may supplement the action of the choanocytes in driving water through the sponge, these animals have been regarded as combined passive-active suspension feeders (Vogel, 1974). However, Riisgård et al. (1993) argue on energetic grounds that passive current-induced filtration is of insignificant importance to most sponges. A general review of sponge feeding biology is given by Frost (1976).



### *Food source and particle size*

Because of their reliance on intracellular digestion, sponges are specialized for feeding on the smallest seston fractions, and are the only group of suspension-feeders able to retain particles down to ~ 0.1  $\mu\text{m}$  (Reiswig, 1975b). Pile et al. (1996) found that the sponge *Mycale lingua* nonselectively retained all types of plankton < 10  $\mu\text{m}$  diameter, including bacteria, cyanobacteria and small eukaryotes. Maximum retention sizes of 6 - 10  $\mu\text{m}$  have been recorded for some sponge species (Wolfrath and Bartel, 1989; Witte et al., 1997), while others may be able to ingest particles as large as 50  $\mu\text{m}$  (Reiswig, 1971a; Kowalke, 2000).

Reiswig (1971a) found that the diet of three tropical sponges consisted largely (~ 80%) of non-living POM unresolvable by direct microscopy, while a similar proportion (74%) of the carbon ingested by *Mycale lingua* was estimated to be derived from living plankton (Pile et al., 1996). Sponge diet composition therefore seems likely to depend on the relative amounts of living and non-living seston available in the local water column.

Sponges typically show high Retention Efficiencies for particles in the appropriate size range. Published estimates for various species feeding on bacteria, micro-eukaryotes and non-living POM include 79-82% (Reiswig, 1971a), 72-93% (Pile et al., 1996), 58-99% (Pile et al., 1997), and 55-75% (Kowalke, 2000).

### *Individual suspension-feeding rates*

Thomassen and Riisgård (1995) provide a tabulation of measured Pumping or Clearance Rates of sponge species. Comparison of results is difficult because of the different ways in which authors express their results (eg. some report rates  $\text{cm sponge tissue}^{-3}$ , others  $\text{g dry mass}^{-1}$ , with the relevant conversion factors not always provided). Recent studies of temperate-zone sponges using modern techniques are probably the most useful in the BIOFAQS context. Riisgård et al. (1993) found that *Halichondria panicea* and *Haliclona urceolus* both had a Clearance Rate of ~ 3600  $\text{ml g dry mass}^{-1} \text{h}^{-1}$ . Further work on *Halichondria panicea* (Thomassen and Riisgård, 1995) recorded a Clearance Rate of ~ 1700  $\text{ml g dry mass}^{-1} \text{h}^{-1}$ . Very similar values of ~ 2700  $\text{ml g dry mass}^{-1} \text{h}^{-1}$  were recorded for two coral reef sponges by Reiswig (1974), while a third reef species (*Mycale* sp.) showed a higher rate of ~ 12600  $\text{ml g dry mass}^{-1} \text{h}^{-1}$ . Sponges appear to have a relatively low water pumping capacity in comparison with other active suspension-feeders, but compensate for this by having a high Retention Efficiency for very small particulate matter.

Reiswig (1971b) demonstrated the periodic cessation of pumping activity in coral reef sponges, mediated by tissue contraction and closure of the oscula. Instantaneous rates of water transport (from either field or laboratory observations) therefore cannot be validly extrapolated over long time periods without some information on the activity pattern of the species concerned.

### *Population suspension-feeding rates*

There have been no direct measurements of seston uptake by sponge populations in the field. The closest approximation is that of Pile et al. (1997), studying freshwater sponges in Lake Baikal. *In situ* measurements on individual sponges (Savarese et al. 1997) were used to estimate a Seston Uptake Rate of 1.97  $\text{g C m}^{-2} \text{day}^{-1}$ , mostly derived from prokaryotic cells. Field measurements showed that picoplankton (plankton < 2  $\mu\text{m}$ ) concentrations in the benthic boundary layer could be depleted by sponge filtering.

Reiswig (1974) and Frost (1978) both used Pumping Rate measurements on individual sponges to estimate the population-level volumetric turnover of water, but did not express results in terms of seston uptake. The freshwater sponges studied by Frost were estimated to process every six days a volume of water equivalent to that of the pond in which they were living.



### 3.4. Suspension-Feeding Capacity Of Multi-Species Communities

The preceding chapter section has reviewed published studies of the collective suspension-feeding capacity of single-species populations. In nature, communities of suspension-feeding invertebrates usually include a mixture of species, and several attempts have been made to measure or estimate rates of Clearance or Seston Uptake at the community level. The widely divergent biologies of the major suspension-feeding taxa make this a more complicated task than for single-species communities. The presence of more than one species creates the potential for interspecific interactions, either competitive - where two or more species exploit the same seston fraction, or synergistic - where different species exploit different resources or enhance each other's feeding success (eg. by combination of feeding currents). Community suspension-feeding estimates have been made at the level of large, geographically-defined areas such as bays, fjords or seagrass beds, and at a smaller spatial scale, focusing on uptake by assemblages on fouling panels or mussel ropes. There are more published examples of geographic-scale studies than of measurements at the smaller scale, which is unfortunate given that the latter are more directly relevant to the needs of BIOFAQS.

After reviewing the published examples of community-level suspension-feeding, this section of the chapter will conclude with a summary of points gathered from the literature which relate to the biology of suspension-feeding animals and which should be taken into account when attempting to model the uptake of seston from aquaculture cage sites.

#### 3.4.1. Large-scale studies

The published work in this category is of only limited relevance to BIOFAQS and will therefore be summarized very briefly. Glynn (1973) is one of the few authors to have directly measured the uptake of seston by a mixed community of suspension-feeders in the field. By sampling the plankton upstream and downstream of a Caribbean reef flat he determined that suspension-feeding reduced the diatom standing stock by 91% and that of zooplankton by 60%. The uptake of planktonic carbon by the reef community averaged over the year was estimated as  $0.18 \text{ g C m}^{-2} \text{ d}^{-1}$ .

Evidence of a correlation between periods of low phytoplankton biomass and high suspension-feeding activity by bivalves in San Francisco Bay led to suggestions that suspension-feeding could act as a natural control on eutrophication (Cloern, 1982; Officer et al., 1982; Nichols, 1985). These studies, and later ones inspired by them, have typically used laboratory measurements of Clearance Rates, scaled-up to field population densities, to estimate population-level clearance at the sites of interest. As an example, using rates obtained by Møhlenburg and Riisgård (1979), Cloern (1982) estimated that suspension-feeding bivalves in south San Francisco Bay were sufficiently abundant to filter a volume equivalent to that of the bay each day. The same approach (ie. scaling-up from laboratory-measured activity rates) has been used to estimate seston uptake by infaunal bivalves in the Kattegat (Loo and Rosenberg, 1989), by ascidians, bivalves and brittlestars in the Bay of Brest (Hily, 1991) and by a diverse community of suspension-feeders in Australian seagrass beds (Lemmens et al., 1996). All these studies concluded that suspension-feeding had a major influence on water column seston concentrations, and therefore on the flow of carbon through the local ecosystem.

### 3.4.2. Small-scale studies

Only a few authors have attempted to quantify the suspension-feeding activity of mixed communities at a small spatial scale. Buss and Jackson (1981) measured *in situ* particle depletion in a small experimental enclosure on a Caribbean coral reef. They measured a correlation between reduced densities of bacteria and naked eukaryotic cells and the spatial coverage of sponges and bryozoans. Data suggested that these two taxa competed for the microflagellate component of the plankton, while bacteria were consumed only by the sponges. Mook (1981) measured particle clearance by fouling communities (including barnacles, bryozoans, hydroids and sponges) on tiles held in closed-system containers of sea water. Pre-starved communities showed a uniform retention of particles across the measured size range (1 - 40 µm) for the first two hours. Later recorded increases in the concentration of particles in particular size categories were attributed to faecal pellet production by suspension-feeders. Mook suggested that pellets emitted by some species were reconsumed by others, and that a mixed community was able to utilize a greater proportion of the total seston than any single species alone.

