

Name of key topic: Population Dynamics
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Background

Overview

Population dynamics is the quantitative analysis of the abundance and structural dynamics of populations, underlying processes, and management consequences. The aims of this key sheet are to introduce principles of population dynamics, and to show how population dynamics approaches can aid the management of aquaculture systems and aquaculture-enhanced fisheries.

Cultured populations are defined here as being subject to management intervention other than harvesting. The degree of intervention defines culture intensity as extensive (stocking and harvesting only, production based on natural aquatic productivity), semi-intensive (natural productivity enhanced by fertilisation and some feeding), and intensive (production based mainly on complete feeds).

The key topic is organised in three major sections: (1) population dynamics and key processes, (2) comparative population dynamics of farmed and wild fish, and (3) management applications.

Population dynamics and key processes

Overview

The dynamics of farmed populations are determined by the management actions of stocking and harvesting, and the biological processes of body growth, mortality and reproduction. Management actions influence biological processes through measures such as feeding, fertilization, temperature regulation, and predator and disease control. Quantitative analysis and modelling of population processes provides a basis for the design of stock management systems in aquaculture and enhanced fisheries. In such analyses, population processes may either be described for a given husbandry system (e.g. feeding, water quality management and disease control regime), or more complex process models may be employed that relate population processes to particular aspects of husbandry (e.g. a growth model that accounts for feeding level).

All population processes are influenced by innate characteristics of the cultured organism, as well as by external factors. External factors can act directly (e.g. mortality due to lack of oxygen), or influence the biological characteristics of cultured organisms through phenotypic (developmental) plasticity. Fish show greater phenotypic plasticity than mammals, and the same almost certainly applies to cultured invertebrates. The respective role of genotype and phenotypic plasticity in determining traits such as growth and mortality regularly causes debate and confusion. This can be resolved conceptually by thinking of 'genotype' as determining the way in which a particular organism responds to environmental factors, rather than specifying a fixed phenotype.

Population regulation through density-dependent processes plays a crucial role in natural populations where it determines the carrying capacity (long-term average abundance) and the potential for sustainable exploitation. In aquaculture, segregation of life stages and a high degree of management control over biological processes imply that regulation by natural processes is not as directly linked to population abundance and structure. Nonetheless, density dependent processes still determine carrying capacity within culture facilities, even though the underlying biological mechanism may be different (e.g. water quality deterioration instead of competition for limited food resources).

Growth

Individual growth is of key importance to the management of cultured (and wild) stocks, for two reasons. First, body size influences requirements of the organism in terms of food and physical environment, and its survival. Because fish typically grow by many orders of magnitude in weight throughout their life, growth is a major factor influencing all aspect of aquaculture management. Secondly, growth is in itself of key interest to aquaculture production and the focus of a great deal of management effort.

Many different mathematical models have been developed to describe the growth of fish, molluscus and crustaceans. Most widely used in management practice are empirical models which describe observed growth patterns by simple equations without explicitly considering physiological processes. Physiological and bio-energetic growth models are more complex and require additional information. Such models are outside the scope of this key sheet, but interested readers are referred to Liu and Chang (1992); Van Dam and Pauly (1995); and Yi (1998).

The most widely used growth model for fish and aquatic invertebrates is the von Bertalanffy growth function (VBGF) (von Bertalanffy 1957). The model is asymptotic, i.e. organisms grow towards a maximum size at high age. The VBGF is illustrated in Figure 1, where the model is used to describe growth in pond cultured tilapias. The VBGF often provides a very good description of lifetime growth patters in aquatic organisms from the advanced juvenile stage onwards. Simpler linear or exponential models may be used to describe growth over shorter periods of time, and there are also alternative asymptotic models to the VBGF (see Moreau 1987 for a review of fish growth models).

