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Recent advances in Mediterranean aquaculture finfish species diversification

Zaragoza : CIHEAM Cahiers Options Méditerranéennes; n. 47

2000 pages 53-59

Article available on line / Article disponible en ligne à l'adresse :

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To cite this article / Pour citer cet article

Kaushik S.J. **Feed allowance and feeding practices.** *Recent advances in Mediterranean aquaculture finfish species diversification.* Zaragoza : CIHEAM, 2000. p. 53-59 (Cahiers Options Méditerranéennes; n. 47)



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Feed allowance and feeding practices

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SUMMARY - Under aquaculture conditions, feeding practices have great implications both in terms of economics and in terms of ecology. Indeed, even with nutritionally adequate and balanced "environmental friendly" diets, bad feeding practices can lead to significant feed losses causing adverse effects on water quality and decrease the sustainability of aquatic animal production. The following points are of interest: feeding frequency, feed allowance and feeding strategy. The feeding frequencies should be considered depending upon two major factors (body size, temperature) both of which affect the rate of passage of feedstuffs through the digestive tract. From a practical point of view, in order to optimise ration levels, fish farmers generally rely upon either feeding charts provided by feed manufacturers or they themselves empirically derive feeding charts. This latter is done generally by predicting weight gain and assuming feed efficiency levels based on past history of farm husbandry and performance. More recently, proposals have been made to derive specific feeding charts based on nutritional bioenergetic principles: this again consists of growth prediction, but further proceeds to evaluate digestible energy (DE) required to achieve a given growth and body composition. Once the DE needs are known, the feed allowance can be made provided data on dietary DE levels are available. The basic idea behind is that the voluntary feed intake (VFI) is driven by DE needs. Recent research data strongly suggest that this general principle is applicable also to marine finfish. In the absence of data on dietary DE levels and on DE needs per unit gain of a given species, a very interesting alternative is to let the fish eat to satiety by themselves. There are currently a number of more or less sophisticated feed distribution systems for use in aquaculture. The choice will depend upon how well are they adapted to the species and size of fish and to the culture site. Demand feeding systems have the advantages of taking into account the behavioural rhythms and the nutritional guality of the diets. There is accumulating evidence to show that even marine species grown in cages can adapt themselves to such demand feeders. Such devices also hold much promise for understanding the specific feeding rhythms of new species and for obtaining quantitative data on the control of VFI as affected by dietary nutrients.

Key words: Aquaculture, feed intake, feeding standards, feeding practices.

RESUME – "Ration alimentaire et pratiques d'alimentation". Dans les conditions de l'aquaculture, les pratiques alimentaires ont de grandes implications en termes d'économie ainsi que d'écologie. En fait, même avec des régimes adéquats nutritionnellement et équilibrés, respectueux de l'environnement, de mauvaises pratiques alimentaires peuvent mener à des pertes alimentaires significatives qui causent des effets adverses sur la qualité de l'eau et diminuent la durabilité de la production animale aquatique. Les points suivants sont d'intérêt : la fréquence de l'alimentation, la ration alimentaire et la stratégie d'alimentation. Les fréquences alimentaires devraient être considérées en fonction de deux grands facteurs (taille corporelle, température) qui tous deux affectent le taux de transit alimentaire à travers le tractus digestif. D'un point de vue pratique, afin d'optimiser les niveaux des rations, les aquaculteurs en général suivent les tables d'alimentation fournies par les fabricants d'aliments ou ils mettent au point de facon empirique leurs propres tables d'alimentation. Ce dernier est généralement fait en prédisant le gain de poids et en supposant des niveaux d'efficacité alimentaire basés sur l'histoire passée de l'élevage à la ferme et les performances. Plus récemment, des propositions ont été faites pour en déduire des tables d'alimentation spécifiques basées sur des principes nutritionnels bioénergétiques : ceci revient encore une fois à la prédiction de la croissance, mais en évaluant maintenant l'énergie digestible (ED) nécessaire pour obtenir une croissance donnée et une certaine composition corporelle. Une fois que l'on connaît les besoins en ED, la ration alimentaire peut être calculée à condition que des informations soient disponibles sur les niveaux de ED alimentaire. L'idée fondamentale sous-jacente est que l'ingestion alimentaire volontaire (VFI) est en fonction des besoins en ED. Des données provenant de recherches récentes suggèrent fortement que ce principe général est applicable également aux poissons marins. En l'absence de données sur les niveaux de ED alimentaire et sur les besoins en ED par unité de gain pour une espèce donnée, une alternative très intéressante est de laisser les animaux se nourrir eux-mêmes jusqu'à satiété. Il y a actuellement de nombreux systèmes plus ou moins sophistiqués de distribution d'aliments en aquaculture. Le choix dépendra de leur plus ou moins bonne adaptation aux espèces et à la taille des poissons, et au site d'élevage. Les systèmes d'alimentation à la demande ont l'avantage de prendre en compte les rythmes de comportement et la qualité nutritionnelle des régimes. Il y a de plus en plus d'éléments démontrant que même les espèces marines élevées en cages peuvent s'adapter à ces nourrisseurs sur demande. Ces dispositifs sont également très prometteurs pour la compréhension des rythmes d'alimentation propres aux nouvelles espèces et pour l'obtention de données quantitatives sur le contrôle de la VFI par rapport aux nutriments du régime.