The study by Lesser et al. (1992) probably shows the closest approximation to the situation of interest to BIOFAQS. Competition for food between rope-cultured mussels (*Mytilus edulis*) and a variety of co-occurring suspension-feeders was investigated. The potentially competing epifauna were the ascidians *Ciona intestinalis* and *Botryllus schlosseri*, the gastropod *Crepidula fornicata* and the barnacle *Semibalanus balanoides*. Clearance Rates and particle size retention were measured on individual animals in aquaria. Results can be summarized as follows:

Species	Selective particle uptake	Clearance Rate Particles ml <sup>-1</sup> ind <sup>-1</sup> h <sup>-1</sup>
<i>Mytilus edulis</i>	Small phytoplankton (3 - 5 µm)	1000 - 1500
<i>Ciona intestinalis</i>	Large phytoplankton (> 16 µm)	250 - 500

Data for *Crepidula fornicata* were similar to those obtained from *Ciona intestinalis*. Clearance Rates of *Botryllus schlosseri* and *Semibalanus balanoides* were found to be very low compared to those listed above. The authors concluded that none of the other epifaunal species were likely to compete significantly for food with *Mytilus edulis* owing to size-partitioning of the phytoplankton resource and the much higher Clearance Rate of the mussels. However, it must be borne in mind that all data were collected from individual animals in isolation rather than from mixed communities *in situ*, and the question of interspecific interactions was not addressed. These data can therefore only be applied with caution to the behaviour of multi-species assemblages of suspension-feeders.

### 3.4.3. Modelling of seston uptake by suspension-feeding communities

A number of important themes can be identified from a review of the literature on benthic suspension-feeding, which reflect the current state of knowledge of the process. These points should be taken into account in future work undertaken within BIOFAQS, specifically when attempting to model the potential of suspension-feeder assemblages to mitigate the local effects of cage aquaculture installations.

#### *Selection of single-species data from the literature*

A number of authors advise that it may be invalid to extrapolate Pumping or Clearance Rates of field populations from short-term measurements made on isolated animals in aquaria. The factors leading to this conclusion include:

- Position-dependent feeding success: Animals in the centre of dense aggregations or in downstream locations may experience reduced feeding success owing to the prior filtration of water by individuals in more favourable sites (Wildish and Kristmanson, 1985; Navarro et al., 1991).
- Temporal variability in activity rates: There is evidence that bed-forming bivalves may not always suspension-feed at full capacity (Prins et al., 1994; Cranford and Hill, 1999). This may lead to an overestimation of seston uptake if results from short-term experiments are extrapolated over longer time periods.
- Dependence of feeding rates on seston characteristics: In a comparison of eight models designed to predict biodeposition by bivalves, those based on data from bivalves filtering natural seston mixtures gave estimates which agreed better with observed values than others based on filtration of dyes or algal monocultures (Doering and Oviatt, 1986). The latter overestimated biodeposition rate by up to an order of magnitude.

#### *Interspecific interactions*

In a natural community of suspension-feeders, different taxa will compete for attachment space and may also compete for some fraction of the available seston (Stuart and Klumpp, 1984). The complex interaction of feeding currents generated by the various members of the community (which may include the re-filtration of water already processed by other organisms) may lead to individual Seston Uptake Rates quite different from those achievable by the same animals in isolation.

#### *Biodeposition and nutrient release*

It is important to note that suspension-feeding animals are not unidirectional sinks for particulate matter from the water column. All taxa will expel unassimilated solid waste as faeces, and some, notably bivalve molluscs, will also concentrate and deposit non-ingested matter as pseudofaeces. Significant quantities of solid deposits may be produced by bivalves. Filtration by the oyster *Crassostrea* results in the deposition of solid matter (faeces plus pseudofaeces) at a rate seven times faster than settlement of the same mass of particulates by gravity alone (Haven and Morales-Alamo, 1966). An oyster bed measuring ~ 0.4 hectares in area was estimated to produce 981 kg dry mass biodeposits week<sup>-1</sup>.

Nutrient release must also be taken into account before concluding that invertebrate suspension-feeding will act as a control on eutrophication. Mussels and other marine invertebrates release ammonium as an excretory product. Asmus and Asmus (1991) calculated that phytoplankton production stimulated by excretory ammonium from a mussel bed could potentially exceed the uptake of algal biomass by suspension-feeding.

### **3.5. Suspension-Feeding As A Process For Mitigating The Impacts Of Aquaculture**

This concluding section of the chapter will attempt to synthesize the main findings of the review of the literature on suspension-feeding in order to suggest which taxa have the greatest potential for use as biofilters in aquaculture. This will be followed by a brief review of the published literature describing practical studies of the use of suspension-feeders as mitigators of aquaculture impacts.

3.5.1. *Potential of suspension-feeding taxa as mitigating agents*

For a suspension-feeding taxon to have potential as a mitigating agent in aquaculture, the following desirable characteristics can be identified:

1. Active suspension-feeding. Suspension-feeders able to generate their own feeding currents will be largely or entirely independent of external water movement and will be useful in a wider range of aquaculture locations.
2. Sessile or strongly sedentary in habit. Highly mobile animals may not remain on the artificial substratum units intended for deployment in BIOFAQs field studies.
3. Ability to retain and ingest particles in the size range released in aquaculture effluent. It may be necessary to sample and characterize the size range of detrital particles released from fish cages or shellfish rafts. Clearly, suspension-feeding invertebrates are unlikely to be effective at removal of particles in the mm-cm size range (eg. uneaten food pellets or large masses of fish faeces).
4. Ability to survive and grow on a diet of non-living organic detritus (and/or bacteria?). Taxa dependent on living phyto- or zooplankton for food may still play some part in reducing the indirect effects of nutrient release from aquaculture sites, but the ideal aim is to absorb non-living POM directly and circumvent the pathway of bacterial breakdown and conversion into planktonic biomass.
5. High Pumping and Clearance Rates. High rates of water processing and particle uptake will maximize the environmental benefit gained from deployment of biofilters.

The following table summarizes the characteristics of the major taxa of benthic suspension-feeders in relation to features 1 - 4 defined above. This tabulation requires some very broad generalizations, and the overlooking of exceptions that undoubtedly exist. However it does allow some general conclusions to be drawn. For the sake of simplicity, the Active suspension-feeding category covers all taxa able to generate their own feeding currents (ie. it includes the Facultative and Combined active/passive categories defined in Section 2.3). The 'Sedentary' category includes animals which habitually remain in one location or are capable only of very slow movement across the substratum, but which are not permanently attached to their site of larval settlement. Water processing rates are considered later.

Taxon	Suspension-feeding mode	Mode of life	Particle size ingested	Main food source	Ingestion of non-living POM
Hydroids	Passive	Sessile	1-5000 µm*	Zooplankton	Few species
Octocorals	Passive	Sessile	250-350 µm**	Zooplankton	No
Sea anemones	Passive	Sedentary	200-6000 µm***	Zooplankton	No
Crinoids	Passive	Mobile	7-1000 µm****	Zooplankton, phytoplankton, POM	Yes

Brittlestars	Passive	Mobile	80- >500 $\mu\text{m}$ *****	Zooplankton, phytoplankton, POM	Yes
Polychaetes	Active	Sedentary or sessile	Optimal retention at 1-10 $\mu\text{m}$	Phytoplankton, (POM?)	Some species?
Bryozoans	Active	Sessile	5 - 50 $\mu\text{m}$	Phytoplankton	No
Ascidians	Active	Sessile	1 - 100 $\mu\text{m}$	Phytoplankton, bacteria, POM	Yes
Bivalves	Active	Mobile, sedentary or sessile	< 1 $\mu\text{m}$ - ?	Phytoplankton, bacteria, POM	Yes
Barnacles	Active	Sessile	< 2 $\mu\text{m}$ - > 1 mm	Zooplankton, phytoplankton, POM	Yes
Sponges	Active	Sessile	0.1 - 50 $\mu\text{m}$	Microplankton, bacteria, POM	Yes

- \* *Tubularia larynx*
- \*\* *Alcyonium siderium*
- \*\*\* *Metridium senile*
- \*\*\*\* *Antedon bifida*
- \*\*\*\*\* *Ophiothrix fragilis*

It can be seen from the summary table that hydroids, octocorals and sea anemones are likely to be of little use to BIOFAQS owing to their reliance on living zooplankton as food. Shallow-water bryozoans are primarily phytoplankton feeders and have not been recorded ingesting non-living POM. Crinoids and brittlestars may ingest POM but their mobility and reliance on passive suspension-feeding may render them unsuitable for use as biofilters in aquaculture.

The desired combination of active suspension-feeding, sedentary or sessile mode of life and ingestion of non-living POM can be found in some or all species of ascidians, bivalves, barnacles and sponges. Ingestion of POM by suspension-feeding polychaetes does not seem to have been investigated but is likely to occur in some species. The diversity of species in all these groups makes it difficult to summarize their relative suspension-feeding capacity. For the sake of comparison, data are given below for Clearance Rates of species which often occur in temperate water fouling communities. *Nereis diversicolor* is not a typical fouling species but is included as a well-studied example of a mucus-net feeding polychaete. No barnacle example is given, since the appropriate measurements seem not to have been made in this group. The selection of data from studies by Riisgård and co-authors allows for continuity of experimental technique and should maximize the comparability of results. All rates are expressed for a common nominal size of 1 g dry flesh mass.