The commonly used mathematical forms of the VBGF in aquaculture are:

$$L(t) = L_{\infty} - (L_{\infty} - L(0)) e^{-kt} \quad (\text{Eq. 1})$$

for growth in length and

$$W(t) = (W_{\infty}^{1/3} - (W_{\infty}^{1/3} - W(0)^{1/3}) e^{-kt})^3 \quad (\text{Eq 2})$$

for growth in weight. In these equations, $L(t)$ and $W(t)$ are the length and weight at time t , $L(0)$ and $W(0)$ are the length and weight at time $t=0$, and L_∞ and W_∞ are the asymptotic length and weight towards which the animals grow at rate K .

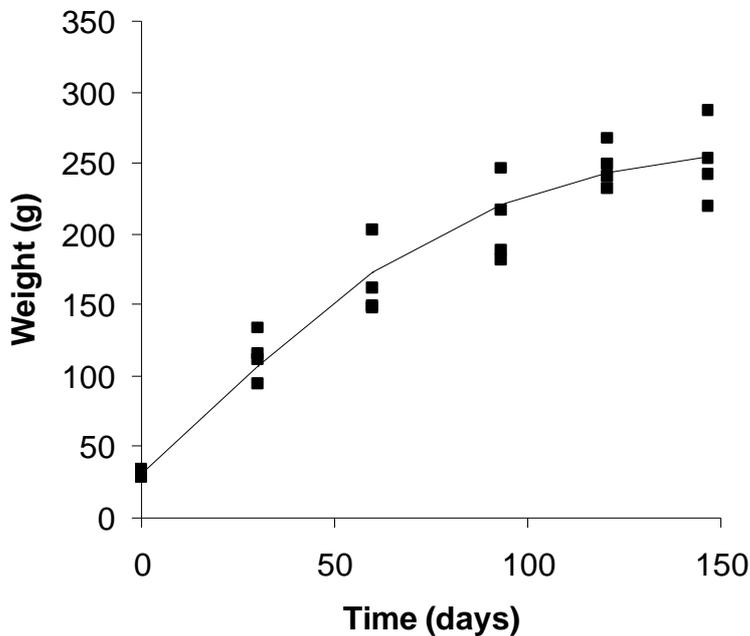


Fig 1. A von Bertalanffy growth function (VBGF) fitted to observed weight growth of Nile tilapia in organically fertilized ponds. The estimated model parameters are $W_\infty = 287$ g and $K = 8.0$ per year. Data from Springborn et. al. (1992).

Growth in aquatic animals is extremely plastic: fish of the same age and genetic background may vary in weight by orders of magnitude, depending on the conditions under which they have been reared. The VBGF has been extended in various ways to account for this plasticity. Pauly et al. 1993 extend the VBGF into a multiple regression model which can be used to account for the influence for various management factors on growth. Length increments are modelled as:

$$(L_2 - L_1) / (t_2 - t_1) = b_0 + b_1 \bar{L} + b_2 X_2 + b_3 X_3 + \dots + b_n X_n \quad (\text{Eq. 3})$$

where $\bar{L} = (L_2 - L_1) / 2$ is the mean length, and $X_1 \dots X_n$ are environmental or treatment variables, and $b_0 \dots b_n$ are regression coefficients. The multiple regression model parameters are related to the VBGF parameters by:

$$K = -b_1 \quad (\text{Eq. 4})$$

And

$$L_\infty = (b_0 + b_2 X_2 + b_3 X_3 + \dots + b_n X_n) / -b_1 \quad (\text{Eq. 5})$$

Alternative multiple regression models related to the VBGF are given by Prein & Pauly (1993) and Jackson & Wang (1998).

Lorenzen 1996a develops a simple extension to the VBGF to account for density dependence in growth by modelling L_{∞} as a linear function of Biomass B

$$L_{\infty}(B) = L_{\infty r} - g (B/B_r) \quad (\text{Eq. 6})$$

where $L_{\infty r}$ is the asymptotic length at reference biomass B_r and g is a coefficient describing the degree of density-dependence in growth.

Growth models such as the VBGF may be fitted using non-linear fitting procedures in standard statistical packages, or optimisation tools in spreadsheet programmes such as Excel. See Lorenzen et al. 1997 or Haddon 2001 for worked examples of model fitting in spreadsheets.