Mots-clés : Aquaculture, ingestion alimentaire, standards alimentaires, pratiques d'alimentation.

Introduction

A diet should meet the daily needs for nutrients and energy for maintenance, growth and reproduction of the animal when fed *ad libitum* or to near satiety. The general concern for both the feed manufacturer and the fish farmer is to define with some degree of precision, the quantitative daily supply of a given diet (set of nutrients and energy) needed to efficiently produce fish of different size classes grown under varying environmental conditions. Inadequate feeding practices result in poor feed utilisation affecting economic returns and lead to sometimes irremediable environmental damage. A significant portion of variability in feed efficiency can be reduced if feeding standards are based on nutritional principles and if feeding practices correspond to the intrinsic behavioural requirements of fish under culture.

Feed allowance

The ideal situation would be where the fish are fed so as to obtain maximum growth with maximum feed efficiency. In fish culture, the relation between feed intake and feed efficiency generally follows a second order polynomial curve (Fig. 1), with an ascending part with increasing supply and decreasing beyond a given ration size. While an insufficient supply will cover only partially the requirements above maintenance, inconsiderate feeding above the required levels in fact reflects excess feed supply released into the environment. Most fish farmers rely upon feeding tables provided by the feed manufacturers themselves and adapt them more or less to suit their own field conditions. To be reliable, these feeding charts should be adjusted for each diet, varying in ingredient and nutrient composition and energy density. A question that arises often is how far such feeding tables are reliable and what is the basis for such tables?

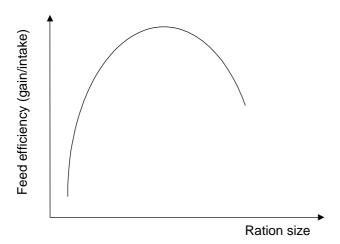


Fig. 1. Relation between feed intake and feed efficiency.

It is practically impossible to conduct trials and obtain data covering all size classes and temperature ranges for any given species. Some approximations can be made with discrete data analysed using response surface curves. However, these will have little significance if the nutritional quality of the diets are not considered.

Determination of optimal feeding levels

For drawing generic feeding charts, some guidelines have been provided for salmonids based on nutritional principles which involves prediction of growth, estimation of digestible energy (DE) needs for such growth and supply feed according to the dietary DE levels (Cho, 1992; Table 1). Such a general model can be adapted to specific production conditions where water quality, genotype, husbandry, etc., might vary (Cho and Bureau, 1998). Available data show that such an approach can be extended to marine finfish species of interest to the Mediterranean area (Kaushik, 1998). The

limitations are that it is essential to have reliable data on the energy requirements of fish for a given growth rate as influenced by body size and temperature and data on the DE levels of the final feed should be available. Such data are scarce for marine finfish species.

Table 1. Evaluation of DE and feed requirements⁺ (Kaushik, 1998, based on Cho, 1992)

Evaluate thermal unit growth coefficient (TGC) and predict weight gain	
Predict retained energy Maintenance energy needs (Hef, in fasting fish, kJ/day)	$(RE) = (W_f - W_i) \times \% DM \times kJ/g DM HEf = [(-1.04 + 3.26) \times T - 0.05T^2] \times kg BW^{0.824}]$
Heat increment of feeding	$(HiE) = HEf \times 0.6$
Non-fecal energy losses	$(NFE) = (RE + HEf + HiE) \times 0.06$
Calculate total DE needs	DE = RE + HEf + HiE + NFE
Determine or calculate dietary DE	
Calculate feed required	Feed = DE need/dietary DE

^{*} W_f = final body weight; W_i = initial body weight; DM = dry matter; T= temperature in °C; BW = body weight; DE = digestible energy.

The fore-said approach is based on the general assumption that voluntary feed intake (VFI) is mainly determined by the concentration of bioavailable energy in an otherwise nutritionally complete diet (Cho and Kaushik, 1990). While such a general principle holds for nutritionally adequate diets, an inconsiderate increase in DE alone without consideration for the relative proportions of essential nutrients per unit DE, might however have adverse consequences of deficiencies in other essential nutrients.