Taxon	Species	Clearance Rate ml h <sup>-1</sup> , for 1 g dry mass	Source
Polychaeta	<i>Sabella penicillus</i>	13620	Riisgård and Ivarsson, 1990
Polychaeta	<i>Nereis diversicolor</i>	8869	Riisgård, 1991
Asciacea	<i>Ciona intestinalis</i>	7080	Petersen and Riisgård, 1992
Bivalvia	<i>Mytilus edulis</i>	7450	Møhlenberg and Riisgård, 1979
Porifera	<i>Halichondria panicea</i>	1701	Thomassen and Riisgård, 1995

It can be seen that the sponge *Halichondria panicea* has the lowest Clearance Rate, and the polychaete *Sabella penicillus* the highest. Rates for the common fouling species *Ciona intestinalis* and *Mytilus edulis* are virtually identical. High densities of ascidians and mussels are likely to occur in the fouling communities of Scottish sea lochs, and in this geographical setting these groups may have the most potential for use in biofiltration.

### 3.5.2. Published studies of suspension-feeder/aquaculture interactions

There have already been several published studies relating to the use of suspension-feeder aggregations as mitigating agents for aquaculture discharges. Stirling and Okumus (1995) measured the growth rates of mussels (*Mytilus edulis*) in two Scottish sea lochs at sites differing in proximity to salmon cages. Near-cage sites were shown to have higher water column concentrations of chlorophyll a and suspended POM. Mussel shell growth rate was higher at salmon farms than away from them. *In situ* production losses were also lower at salmon farms over the winter, suggesting that mussels at these locations did not deplete their stored reserves to the same extent as those further from the cages. These metabolic advantages indicate that mussels were able to utilize the additional seston resources available at the salmon cage sites, but the proportionate mitigation of cage discharges was not measured. A significant control of eutrophication by bivalve feeding was recorded in a Chilean lake by Soto and Mena (1999). In closed tank systems containing salmon, freshwater mussels (*Diplodon chilensis*) reduced concentrations of chlorophyll a by two orders of magnitude in 18 days, converting a hypereutrophic situation to an oligotrophic one. Further evidence supporting the mitigating potential of mussels was reported by Newell and Richardson (2000), who used a computer model to simulate the complex patterns of water flow around mussels suspended on lines. Depletion of seston by up to 50% was indicated by the model and later recorded in field trials.

In contrast to these generally favourable results, Taylor et al. (1992) found no significant enhancement of mussel growth by proximity to salmon cages. Growth of cultured mussels was not significantly correlated with distance from the farms, and there was no evidence of any contribution to mussel nutrition either directly via fish feed or faeces, or indirectly via stimulation of phytoplankton growth. Troell and Norberg (1998) modelled the output and retention of suspended solids in an integrated salmon-mussel culture. They concluded that mussel suspension-feeding is unlikely to exert a significant sustained control on aquaculture effluent discharges. The episodic addition of fish feed led to a large increase in water column seston load, but particle retention by mussels was limited by the threshold level required to induce pseudofaeces production. It was concluded that naturally-occurring seston concentration is the key factor controlling mussel growth, and that increased suspended solids from fish cages may contribute significantly to nutrition only during periods of low plankton productivity.



These conflicting results indicate a need for modelling simulations with all input and output terms accurately-budgeted and based on realistic biological data. Bodvin et al. (1996) have attempted to construct such a model for a remediated multi-species aquaculture system. Using data from the literature, and from field and laboratory tests, they estimated that a standing stock of 300 metric tonnes (MT) salmon would require 112.5 MT mussels to absorb particulate nitrogen and phosphorus, and 45 MT seaweed to bind the dissolved nitrogen and phosphorus produced by the salmon and mussels.

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## Chapter 4

### A review of biofouling on artificial substrates

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#### 4.1 Biofouling

'Biofouling' is commonly used to distinguish the assemblages of animals and plants that grow on artificial structures from those occurring on natural objects (i.e. rocks, stones, etc.). In general these organisms are inter-tidal and sub-littoral species that are commonly observed on most rocky shorelines. These species exhibit certain characteristics that enable them to readily colonise artificial structures either deployed on the sea floor or suspended in the water column. These characteristics are; a free-swimming larval phase, a sedentary adult form that can firmly adhere to the substratum and an ability to extract dissolved nutrients and/ or particulate material from the water column. Examples include; barnacles, bivalves, hydroids, polychaetes (sedentary), bryozoans, anemones, tunicates, diatoms, green, brown and red algae. In addition, many non-sessile animals are able to colonise artificial structures and typically reside within the sessile biofouling community. These animals include; echinoderms, isopods, amphipods, errant polychaetes, crabs, shrimps and pycnogonids (sea spiders) (Claereboudt et al., 1994; Cook, 1999).

Over 2000 species of fouling organisms are thought to exist on the surfaces of artificial structures, including 50 species of bacteria, 110 species of diatom, 450 species of algae and 1900 species of other animals (Hutchins, 1952). In the aquaculture industry, research has mainly concentrated on investigating methods of controlling biofouling, particularly bacterial, diatom and algal fouling on artificial structures (Dempsey, 1981a; Dempsey, 1981b; Hodson and Burke, 1994; Milne and Powell, 1967), as marine fouling can reduce water flow, thus decreasing the oxygen supply to the cages and increase the retention of uneaten food and waste products (Blair, Campbell and Grant, 1982). Little is known, however, on the succession of biofouling communities on artificial structures associated with caged fish culture.

Long term studies on artificial reefs have observed that these structures follow a pattern of colonisation and succession associated with natural objects. This colonisation commences with the attachment of pioneer species, such as bacteria, diatoms, hydroids and serpulids in the first few months of immersion (Jensen et al., 1994). This initial stage is followed by a decline in species richness and diversity as one or two species, such as mussels or barnacles out compete the pioneer species for space on the surface of the artificial structure (Ardizzone, Gravina and Belluscio, 1989; Bombace et al., 1994; Chojnacki, Ceronik and Perkowski, 1993). Finally, after 5 – 10 years of immersion, species diversity and richness increases, as the dominant species become overgrown and a climax community is reached, characterised by polychaetes, crustaceans, bryozoans (Ardizzone, Somaschini and Belluscio, 1996) bivalves, sponges, anemones and echinoderms (Ponti, Abbiati and Ceccherelli, 1999) and kelps (Forteach et al., 1982). The pattern of succession on artificial reefs, however, can be influenced by variations in physico-chemical and biological factors over a localised and geographical scale. Studies on the environmental impact of caged fish culture have shown that this activity can affect the hydrography, the level of dissolved and particulate material in the water column and as a consequence the turbidity of the water in the vicinity of the cages (Pearson and Black, 2001). It is



possible, therefore, that the succession of biofouling communities on artificial structures placed in the close vicinity of caged fish culture could be significantly influenced by this activity. There have been no studies to date, however, that have observed the effects of variations in physico-chemical and biological parameters on biofouling on artificial structures association with caged fish culture.

#### *4.2.1 Physical Parameters*

Studies on artificial structures in European waters have found that variations in light exposure, sediment deposition (Badalamenti et al., 1985; Laihonon et al., 1996), depth (Hanson and Bell, 1976; Leighton, 1979; MacDonald and Bourne, 1989; Wallace and Reinsnes, 1985), hydrography (Baynes and Szmant, 1989; Riggio et al., 1986), salinity (Bombace et al., 1994) and wave action [Katoh, 1980] can influence the pattern of succession of biofouling communities.