Mortality

Mortality is the second population process of major importance to aquaculture. However, mortality is considered less controllable than growth and has been surprisingly little studied.

Traditionally, mortality is described as proportional survival over a culture period in aquaculture, and as an instantaneous rate in fisheries ecology (for a discussion see Hopkins and Pauly, 1993). The development of population numbers over time under the influence of a constant instantaneous mortality rate is described by

$$N(t) = N(0) e^{-Zt} \quad (\text{Eq. 7})$$

where $N(t)$ is the population abundance at time t , $N(0)$ is the initial number at time $t=0$, and Z is the instantaneous mortality rate. Proportional survival S from $t=0$ to t is defined by

$$S = N(t) / N(0) \quad (\text{Eq. 8})$$

Consequently, S and Z are related by

$$S = e^{-Zt} \quad (\text{Eq. 9})$$

Among the advantages of using instantaneous mortality rates are that they are independent of the study period and can therefore be compared easily, and that they are additive. In fisheries ecology, the total mortality rate Z is the sum of the fishing mortality rate F caused by fishing, and the natural mortality rate M due to all other causes (e.g. predation, parasitism, or adverse environmental conditions):

$$Z = M + F \quad (\text{Eq. 10})$$

Natural mortality rates in most aquatic animals are strongly size-dependent, and can be described by a power function of the form

$$M(W)=M_r (W/W_r)^b \quad (\text{Eq. 11})$$

where $M(W)$ is the natural mortality at weight W , M_r is then natural mortality at reference weight W_r , and b is the allometric exponent of the relationship. In natural fish populations the exponent b is about -0.3 (Lorenzen 1996b), which implies that natural mortality is inversely proportional to length (see also Lorenzen 2000a). It is likely that this holds not only for fish but for most aquatic invertebrates (e.g. Perez-Castaneda & Defeo 2003).

Mortality rates are determined by a combination of environmental factors (e.g. temperature, presence of predators or pathogens), and biological attributes of the organism (e.g. predator avoidance behaviour, susceptibility to pathogens). These factors and their interactions remain poorly understood, particularly in farmed populations. Comparative studies of mortality rates in different ecosystems provide some insights and management guidance, which are discussed below. One area of particular interest to cultured populations is mortality related to infectious diseases, either as a direct consequence of disease or as an indirect effect mediated by culling for disease control. This aspect is discussed further in the applications section.

Reproduction and recruitment

Key reproductive parameters are age A_m and length L_m at maturity, and fecundity (the number of eggs produced by a mature female). In wild populations, the ratio of length at maturity to asymptotic length L_m/L_∞ is normally between 0.6 and 0.8. This is the result of fitness tradeoffs, which lead to relationships between life history traits known as invariants (Charnov 1993). Fecundity in fish and aquatic invertebrates is approximately proportional to body weight. As in growth, phenotypic variation in reproductive traits is typically very large in aquatic organisms.

In aquaculture, well developed hatchery and nursery technologies allow a relatively predictable survival from egg to juvenile and adult stage. This is much less the case in natural environments, where mortality in early life stages and juveniles of fish is highly variable as well as density-dependent. Hence the number of eggs produced by a wild fish population is a poor predictor of the number of offspring that will eventually “recruit” to form the next generation of spawners. In fisheries stock assessment it is therefore common to lump the processes of spawning, egg and juvenile survival into a black box process known as a stock recruitment relationship. This is simply an empirical relationship between the number or biomass of mature fish, and the resulting recruitment of offspring. In the aquaculture context, stock-recruitment relationships are important in the management of stock enhancements (see application section).

Density-dependence and carrying capacity

Many population processes including mortality, growth and reproduction in fish, crustaceans and mollusks have been shown to exhibit density-dependence. Density-dependence tends to be compensatory in nature, i.e. survival, growth or reproductive output decline with increasing density and thereby limit abundance or biomass to a level known as the carrying capacity. Density-dependence may operate at several life stages, defining stage-specific carrying capacities. Different mechanisms may dominate regulation at different stages. In wild fish, vital rates of egg and larval stages tend to be density-independent, juvenile stages are subject to density-dependent mortality, and late juveniles and adults are subject to density-dependent growth and reproductive output (Myers & Cadigan 1993a,b; Lorenzen & Enberg 2002; Lorenzen 2005). In extensive aquaculture systems and enhanced fisheries, mechanisms similar to those found in wild stocks are likely to hold.