Voluntary feed intake

In the lack of knowledge on the role of brain, the control factors and the integrative or feed-back mechanisms involved, it is difficult to envisage manipulation of VFI (Forbes, 1986). How far the central nervous system is involved in the control of appetite, satiety and voluntary feeding in fish is not clearly known. Our knowledge with fish is still at a descriptive stage, mainly concerned with some environmental and biotic factors and to a less extent on dietary on nutritional factors. Within a given species, VFI will vary also depending upon the physiological status (e.g. gametogenesis). A generally established fact is that feed intake per unit body weight decreases with increasing body weight and increases with increasing water temperature within the thermal preferendum zone of a given species. Under stressful conditions such as hypoxia or high ambient ammonia levels the VFI is also reduced.

Digestible energy

There is evidence that under satiation feeding conditions, fish are capable of adjusting their voluntary feed intake depending upon the quality of the diets and especially upon the dietary DE levels. Very early studies using separate-feeding techniques (Kaushik *et al.*, 1981; Kaushik and Luquet, 1983) had pointed out that overall feed intake was governed by energy supply. Subsequent studies have confirmed that, like in the case of higher vertebrates, whenever there is an increase in the energy density of the feed, the voluntary feed intake is reduced in salmonids (Boujard and Médale, 1994; Paspatis and Boujard, 1996). With the advent of high energy diets, the question arises as to whether fish fed high fat diets respond in a similar manner or whether they induce hyperphagia as observed in rats (Horn *et al.*, 1996). Recent studies in our own group have confirmed that both rainbow trout and sea bass fed a high fat diet (30%) had decreased their feed intake while maintaining their growth rates with improved feed efficiency (Gélineau *et al.*, 1999, unpublished).

Other nutrients

A close look at a number of published works on the determination of nutrient requirements show

that a dietary deficiency leads in general to a decline in voluntary feed intake in fish. How far individual amino acids such as tryptophan involved in the production of serotonin which is a brain neurotransmitter affecting VFI in higher animals (Henry *et al.*, 1996) play a role in controlling appetite in fish is not known. Similarly, while in terrestrial animals, tissue metabolite concentrations (glucose, amino acids) are known to have a clear feed-back effect on VFI (Forbes, 1986), little is known in the case of fish. There has also been some suggestion that factors such as fat body mass might influence feed intake (Jobling and Miglays, 1993). Whether this is the cause or an effect remains to be verified through further controlled studies in which one can truly manipulate tissue nutrient or metabolite concentrations.

Phagostimulants

Addition of specific feed attractants are generally considered to increase VFI. A few phagostimulants have been identified which appear to differ between species (Mackie and Mitchell, 1985; Hara, 1994). Thus, while inosine monophosphate is considered an important attractant for turbot, a mixture of L-amino acids resembling that of squid extract is found to elicit good feeding response in other species. When a substantial amount of fishmeal is replaced with plant proteins, a general observation is a decline in VFI (Gomes *et al.*, 1995; Médale *et al.*, 1998). With plant protein rich diets, addition of the limiting sulphur amino acid (Médale *et al.*, 1998) or a mixture of L-amino acids (Dias *et al.*, 1997) have been found to increase voluntary feed intake and consequently growth. But, Cowey and Cho (1992) observed that addition of putrescine to a soybean meal based diet did not increase the feed intake of rainbow trout. Rainbow trout are also capable of discrimination between diets containing coated or uncoated potential feeding deterrants (Boujard and Le Gouvello, 1997).

Diet selection

Cuenca and de la Higuera (1993) observed that rainbow trout were capable of discriminating between two diets varying in zinc levels and that given a choice between zinc-deficient (5.5 p.p.m.) or zinc-sufficient (44 p.p.m.) diets, fish selected diets which were zinc-sufficient. A recent study by Sánchez-Vázquez *et al.* (1998b) also clearly showed that goldfish are capable of selecting between macronutrients thus "formulating" their own diets. An earlier study by Kentouri *et al.* (1993) under cage culture conditions had shown that sea bream is capable of selecting between diets and thus adjusting the overall feed intake depending upon dietary energy density.

Monitoring VFI

Most fish are capable of using demand feeders (Landless, 1976; Burel *et al.*, 1997). Specific devices have been developed in the recent past to monitor VFI in fish (Boujard *et al.*, 1992; Cuenca and de la Higuera, 1994a) for experimental purposes using such demand feeders. With such devices, each activation of a demand results in the delivery of either a single pellet or a given amount of pellets, with a possible feed-back control by a computer which also records the demands and amount delivered. Under practical conditions, it is common to use the criterion of visual satiety (observation of decreased feeding activity) as an approach close to *ad libitum* feeding. Such a practice may not be applicable to bottom-feeders nor under cage or pond culture conditions.

Some techniques are also available for monitoring individual feed intakes using radiography of fish fed diets containing opaque material (Talbot and Higgins, 1983). Although of great use in following individual variability in feed intake such methods are of limited use under farming conditions.