##### *Light Intensity*

The majority of the artificial structures associated with caged fish culture are located in the photic zone (approx. depth – 9 m; C.J. Crome, personal communication). Studies on artificial reefs (Riggio, 1989; Spanier, Kress and Tom, 1999) and submerged structures on oil platforms (Forteath et al., 1982) located in this zone have found that these structures are typically dominated by macroalgae. As the light intensity is reduced, either by increasing depth or water turbidity a reduction in algal coverage is observed (Laihonon et al., 1996). This was highlighted by studies on the Loano Artificial Reef (Fig. 1F) where the algal coverage on atoxic panels suspended in the water columns was found to decrease with depth (Relini and Cormagi, 1989b; Relini, Torchia and Relini, 1994). The maximum algal coverage was at a depth of – 5 m. In addition, studies in the Adriatic and Baltic Seas have found that the photic zone can be significantly reduced on a localised scale by eutrophication, where the high turbidity of the water can restrict the photosynthetically active layer to the uppermost portion of the water layer. In the Adriatic Sea the high turbidity is attributed to the efficient water exchange in the coastal regions in the northern and central basin caused by the shallow nature of the basin and heavy river runoff (Cruzado, 1985) leading to elevated levels of phytoplankton and suspended particulate material. Similarly, the Baltic Sea has severe eutrophication problems due to the high levels of nutrients that enter the Sea from the adjacent land masses (Laihonon et al., 1996). In severe cases of eutrophication, the associated high turbidity can even lead to the complete absence of macroalgae from benthic communities (Badalamenti et al., 1992). Certain fouling species, however, prefer surfaces with a reduced exposure to light (Spanier et al., 1999) and would favour conditions of high turbidity. These species are typically associated with caves and crevices and include; madreporarians, demosponges, bryozoans, encrusting algae, barnacles and serpulids (Ardizzone et al., 1996; Riggio, 1989).

On a European scale, the light intensity and consequently the photic zone can vary significantly dependant on the latitude of the water mass. Artificial structures, therefore, placed in U.K. waters would be colonised by green algae at depths of between 0 – 5 m (Forteath et al., 1982) and red algae between -10 m to -12 m depth (Collins et al., 1999; Jensen et al., 1994), whereas in the Mediterranean Sea, where the photic zone extends to greater depths in the water column, small filamentous green algae can be observed on artificial reefs at depths of - 18.5 m (Spanier et al., 1999) and –20 m to –30 m (Moreno et al., 1994).

##### *Sedimentation*

Particulate waste products associated with caged fish culture can include, uneaten processed fish meal, trash fish and fish faeces (Black, 1998). A study using sediment traps under cages at Scottish fish farms determined particulate sedimentation rates ranging between 11 – 33 g solids



$\text{m}^{-2} \text{ day}^{-1}$  (T.D. Nickell, personal communication). In comparison, a study on the sedimentation rates near long-sea sewage outfalls around the British coast found that a rate of  $<1 \text{ g C m}^{-2} \text{ day}^{-1}$  was typical for these outfalls and this was attributed mainly to their exposed, dispersive locations (Cromey et al., 1998). The deposition of particulate material, combined with an increased turbidity has been found to significantly influence the succession of biofouling communities. Horizontal surfaces, in particular, exhibiting a lower species diversity (Loya, 1972; Loya, 1976; Loya and Slobodkin, 1971; Riggio et al., 1985; Roy and Smith, 1971) and a greater dominance of detritivores and sediment dwelling organisms (Riggio et al., 1986) than vertical surfaces on these reefs. A study on the Fregene artificial reef (Fig. 1H) also attributed the decline in filter feeders, predominately mussels and barnacles and increase in deposit-feeders and carnivores, to the high sedimentation rates which smothered byssal filaments and impeded mussel valves (Ardizzone et al., 1989). Reduced colonisation, growth and maturation of infra-circa littoral populations in the Gulf of Trieste compared to the Mediterranean was also attributed predominantly to intense sedimentation and reduced water transparency (Falace and Bressan, 1996 b; Falace and Bressan, 1996a).

### *Depth*

Seabed depth under caged farm culture varies considerably between sites, however, moorings have been known to extend to a depth of approximately - 50 m beneath cages on the west coast of Scotland (C. J. Cromey, personal communication). Depth has been found to influence the total biomass of fouling organisms (Claerebout et al., 1994; Hanson and Bell, 1976; Leighton, 1979; MacDonald and Bourne, 1989; Wallace and Reinsnes, 1985) and the distribution of certain taxa (Ardizzone and Bombace, 1983). (Claerebout et al., 1994) attributed the reduction in total biomass with increasing depth to a temperature-driven stratification in the water column, a reduction in food abundance and a decline in larval settlement rates with depth. Certain species, however, tend to favour a specific depth range for settlement. For example, studies throughout Europe have found that mussels typically dominate artificial structures deployed in depths of up to - 15 m (Ardizzone et al., 1989; Bombace et al., 1994; Chojnacki et al., 1993; Laihonon et al., 1996; Ponti et al., 1999; Sell, 1992). At depths exceeding - 15 m, fouling communities recorded on the platforms in the North Sea (Forteath et al., 1982; Sell, 1992) and on artificial reefs in the Mediterranean Sea (Moreno et al., 1994; Relini and Cormagi, 1989a) tend to be dominated with organisms, such as bryozoans, serpulids, hydroids and barnacles. Oysters, tunicates and sponges have also been observed to colonise artificial reefs at these depths in the Mediterranean Sea (Moreno et al., 1994; Ponti et al., 1999; Relini et al., 1986; Relini and Relini, 1989).

### *Hydrography*

Cage structures are often located in sheltered environments, thus protecting staff and equipment (Black, 1998). The hydrographic conditions, however, can vary considerably on a local immediate environment through to a regional and European level. In the immediate environment, the current speed can typically be reduced by 25 % on transmission through a 12 – 18 mm clean net. Current speed can, therefore, be substantially reduced through a series of such nets in a cage array, particularly if the nets are fouled or have fine mesh sizes (Black, 1998). On a European level, the Mediterranean Sea, for example, due to its restricted nature, has an insignificant tidal range and currents compared to coastal sites in the North West Atlantic (Pearson and Black, 2001). Water movement, however, is essential in caged fish culture, for the supply of oxygen to the cages and in the removal of waste products (Black, 1998). Similarly, sessile benthic fauna benefit from elevated water movement, in terms of enhanced supply of oxygen/ nutrients and the removal of dissolved and suspended material, favourable conditions for larval settlement (Crisp, 1955) and lower sedimentation rates (Baynes and Szmant, 1989). Studies have shown that current and tidal regimes can influence the colonisation and succession of biofouling communities on artificial structures (Baynes and Szmant, 1989; Riggio et al., 1986).

(Angel and Spanier, 1999) observed that tunicates were distributed primarily on the outermost surfaces of artificial reefs in Eilat (Fig. 10) and this was attributed to the elevated flux of particulate matter and dissolved oxygen experienced by these regions compared to the inner regions of the reef.

### *Salinity*

The salinity of seawater is remarkably constant and caged fish culture is typically located in areas subject to only minor fluctuations in salinity (C.J. Cromey, personal communication). Surface waters adjacent to freshwater discharge and semi-enclosed areas such as the Red Sea, where evaporation can exceed the precipitation rate (Barnes and Hughes, 1992) can experience larger fluctuations in their salinity. It has been suggested that salinity can influence the succession of biofouling communities. (Bombace et al., 1994) attributed a decline in the mussel *Mytilus galloprovincialis* population on an artificial reef in the Adriatic Sea, to the freshwater discharge from a river adjacent to the reef site. (Laihonen et al., 1996) also observed an absence of certain species of filamentous algae in the Baltic Sea and attributed this to low salinity levels caused by a large freshwater input to this area.

### *4.2.2 Biological Parameters*

Studies have identified predation (Day, 1977; Hixon and Brostoff, 1983), food availability (Badalamenti et al., 1992; Bombace, 1989) and inter- and intra-species competition (Bombace et al., 1994) as biological parameters that can influence the succession of biofouling communities on artificial structures.

### *Predation*

The main predators associated with caged fish culture are various species of wild fish. These predators are attracted by food, either directly or indirectly through an increase in algal and zooplankton biomass and by the provision of a refuge by the cage structures (Black, 1998). Little is known about the fish populations around marine cages. (Carss, 1990), however, found that wild fish may congregate in large numbers around Atlantic salmon cages in Scottish sea lochs. Similarly, large aggregations of wild and escaped fish have been observed around cages in Greece (K.D. Black, personal communication). Grazing by predators can significantly influence succession in biofouling communities. Sea urchins and fish are generally regarded as the main grazing organisms on artificial structures and their grazing activity can promote the growth of calcified organisms and filamentous algae (Day, 1977; Hixon and Brostoff, 1983). There are no studies, however, on the influence of predation on the structure of biofouling communities on artificial structures associated with caged fish culture in European waters.