Walter (1934) reported a set of experiments on the extensive culture of common carp in ponds which are particularly useful for understanding the concept of carrying capacity and the role of regulatory processes in defining it. Figure 2 shows the development of numerical density and weight over a six month period in cohorts of common carp stocked at different densities and initial weights. Final weights decline with increasing density so that final biomass is approximately constant, defining the carrying capacity for carp in the experimental ponds (indicated by the diagonal line). Cohorts stocked at very low density do not reach the carrying capacity within the culture period. Cohorts stocked at small size and very high density not only grow very little, but also show a significant level of mortality. In the other cohorts, including those stocked at a biomass above the carrying capacity, there was very little mortality. This example shows that carrying capacity in extensive growout systems tends to be defined by density dependence in growth, with density dependence in mortality being significant in small fish and at very high densities.

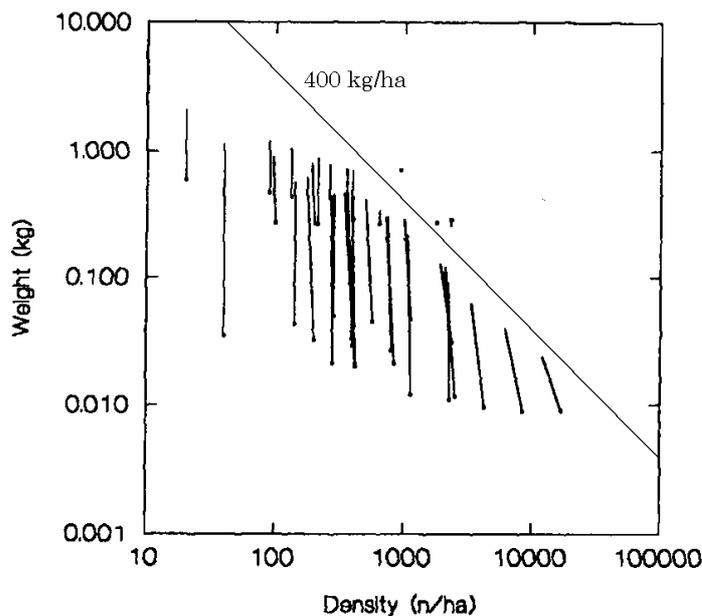


Fig 2. Development of population density and body weight in cohorts of common carp stocked at different densities and initial weights. The diagonal line indicates a biomass of 400kg/ha, the approximate pond carrying capacity as defined by the density-dependent growth and mortality processes. Modified from Lorenzen (1996a), based on data from Walter (1934).

In sedentary or highly territorial species where competition between individuals is asymmetric (there are winners and losers), mortality may be closely related to growth in a phenomenon known as self-thinning. This process can be important for example in bivalve cultivation (Frechette et al 1996; Frechette & Bacher 1998).

Comparatively little is known about density-dependent processes in intensive culture. However, density-dependence in survival and growth clearly exists even in highly controlled environments (Irwin et al. 1999; Alvarez-Gonzalez 2001). Moreover, high stocking densities may increase the risk of catastrophic mortalities due to water quality problems or disease outbreaks. The normal practice is to define carrying capacities in intensive systems by criteria such as the maximum density under which certain water quality criteria can be met under normal operating conditions. Quantitative assessment of carrying capacity based on density-dependence of fish performance indicators may allow the best utilization of system capacity however and thus improve efficiency.

Comparative information on population processes

Comparative information on population processes in different aquaculture systems and in wild population provides insights into the biology of aquaculture systems and is highly valuable to a range of management problems. These include the design of culture systems, management strategies for aquaculture-based fisheries enhancements, and the selection of species for culture.