Over the recent past, more or less sophisticated devices have also been developed to record demands and deliver diets (Kadri *et al.*, 1991; Alanara, 1992; Juell *et al.*, 1993; Jobling *et al.*, 1995) for fish grown in cages. Whether such devices really allow satiation feeding becomes questionable in the light of observations of Gélineau *et al.* (1998) with rainbow trout. Their data show that at least under their experimental conditions, fish when on demand with self feeders did not ingest as much feed as they would be able to, and might not be satiated, but did express their hunger in terms of trigger activity. So, it appears necessary that such self feeders should be able to offer reward equivalent to the effort or demand (Brännäs and Alanärä, 1994).

Feeding practices

Feeding rhythms

Species-specific feeding rhythms which are both endogenous as well as entrained by different environmental cues have been demonstrated in several species (Sundararaj *et al.*, 1982; Boujard and Leatherland, 1992; Cuenca and de la Higuera, 1994b). Salmonids such as rainbow trout or Atlantic salmon and cichlids such as tilapia appear to show high feeding activity both at dawn and dusk, the former being quantitatively more important than the latter. Many of the catfishes show a high feeding activity only during the dark phases of the a daily cycle (Sundararaj *et al.*, 1982; Boujard and Luquet, 1996). Some species such as the sea bass or the common carp appear to be more capable of phase shifting their feeding rhythms. Isolation of fish also entrains a shift in feeding rhythm in silurids (Boujard and Luquet, 1996). In European sea bass, the endogenous rhythms appear to be entrained both by feeding and by photoperiod (Sánchez-Vázquez *et al.*, 1995). Even under extensive culture conditions, such a plasticity has been observed in sea bass (Begout Anras, 1995). Seasonal phase inversion has also been demonstrated in this species (Sánchez-Vázquez *et al.*, 1998a).

Feeding at specific periods of the diel cycle also affects growth, feed efficiency and body composition (Sundararaj *et al.*, 1982; Gélineau *et al.*, 1998). Such data would imply that the feeding practices should be in tune with such biological rhythms and otherwise a decrease in feed efficiency and even change in body composition might result.

Frequency of feeding

The frequency of feeding depends upon two major factors: body size and water temperature. Both these factors affect the rate of passage of feedstuffs through the digestive tract. Thus there is a close relation between gut fullness and return of appetite (Vahl, 1979). For instance, in small larvae, with a very short digestive tract, the frequency of feeding can be several times an hour (Kaushik, 1985), whereas in broodstock fish, a single meal a day might be sufficient. A large number of studies have shown that for the greater part of the growth cycle of fish (say between 20 g to harvest), two meals are sufficient (Luquet *et al.*, 1981).

Feeding strategies

The ideal feeding strategy would be the one which leads to homogenous growth of all individuals in a group. In any aquaculture system, day to day variation as well as inter-individual differences in feed intake are bound to occur. Under restricted feeding conditions, this might exacerbate possible endogenous differences between individuals. A close relation between inter-individual variability and ration size is seen from the data of McCarthy *et al.* (1993). Optimal feed supply decreases competition for feed and hence size heterogeneity. By providing feed to satiety at all areas of the growing pond/cage/raceway, we can decrease competition for food and thus decrease size heterogeneity. Even in early larval stages, considerable reduction in cannibalism can be achieved through proper feed distribution.

There are a currently a number of more or less sophisticated devices to automatise feed distribution under fish farm conditions. Of the three major strategies that are available to distribute feed (hand-feeding, automatic/mechanical feeders and demand-feeders), the most ideal is the one which optimises feed utilisation and decreases feed wastage and consequently the environmental load. The use of demand feeders well adapted to the species and size of fish and to the culture site has the advantages of taking into consideration the behavioural demands (rhythms) and the nutritional quality of the diets, thus meeting both requirements. Other systems incorporate an underwater sensor to detect excess feed particles exerting either a feedback control of feed supply or a signal to the farmer.

Conclusions

Biological, environmental and nutritional factors govern voluntary feed intake in an integrated fashion. Although digestible energy plays a major role in VFI, much needs to be known on other

nutritional factors that affect appetite and voluntary feed intake in fish. Over the past decade, much progress has been made in understanding the feeding rhythms and feeding behaviour of fish under aquaculture conditions. Besides the question on what and how much, when to feed is being addressed in different species. Currently, there are a number of more or less sophisticated devices to automatise feed distribution for experimental purposes as well as under fish farm conditions. Given that the demand feeding capacity has been demonstrated in several finfish species, incorporation of such systems in marine finfish culture has the dual advantage of meeting the behavioural needs as well as the metabolic demands in relation with the nutritional quality of the diets. Optimisation of feeding practices has implications both from the practical and from the physiological point of view.

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