### *Food Availability*

Caged fish culture releases dissolved components and particulate material directly into the water column. The dissolved components include: ammonia, phosphorus, silicates and dissolved organic carbon (DOC), that contains fractions rich in nitrogen (DON) and phosphorus (DOP). The particulate material can consist of uneaten processed fish feed, trash fish and fish faeces. Both the dissolved and particulate components are released in a highly biologically active form and the effects of the particulate material on the benthic environment have been well established (Brown, Gowen and McLusky, 1987; Findlay, Watling and Mayer, 1995; Weston, 1990). Less information is available on the effects of the dissolved components on the immediate environment because of the speed at which these nutrients are typically diluted (Pearson and Black, 2001). A recent study in the Mediterranean Sea, however, reported elevated concentrations of phosphate and ammonium near three fish farms (Pitta et al., 1998). Nutrient enrichment of the water column by fishpond effluents has been found to stimulate the growth of the macroalgae, *Ulva lactuca* (Neori, Cohen and Gordin, 1991). It has also been suggested that

the organic loading of the water column will also influence the diversity and growth of biofouling communities, as eutrophic produce very different communities than oligotrophic waters (Bombace, 1989). For example, a dominance of vagile and sessile organisms and a very high production of filter feeders, such as mussels and oysters have been described on the artificial reefs in the eutrophic waters of the Adriatic Sea (Badalamenti et al., 1992).

#### *Competition*

Little is known about inter- and intra species competition between fouling organisms on artificial structures associated with caged fish culture. Aggressive species, such as mussels, tube worms and barnacles have been seen to out compete other less dominate species on moorings and structures associated with the shellfish farming industry in Scotland (E.J.Cook, personal observation) and Northern Ireland (Minchin and Duggan, 1989). Similarly, studies on the Fregene (Fig. 1H), Ancona (Fig. 1L) and Polmerian (Fig. 1P) artificial reefs, have observed the progressive dominance of mussels over the less aggressive pioneer species that initially colonised the reefs (Ardizzone et al., 1989; Bombace et al., 1994; Chojnacki et al., 1993).

### **4.3 Distribution of Biofouling in European Waters**

Studies of biofouling communities in European Waters have concentrated on the colonisation patterns of structures, such as artificial reefs and submerged surfaces on oil platforms. Little information is available on the biofouling communities of aquaculture related structures. The following section, provides a review of the literature available on biofouling communities colonising artificial structures in the North East Atlantic, the North Sea, the Mediterranean Sea, the Red Sea and the Baltic Sea (Figure 1).

#### *4.3.1 United Kingdom*

##### *Poole Bay Artificial Reef, Southern U.K. (Fig. 1A)*

The Poole Bay Artificial Reef consists of concrete blocks deployed at a depth of -10 m below chart datum in conical reef units. Calcareous tube worms, *Pomatoceros triqueter*, ascidians, *Ascidia mentula*, *Botryllus schlosseri* and didemnid species and an indistinct ‘turf’ consisting of hydroids and bryozoans were observed to colonise the blocks in the first few months of immersion. Algae, principally rhodophyte species, such as *Calliblepharis ciliata* and *brongniartella byssoides* later colonised the reef. In the two years following immersion, seasonal fluctuations in the numbers of hydroids, *Aglaophenia* sp. and *Plumularia setacea*, bryozoans, *Bugula plumose*, *Bicellariella ciliata* and *Eschariodes* sp., ascidians, *Aplidium* sp. and barnacles, *Balanus* sp. were recorded. Encrusting sponges, *Dysidea fragilis* and *Amphilectus fucorum* and isolated specimens of anthozoa including *Anemonia viridis*, *Cereus pedunculatus*, *Sagartia troglodytes* and *Urticina felina* were observed on the reef after 2 years (Jensen et al., 1994).

##### *Poole Bay Artificial Tyre Reef, Southern U.K. (Fig. 1A)*

The Poole Bay Artificial Tyre Reef consists of 500 scrap tyres deployed at a depth of -12 m. Algae (red and brown) and hydroids *Halecium* sp. were predominant on all the upper surfaces and bryozoans (including *Bugula flabellata*) were dominant on the vertical surfaces one year after immersion. Ascidians, including *Styella clava* and *Asciidiella aspersa*, tube worms, barnacles and sponges were also recorded on the horizontal surfaces of the blocks but occurred at much lower frequencies (Collins et al., 1999).

*Mulroy Bay, North Ireland (Fig. 1B)*

Moorings and structures suspended in the water column (depth unknown) and used for shellfish cultivation in Mulroy Bay were fouled by the mussel *Mytilus edulis* (Minchin and Duggan, 1989). Barnacle and tube-worm fouling (species unknown) has also been reported by oyster farmers on the north-west coast of Ireland (Minchin and Duggan, 1989).

*Loch Fyne/ Lynne of Lorne, West Scotland (Fig. 1C)*

On the west coast of Scotland, the solitary tunicate, *Ciona intestinalis* and the tube worm, *Spirobis borealis* were the dominant fouling organisms on experimental panels held at -10 m and deployed for 5 months in Loch Fyne (Cook, 1999). Dense aggregations of the mussel, *Mytilus edulis* and sea urchin, *Psammechius miliaris* have also been observed on the nets of submerged fish farm cages in the Lynne of Lorne (E.J. Cook, personal observation).

*Montrose Alpha Oil Platform, North East U.K. (Fig. 1D)*

The Montrose Alpha oil platform was installed in 1975 and detailed examination of the marine fouling on the jacket has been conducted since 1977. In the depth range Mean Low Water (M.L.W.) to - 10 m, a dense community of seaweeds covered the outer surfaces of vertical structures and the upper surfaces of horizontal structures. The sea-lettuce *Ulva lactuca* and the filamentous green alga *Enteromorpha intestinalis* covered the majority of the substrate between M.L.W. and - 1.5 m, whereas the red alga *Polysiphonia urceolata* and *P. brodiaei* dominated the fouling community between - 6 m and - 10 m. The kelps *Laminaria hyperborea*, *L. digitata* and *Alaria esculenta* were present in small groups. Hydroids, particularly *Obelia dichotoma* and *Bougainvillia ramose* and the mussel *Mytilus edulis* were also observed amongst the seaweeds. On the inner and lower surfaces of the structure, the profuse cover of seaweeds was entirely replaced by hydroids and bryozoans. Below - 10 m to a depth of - 31 m, the community structure changed significantly and the dominant organism was the bryozoan *Electra pilosa*. The hydroids *Obelia dichotoma*, *Laomedea flexuosa* and *Bougainvillia ramose* and the arborescent bryozoans *Bicellariella ciliata* and *Bugula avicularia* were also common in this depth range (Forteath et al., 1982).

*Claymore A Oil Platform, North Sea, NW U.K. (Fig. 1E)*

The Claymore A oil platform was installed in 1989. Examination of the fouling community (Sell, 1992) has observed that the dominant species from M.L.W to - 20 m were mussels *Mytilus edulis*, soft corals *Alcyonium digitatum*, seaweeds and hydroids. In particular, the mussels tended to completely dominate the structure between - 7 m to - 15 m, unlike the Montrose Alpha platform. At depths greater than - 20 m, the plumose anemone *Metridium senile*, hydroids, the solitary tubeworm *Pomatoceros triqueter* and the barnacle, mainly *Balanus crenatus* dominated the fouling community.

#### 4.3.2 Mediterranean Sea

*Loano Artificial Reef, Ligurian Sea, NW Mediterranean (Fig. 1F)*

The Loano Artificial Reef consists of large concrete blocks arranged in pyramids and single small concrete blocks at a depth range of - 5 m to - 45 m. The main reef is situated between a depth of - 18 m and - 24 m (Relini and Cormagi, 1989a). The development of sessile macrobenthos communities on atoxic panels and concrete blocks at this site was studied in detail (Relini et al., 1994). On the panels, it was observed that the dominant encrusting species after 1 year were bryozoans, serpulids, hydroids, barnacles, ascidians, bivalves and algae (also Corallinaceae). On the reef blocks, colonial bryozoans, algae, barnacles, serpulids and bivalves are all present at the end of the first year of immersion. Mussels were never dominant at this reef site. After 2 years, photophyle algae, in particular *Dictyota*, bryozoans, such as *Schizoporella* and serpulids,

*Salmacina*, *Serpula* and *Pomatoceros* were observed. After 4 years, the upper horizontal surfaces of the blocks became colonised by the large brown alga, *Sargassum vulgare* Agardh, *Dictyota dichotoma*, *Cystoseira* spp., *Dictyopteris membranacea* and *Padina pavonica* (Relini et al., 1994). In addition, a detailed study of the algal flora on the Loano reef in 1994/ 5 was conducted by (Falace and Bressan, 1999).