On the whole, fish grow faster, mature earlier, and suffer lower rates of natural mortality in aquaculture compared to natural ecosystems. Accelerated growth and maturation result from the fact that cultured fish are provided with resources at higher levels than typically available in natural systems (Thorpe 2004). Protection from predators reduces natural mortality, and also allows fish to divert energy from predator avoidance to growth and reproduction.

Growth

Growth may be compared in terms of the VBGF parameters, or through indices that synthesize von of growth performance in a single number. Pauly (1981) defined the growth performance index P, which is proportional to the logarithm of the maximum weight growth rate ($(4/9) KW_{\infty}$) in the VBGF:

$$P = \log_{10}(KW_{\infty}) \quad (\text{Eq. 12})$$

Although other indices of growth performance have been proposed (Moreau *et al.*, 1986), P is the most readily interpretable in terms of the maximum growth rate.

Extensive, comparative studies of tilapia growth performance in wild stocks and in aquaculture have been reported by Moreau *et al.* (1986) and Pauly *et al.* (1988). An overview of observed growth parameters in natural and cultured populations of *O. niloticus* is given in Figure 3(a). There are two clearly separated clusters, one of wild populations with high W_{∞} and low K , and one of cultured populations with low W_{∞} and high K . The line of slope -1 indicated in Figure 4(a) connects points of equal growth performance P (Eq. 8). The average growth performance P and therefore maximum

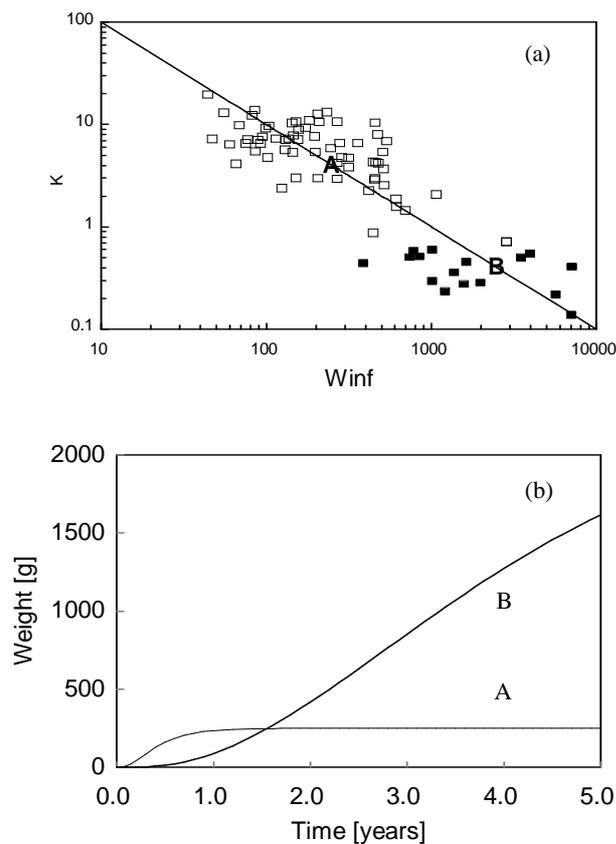


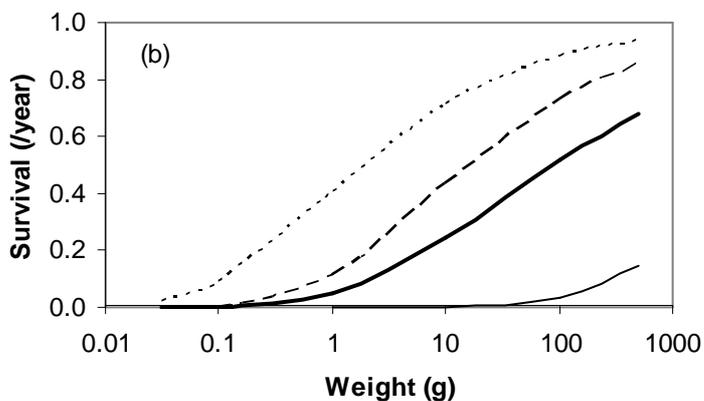
Fig. 3 Growth patterns in populations of *O. niloticus*. (a) VBGF parameters in wild (■) and farmed (□) populations. The solid line of slope -1 denotes equal growth performance index P . (b) growth trajectories associated with points A and B. Both parameter combinations have the same growth performance index P (and therefore the same maximum growth rate), but lead to very different growth trajectories. From Lorenzen 2000b, based on data from Moreau *et al.* (1986) and Pauly *et al.* (1988).

growth rates in natural and farmed populations of *O. niloticus* overlap widely, although on average P is higher in culture. The different growth patterns implied by different points on the same isoline of P are illustrated on Figure 3(b). Farmed populations of

O. niloticus grow to lower asymptotic size at a higher rate K than wild populations, and show a moderately higher maximum weight growth rate. Similar results have been obtained for other tilapia species (Pauly *et al.* 1998).

Natural mortality

A comparative analysis of mortality–weight relationships across a wide range fish species (Lorenzen, 1996b) showed that natural ecosystems are characterised by a common natural mortality-weight relationship with an allometric exponent of $b = -0.29$ (Eq. 11) (Figure 4). Natural mortality in aquaculture systems is lower overall than in natural ecosystems, but more strongly weight-dependent with an allometric exponent of $b = -0.43$. Tank systems Natural mortality rates in aquaculture are more strongly size dependent than in wild stocks. Consequently, natural mortality rates of large/mature fish are far lower in culture than in natural stocks. Mortality in tank systems is lower than in pond or cage systems, but the allometric exponent is the same in all aquaculture systems. Also shown in Figure 4 is an average mortality-weight relationship for cultured fish released into natural ecosystems for culture-based fisheries or stock enhancements (Lorenzen 2000a). Mortality in cultured fish released into natural systems has the same allometry as in wild fish, but is much higher on average by a factor of five. The mortality and survival figures given here may be used in exploratory population management and system design studies where specific data are lacking.



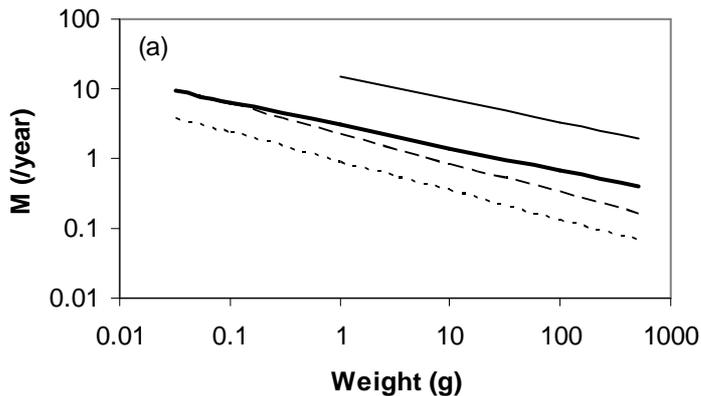


Fig. 4. Empirical relationships between (a) the natural mortality rate M and (b) the equivalent proportional survival S and body weight in wild fish (heavy solid line), pond and cage aquaculture (dashed line), tank aquaculture (dotted line), and cultured fish released into natural ecosystems (light solid line). Based on Lorenzen (1996b, 2000a).

Reproduction

Farmed fish tend to mature earlier and at a smaller size, are more fecund per unit of body weight, and may also reproduce more often than wild fish of the same species (Lorenzen 2000b, Thorpe 2004). Reported age at maturity in the tilapia *Oreochromis niloticus* for example ranged from 3 months in culture to over 2 years in natural lakes, while length at maturity varied between 10 cm and 39 cm (Lorenzen 2000b).

Where to find comparative information

Comparative empirical data on population processes and parameters are very useful for two reasons. They provide a basis for answering biological and management questions through statistical analysis, and they give a priori information for preliminary analyses of population dynamics in systems for which specific information is lacking. The database FISHBASE (www.fishbase.org) contains growth data for many species in natural and aquaculture systems, as well as data on reproductive traits and natural mortality in wild fish. FISHBASE also produces a variety of plots for visual comparative analyses. Comparative data and statistical models of mortality-size relationships are given in Lorenzen (1996b, 2000a) for wild and cultured fish, and for cultured fish released into natural systems. Lorenzen & Enberg (2002) provide limited comparative data and a statistical model for the degree of density-dependence in fish growth. Myers (2001) synthesizes generalisations about the stock-recruitment relationship in marine fish.