*Marconi Gulf Artificial Reef, Ligurian Sea, NW Mediterranean* (Fig. 1G)

The Marconi Gulf Artificial Reef consisted of barges, dock-gates and reinforced blocks of concrete. It was deployed between 1980 and 1984 and the majority of the hard substrate suitable for settlement is located between – 25 m and - 45 m. Newly immersed structures, at depths greater than - 15 m were rapidly colonised by pioneer species such as serpulids and bryozoans. The dominant organisms on the reef were oysters and erect species, including sponges, soft corals, *Alcyonium palmatum*, ascidians, *Phallusia mamillata* and *Ascidia mentula*, calcareous tube worms, *Spirographis spallanzanii* and *Filograna* sp. and the gorgonian, *Lophogorgia sarmentosa* (Relini et al., 1986; Relini and Relini, 1989). In contrast with the Fregene (Fig. 1H) and Ancona (Fig. 1L) artificial reefs, mussels were absent and this difference was attributed to the depth of the Marconi Gulf reef (Ardizzone and Bombace, 1983).

*Fregene Artificial Reef, Central Tyrrhenian Sea* (Fig. 1H)

The Fregene Artificial Reef is constructed from concrete blocks and is located at a depth of – 12 m to - 14 m. The benthic colonisation has been studied over an 11 year period and four main developmental stages have been observed. In the first year of immersion, the reef community was dominated by pioneer species, including diatoms, hydroids, *Obelia dichotoma* and *Bouganvillia ramosa*, serpulids, *Pomatoceros lamarkii*, *P. triqueter* and *Hydroides pseuduncinata* and barnacles, *Balanus perforatus* and *B. eburneus*. Settlement of juvenile mussels, *Mytilus galloprovincialis* also occurred. In the second and third years, the reef was dominated by mussels and barnacles and species richness and diversity decreased. After 3 years, the community structure began to change, as the entrapment of sediment particles and mussel pseudofaeces between the byssus filaments and numerous mussel valves reduced the number of filter-feeders and lead to an increase in species diversity and richness. After 4 years, the mussel beds had disappeared and the reef community was dominated by deposit-feeders and carnivores (Ardizzone et al., 1989). After 10 years, the community had reached a 'Climax type' steady state and was characterised by polychaetes, crustaceans and bryozoans. Throughout the study period there was a notable absence of macroalgae and this was attributed to the considerable turbidity of the water (Ardizzone et al., 1996).

*Terrasini Artificial Reef, NW Sicily* (Fig. 1I)

The Terrasini Artificial Reef consists of 2 pyramids (Height approx. 4.2 m) constructed from large cubic concrete blocks, at a depth of approximately -18 m. Sequential surveys of the reef following immersion in 1981 observed (Badalamenti et al., 1985; Riggio et al., 1986; Riggio et al., 1985) that the early stages of colonisation were dominated by tube-dwelling Serpulids, gastropods, particularly Rissoacea and encrusting Bryozoa. This was followed by an increase in the taxonomic composition and abundance of polychaetes and the proportion of carnivorous and deposit feeding species on the reef. The gastropods, *Bittium latreilli* and *B. jadertinum* were the most abundant molluscs on the reef and the bivalves, including *Spondylus gaederopus*, *Pseudochama gryphina*, *Arca noae* and *Lima lima* increased in abundance over the three years following immersion. The reef also supported a luxuriant algal growth, which consisted of algal turfs and a dominance of the brown alga *Cystoseira compressa*, particularly on the horizontal surfaces of the upper layer of the reef. *Cystoseira saugeauana* was found on the vertical walls of the lower layers (Riggio et al., 1986). The red alga, *Lophocladia lallemandii*, *Halopteris filicina* and *Jania rubens* were found on the outermost exposed surfaces on the reef after one year



of submergence (Badalamenti et al., 1985). A complete absence of the Ascidiacea and Echinoderms was noted (Riggio et al., 1986). This succession is in distinct contrast to the artificial reefs in the Adriatic Sea (Bombace 1981; 1983 and Bombace et al., 1994) and the Central Tyrrhenian Sea (Ardizzone et al., 1982, 1989) where filter-feeders quickly dominated the biofouling community.

*Alcamo Marina Artificial Reef, NW Sicily (Fig. 1J)*

The Alcamo Marina Artificial Reef consists of 32 pyramids, each consisting of 14 concrete blocks and deployed at depths of – 5 m to – 50 m. Initial colonisation of the reef was by serpulid polychaetes, encrusting and erect bryozoans and ostreid bivalves. The oyster *Ostrea edulis* dominated the upper boulders in each pyramid. Over the following years, the most illuminated surfaces became colonised by seaweeds and the remainder of the reef became dominated by active and passive filter feeders (Riggio, 1989).

*Balearic Artificial Reef, Western Mediterranean (Fig. 1K)*

This reef consists of concrete “boulders” and was deployed between depths of – 20 m and – 30 m. The initial colonisation of the boulders was by small filamentous algae of the group ectocarpal feoficea, hydroids, *Clytia hemisphaerica*, *C. linearis* and *Obelia dichotoma*, bryozoans, *Aetea truncata*, serpulid polychaetes and sponges such as the *Calcarea Grantia* and *Sycon*. After 14 months of submersion, algal, hydroid and bryozoan diversity and serpulid numbers increased and at 18 months the dominant organisms were typically species that formed encrusting and laminar colonies such as the bryozoan, *Calpensia*, tunicate, *Diademnum* and sponges, *Demospongia Spirastrella cuncatrix* and *Hemimycale columella* (Moreno et al., 1994).

*Ancona Artificial Reefs, Northern Adriatic Sea (Fig. 1L)*

Five artificial reefs were constructed along the Italian Adriatic coast from Ancona northwards to the Po River. The reefs consisted of concrete blocks arranged in pyramids at depths of between – 10 m and –14 m. The reefs were initially colonised by hydroids, bryozoans and serpulid polychaetes, however, after a few months of submersion the mussel *Mytilus galloprovincialis* dominated the majority of the reefs and the oysters, *Ostrea edulis* and *Crassostrea gigas* were typically found at lower densities on the base blocks. In contrast, the most northern reef remained dominated by serpulids, *Pomatoceros triqueter* and *Serpula vermicularis*, ascidians, actinias and a few bivalves, *Hiatella arctica*, *Anomia ephippium*, *Chlamys varia* and juveniles of *Aequipecten opercularis* and *Scapharca* cf. *inaequivalvis*. The low proportion of mussels at this site was attributed to the large freshwater inflow from the Po River (Bombace et al., 1994).

*“Paguro” Drilling Platform, Northern Adriatic Sea (Fig. 1M)*

The “Paguro” drilling platform sank in 1965 and is located in a water depth of – 10 m to – 34 m. A recent visual survey of the platform found that the mussel *Mytilus galloprovincialis* dominated surfaces between 8 m and 13 m, whereas below this depth the oysters *Crassostrea gigas* and *Ostrea edulis* became the dominant species. Encrusting sponges, including *Laxosuberites rugosus* and large colonies of the encrusting coral, *Epizoanthus arenaceus* were also present amongst the oyster-beds. In addition, hydroids, anemones, molluscs, including the bivalve *Hiatella arctica*, polychaetes, including *Syllis gracilis*, *Ceratonereis costae*, *Pomatoceros triqueter* and *Serpula vermicularis*, crustaceans, including the barnacles *Verruca stroemia* and *Balanus trigonus* and the amphipod *Corophium sextonae*, echinoderms, including *Marthasterias glacialis*, *Echinus acutus*, *Cucumaria palnci* and *Ophiothrix fragilis* also colonised the wreck (Ponti et al., 1999).



#### *Haifa Artificial Reef, SE Mediterranean (Fig. 1N)*

Concrete blocks were deployed at a depth of 18.5 m off the coast of Haifa, Israel. Sub-samples of these blocks were studied every 3 - 4 months for their biotic coverage. The concrete blocks were slow to colonise with very low levels of fouling observed in the first 3 months. A diverse sessile community, however, did develop on the reef over the following 30 months and the dominant fouling organisms on the blocks were: bryozoa of the genera, *Schizoporella*, *Celleporaria*, *Thalamoporella*, *Electra* and *Beania*, followed by barnacles of the species, *Balanus trigonus*, *B. amphitrite* and *B. perforatus*. Other sessile marine taxa recorded on the blocks were filamentous green algae, *Entromorpha* sp., serpulid worms of the species, *Pomatoceros triqueter*, *Serpula ancharum*, *Hydroides uncinata* and *Spirorbis* sp., the hydroid *Aglaophenia pluma* and the bivalves *Pinctada radiata* and *Spondylus spinosus* (Spanier et al., 1999).