Application to aquaculture management

Population dynamics approaches are useful to a range of management problems in aquaculture and fisheries enhancement. Quantitative predictions of numbers, size

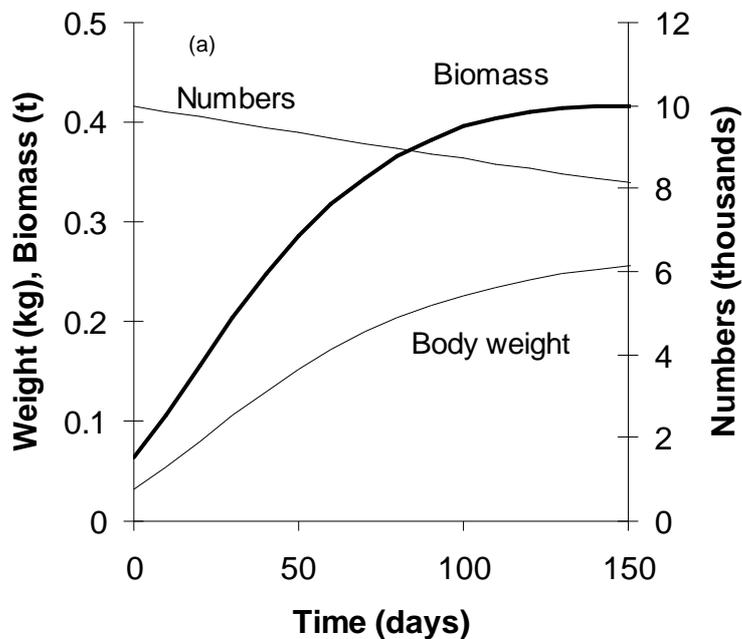
structure, yield etc. are easily combined with information on costs and prices for the bio-economic evaluation of stock management strategies.

Key applications considered here are

- Management of single in intensive and semi-intensive culture
- Extensive aquaculture or culture-based fisheries
- Stock enhancement
- Disease epidemiology and control

Dynamics and management of single cohorts

A cohort is a group of fish that share the same age, and are usually similar in other characteristics such as size. Whereas most wild populations are composed of several cohorts, i.e. contain fish of different age, cohorts are separated in most aquaculture systems. The problem of population management thus becomes one of optimally stocking and harvesting single cohorts within the constraints of physical facilities and other management inputs.