#### 4.3.3 Red Sea

##### *Eilat Artificial Reefs, Gulf of Aquaba (Fig. 1O)*

Two artificial reefs consisting of cylinders, composed of high-density polyethylene fence material were deployed in April 1999 at a depth of - 20 m on the seafloor off the coast of Eilat. The reefs were quickly colonised by solitary tunicates and bryozoans. Five months after deployment, however, the tunicate populations were seen to crash and the population density was significantly reduced. Other macro-invertebrates recorded on the reefs were sea urchins, anemones, crinoids, sponges, bivalves, gastropods, tube-building polychaetes and crustaceans, including barnacles (Angel and Spanier, 1999). In an earlier study off the coast of Eilat, (Goren, 1979) suspended asbestos plates in the water column at a depth of approximately - 20 cm for one year. The study found that at this depth the dominant species throughout the study period were the tube-dwelling polychaetes, *Filograna implexa* and *Spirorbis* sp. Other species, such as; the corals *Boloceroides* sp. and *Aiptasia* sp., the barnacle *Balanus amphitrite*, the crustacean *Leptochelia savignyi*, the bryozoans *Bugula neritina*, *Celleporaria* sp. and *Crisia elongata*, the bivalves *Ostrea* sp. and *Placunanomia* sp. and the tunicate *Styela canopus* were also abundant on the plates at certain stages of the community succession. Artificial reefs consisting of limestone rocks have also been placed at a depth of - 15 m off the coast of Eilat and a four year study has been conducted to observe fish and invertebrate recruitment. Detailed information, however, on the individual species recorded on the reefs has yet to be published (Abelson and Shlesinger, 1999).

#### 4.3.4 Baltic Sea

##### *Polmerian Bay Artificial Reefs, Southern Baltic (Fig. 1P)*

The reefs consisted of concrete pipes, situated between depths of - 9 m and - 12 m. The dominant species colonising the reefs were mussels *Mytilus edulis* and barnacles *Balanus improvisus* (Chojnacki et al., 1993).

##### *Puck Bay Artificial Reef, Southern Baltic (Fig. 1Q)*

The reefs consisted of net materials and are situated at an unspecified depth. The dominant reef species were mussels and barnacles, as in Polmerian Bay, with the addition of the blue-green algae, *Pilayella littoralis* (Szatybelko and Matulaniec, 1994).

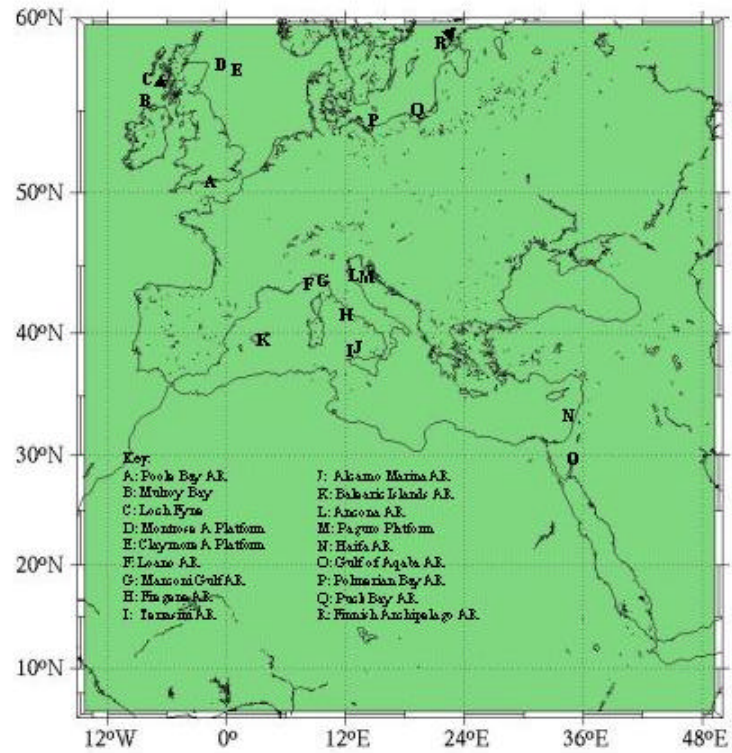
##### *Finnish Archipelago Artificial Reefs, Northern Baltic (Fig. 1R)*

Floating artificial reefs were constructed of PVC ropes attached to an aluminium frame and deployed at a depth of - 15 m. The dominant reef species after six months immersion were barnacles *Balanus improvisus*. The mussel *Mytilus edulis* and the bryozoan, *Electra crustulenta* were also abundant on the reef and Chironomidae, Amphipoda and the hydroid, *Obelia loveni* were present in small numbers (Laihonen et al., 1996).

#### 4.4 Summary

A number of studies have observed the impact of caged fish culture on benthic community in the local environment (Brown et al., 1987; Duplisea and Hargrave, 1996; Findlay et al., 1995; Weston, 1990). However, the influence of the aquaculture industry on the biofouling community of artificial structures, either deployed on the seabed or suspended in the water column has received little attention. It is clear from the literature available on biofouling that the increased levels of particulate material and elevated levels of ammonia, phosphorous and dissolved organic carbon (DOC) and the less dynamic hydrographic conditions (i.e. areas of restricted exchange) typically associated with caged fish culture will have an influence on the colonisation of artificial structures placed in close proximity to fin-fish cages by biofouling organisms. If biofouling communities are to be successful, therefore, in reducing the environmental impact of caged fish culture, the position of the artificial structure, in relation to light intensity, sedimentation levels, depth, hydrography, salinity and nutrient availability must be carefully considered in order to maximise the efficiency of the 'bio-filter' in extracting particulate and dissolved nutrients from the water column.

FIGURE 1: Map of studies of biofouling communities on artificial structures throughout Europe



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## Chapter 5

# Synthesis of the Literature Review on Biofiltration and Aquaculture

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### 5.1 Existing attempts to mitigate nutrient inputs of aquaculture through bio-filtration

#### 5.1.1 Artificial reefs as biofilters

Antsulevich, et al. (2000) describe artificial reef studies using panels and buoys in the Gulf of Finland to determine whether the growth capacities of fouling communities in the northern Baltic Sea was high enough to capture significant amounts of nutrients released by fish farms. Green algae, *Enteromorpha intestinalis*, reached a biomass of  $2\text{ kg m}^{-2}$  on the artificial substrates. They calculate that removal of 500 tonnes algae is equivalent to the removal of 500-4000 kg nitrogen and 50-100 kg phosphorus from the water body. However the overall conclusion was that in Finnish waters reefs fouled with algae would not remove sufficient nutrients to be of practical use. Faunal species which could assimilate particulate matter as well as nutrients included:

Colonial hydroids( including *Cordylophora caspia* and *Gonothyraea loveni*) reach a biomass of  $0.3\text{-}0.4\text{ kg m}^{-2}$  within 2 months on fresh surfaces  
Barnacles, *Balanus improvisus*, reached a density of  $1.3\text{ kg m}^{-2}$ .  
Zebra mussel, *Dreissena polymorpha*, 5100 individuals m

Chojnacki (2000) deployed concrete pipe artificial reefs in the Southern Baltic (Pomeranian Bay), recording very high initial colonisation rates, up to 400,000 individuals  $\text{m}^{-2}$ , mainly juvenile *Mytilus edulis* and *Balanus improvisus*. A climax community was achieved within 2 years dominated by these filtering organisms leading the author to suggest that such artificial reefs could contribute to a increase in water quality as well as support fisheries.

In order to understand the functioning of a reef, artificial or natural, as an ecological system its living components must be considered in relation to the surrounding environment. Harmelin and Bellan-Santini (1997) identified at least three reef-interacting biotic compartments: (1) sessile communities (algae and invertebrates); (2) small mobile epifauna; and (3) large mobile epifauna (fish and invertebrates). In the first case biomass is a useful indicator of the relative significance of these groups. Fish numbers (and indirectly biomass) around artificial reefs have been widely studied (e.g. Buckley and Hueckel, 1989; Charbonnel et al., 1997). Mobile invertebrates have been studied to a much lesser extent, with the majority of work related to commercially valuable species such as the lobster (Smith et al., 1998). Moreno (1997) has reviewed the techniques for monitoring epibiotic colonisation. Sessile biomass has been determined by removing small tiles or blocks (Relini et al., 1994) or scraping known areas *in situ*.

Ecological modelling of systems requires a knowledge of the rates of energy flow (Grodzinski et al., 1975; Fasham, 1984). Thus as well as biomass its rate of growth or turnover should be determined. The growth rate of reef epibiota rate could be determined by measuring change in biomass per unit area, with time. This is likely to underestimate the true growth rate since this

cannot account for loss by predation or other means. For a number of benthic infauna species the annual production per unit biomass has been calculated (Schwinghamer et al., 1986). Enclosed chamber (respirometer) experiments have a long history in examining the respiratory exchange and thus the energy utilization of animals (Morrison and West, 1975). Sediment community oxygen consumption is (SCOC) using respirometers is used to study benthic processes in inshore and deep seas (Smith et al., 1994). Light and dark bottle incubation are routinely used to determine the rates of respiration and production of water column plankton (Strickland & Parsons, 1968). Chamber incubation has been applied to the study of single species of algae (Guterstam, 1977; Chisholm and Jaubert, 1997), corals (Yap et al., 1995; Rex et al., 1995) and sponges (Cheshire et al., 1996a). Cheshire et al. (1996b) have also studied photosynthesis and respiration of macro algae communities *in situ*.

Collins et al., 1999 describes the application of an incubation chamber technique to the study of epibiota communities on an artificial reef in Poole Bay, off the south coast of the UK. Dark respiration was found to be related to the mass of epibiota according to the linear regression model:

$$\text{oxygen flux}(\mu\text{molO}_2 \text{ gAFDW}^{-1} \text{ hr}^{-1}) = -30 \text{ mass}(\text{gAFDW}) - 475 \quad (r^2 = 0.71)$$

Similarly algal oxygen production (in the light, 30-50  $\mu\text{E m}^{-2} \text{ s}^{-1}$ ) was linearly related to algal biomass, linear regression model:

$$\text{oxygen flux}(\mu\text{molO}_2 \text{ gAFDW}^{-1} \text{ hr}^{-1}) = 126 \text{ mass}(\text{gAFDW}) + 401 \quad (r^2 = 0.83)$$

Mixed samples of representative algae from the reef ( including *Calliblepharis ciliata*, *Brongniartella byssoides*, *Seirospora interrupta*, *Heterosiphonia plumosa* and *Ceramium* spp.) incubated under similar conditions were found to show the following rates:

$$\begin{array}{ll} \text{algae respiration} & = -25 \pm 22 \mu\text{molO}_2 \text{ gAFDW}^{-1} \text{ hr}^{-1} \\ \text{algae gross production} & = 94 \pm 64 \mu\text{molO}_2 \text{ gAFDW}^{-1} \text{ hr}^{-1} \\ \text{algae net production} & = 119 \pm 86 \mu\text{molO}_2 \text{ gAFDW}^{-1} \text{ hr}^{-1} \end{array}$$

Assuming molecular conversion ratios (Respiratory and photosynthetic quotients) to be equal to 1 then converting the average oxygen fluxes per unit mass of epibiota above yields:

$$\begin{array}{ll} \text{all epibiota respiration} = & 14 \pm 4 \mu\text{gC gAFDW}^{-1} \text{ hr}^{-1} \\ \text{algae net production} = & 159 \pm 118 \mu\text{gC gAFDW}^{-1} \text{ hr}^{-1} \end{array}$$

Gross oxygen production measured by the incubation technique is a good indicator of algal growth, though account must be taken of losses of dissolved organic carbon. Approximately 90% of the reef epibiota biomass is faunal. The respiration value for this is composed of three main components; maintenance and growth and reproduction. Humphreys (1979) calculated a general relationship between annual respiration and annual production suggesting that some 20% of respiration is used for growth. This could be used to estimate total epifaunal production on the reef. The alternative approach of using individual body-size - metabolic rate relationships proposed by Schwinghamer et al. (1986) and Edgar (1990, 1994) to produce production/biomass ratios is difficult to apply to many of the colonial sessile organisms found on reefs.

Oxygen production by algae has only been measured at high light levels (mid-day in summer). Estimates of production should be modelled using measurements of light intensity on biotopes a 24 hour and annual cycle. Temperature affects metabolic rate so should be

considered when estimating annual respiration (and production). Furthermore algae and epifauna growth is seasonal so ideally a range of biomass measurements through the year is required. Given these further calculations the approach described here could produce essential information on the epibiota component of a predictive model of reef energetics such as described by Polovina (1984).

#### *5.1.2 Published studies of suspension-feeder/aquaculture interactions*

There have already been several published studies relating to the use of suspension-feeder aggregations as mitigating agents for aquaculture discharges. Stirling and Okumus (1995) measured the growth rates of mussels (*Mytilus edulis*) in two Scottish sea lochs at sites differing in proximity to salmon cages. Near-cage sites were shown to have higher water column concentrations of chlorophyll a and suspended POM. Mussel shell growth rate was higher at salmon farms than away from them. *In situ* production losses were also lower at salmon farms over the winter, suggesting that mussels at these locations did not deplete their stored reserves to the same extent as those further from the cages. These metabolic advantages indicate that mussels were able to utilize the additional seston resources available at the salmon cage sites, but the proportionate mitigation of cage discharges was not measured. A significant control of eutrophication by bivalve feeding was recorded in a Chilean lake by Soto and Mena (1999). In closed tank systems containing salmon, freshwater mussels (*Diplodon chilensis*) reduced concentrations of chlorophyll a by two orders of magnitude in 18 days, converting a hypereutrophic situation to an oligotrophic one. Further evidence supporting the mitigating potential of mussels was reported by Newell and Richardson (2000), who used a computer model to simulate the complex patterns of water flow around mussels suspended on lines. Depletion of seston by up to 50% was indicated by the model and later recorded in field trials.

In contrast to these generally favourable results, Taylor et al. (1992) found no significant enhancement of mussel growth by proximity to salmon cages. Growth of cultured mussels was not significantly correlated with distance from the farms, and there was no evidence of any contribution to mussel nutrition either directly via fish feed or faeces, or indirectly via stimulation of phytoplankton growth. Troell and Norberg (1998) modelled the output and retention of suspended solids in an integrated salmon-mussel culture. They concluded that mussel suspension-feeding is unlikely to exert a significant sustained control on aquaculture effluent discharges. The episodic addition of fish feed led to a large increase in water column seston load, but particle retention by mussels was limited by the threshold level required to induce pseudofaeces production. It was concluded that naturally-occurring seston concentration is the key factor controlling mussel growth, and that increased suspended solids from fish cages may contribute significantly to nutrition only during periods of low plankton productivity.

These conflicting results indicate a need for modelling simulations with all input and output terms accurately-budgeted and based on realistic biological data. Bodvin et al. (1996) have attempted to construct such a model for a remediated multi-species aquaculture system. Using data from the literature, and from field and laboratory tests, they estimated that a standing stock of 300 metric tonnes (MT) salmon would require 112.5 MT mussels to absorb particulate nitrogen and phosphorus, and 45 MT seaweed to bind the dissolved nitrogen and phosphorus produced by the salmon and mussels.

## **5.2 Synthesis and Summary**

The data presented in this review suggest a large number of potential biofiltration methodologies and biofiltering target species that offer the potential for impact reduction as

well as the possible complete removal of aquaculture impacts. The potential varies geographically in addition to the target species of culture. However, there are few examples of quantitative practical assessments based either on field or commercial-scale trials. The BIOFAQs project will provide the first practical field-based pan-European assessment of biofiltration potential. The project will also provide the opportunity to iterate previously published research, and, in particular, previous modelling attempts.

The model of Bodvin et al. (1996) suggests that the combined total mass of biofiltering material required for a remediated multi-species aquaculture system approximated 50% of the mass of the culture species standing stock. Scaling this estimation up for whole supra-regional production quantities produces huge biomasses of potentially unusable material. The model of Bodvin et al. (1996) can be revisited and possibly revised during the BIOFAQs project. But the scale of biofiltering material required for a whole industry is likely to remain extremely large and impractical. However, biofiltration should not be dismissed as a targeted technology that may aid the aquaculture industry on smaller, more localised scales. Partial remediation through biofiltration remains a viable option, as does total remediation on a small scale. Total remediation may assist aquaculture interests in environmentally or aesthetically sensitive areas. Partial remediation presents a possibility to the industry to increase production within an existing discharge consent envelope.

The eventual removal of the biofiltration material will be required either where a cyclical production schedule is used, or where climax communities develop. How that material is then treated may differ geographically and will also depend on the addition value of the material. Where disposal is the only option then there will be a negative economic value to the material. Where re-use is a possibility then this may influence the target biofiltration species with concomitant influences on the actual efficiency of biofiltration. Legal and economic influences on biofiltration as a method of aquaculture impact mitigation are explored in BIOFAQs workpackages WP05 and WP06.

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