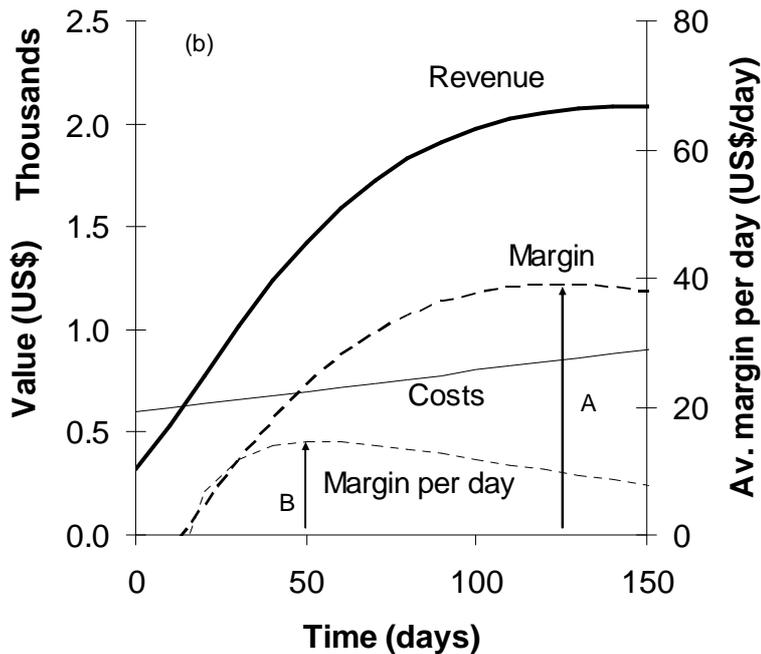


Fig. 5 Population dynamics and associated bio-economic variables in single cohort aquaculture. (a) Development of population numbers, body weight and the resulting total biomass over the culture cycle. (b) Revenue, cost and the resulting gross margin (revenue minus cost), and average margin per day (final margin divided by culture period).

The issues involved in stocking and harvesting a single cohort are best appreciated by looking at a hypothetical example (Figure 5). Assuming that the growth pattern and mortality rate of fish is predetermined by the culture environment and levels of inputs, the management problem is one of optimal harvesting of the farmed fish. Figure 5(a) shows the development of average body weight, population numbers, and the resultant stock biomass (weight x numbers) over a period of 150 days. Biomass reaches its maximum at the end of the 150 day culture period, which therefore is the optimal period for biomass yield. Now consider the development of the product value and costs over the same period (Figure 5(b)). Assuming a fixed price per unit biomass, value increases in the same way as biomass and reaches its maximum at 150 days. Costs consist of a fixed outlay for pond preparation, harvesting and seed fish, plus a variable component for fertilization and routine upkeep that increases with the length of the culture period. Because costs increase with the duration of the culture period, the maximum gross margin (product value minus costs) is achieved at 125 days, i.e. before maximum biomass is reached. A further issue to consider is the fact that culture systems have a finite capacity and that therefore, harvesting one cohort of fish makes space for a new cohort (this is known as the rotation problem). Given that the rate at which the gross margin is generated (i.e. the slope of the margin curve) declines throughout the later stages of the culture period, it is advantageous to replace an old cohort by a new one that generates profit at a higher rate. This of course is possible only if seed fish are available more or less continuously throughout the year. Where this is the case, the

optimal culture period is the one that produces the greatest margin per unit time of occupying the facility. In the example, this is a period of only 50 days. This example illustrates the main economic issues associated with the optimal management of single cohort populations, and the crucial role of population dynamics (quantitative analysis of growth and mortality patterns) as a basis for bio-economic analysis. For more rigorous and mathematical treatments of the bio-economics of harvesting farmed fish see Bjorndal (1988, 1990; Cacho et al. 1991; Springborn et al. 1992 and Heaps 1995).

Within single cohort culture, biomass increases over the culture period and typically reaches the system carrying capacity towards the end of the cycle. Hence carrying capacity is underutilized during the earlier stages of the cycle. This may be addressed by breaking the cycle down into shorter stages grown in systems of increasing capacity, or by simultaneous culture of multiple cohorts, either mixed or segregated by screens within a larger culture unit. Watten (1992) uses a population management model to explore optimal management of multi-cohort systems in intensive culture.

In many aquaculture systems of course, growth patterns of fish are not fixed but are actively manipulated by the choice of stocking density (in extensive and semi-intensive systems) and by feeding (in intensive systems). In this case, growth models are required that can account for such management factors. Also, the effects of husbandry practices on mortality rates are useful to consider, particularly in the culture of juveniles. The multiple regression models of fish growth described by Pauly *et al.* (1993), Prein and Pauly (1993) and Jackson & Wang (1998) allow analysis of a wide range of management impacts on growth, and may aid the improvement of semi-intensive and intensive husbandry systems. Prein (1993a,b) describe the application of these models to the analysis of tilapia growth in pond culture.

The potential of population and related modelling approaches to aid planning, and substantially reduce the experimental effort required to improve culture systems, has not been fully appreciated among aquaculture practitioners. The further development of modelling approaches and a more rigorous application of statistical principles in experimental design and analysis (Riley and Darmi, 1995; Knud-Hansen, 1997) are likely to yield increasingly more powerful population models for many aquaculture systems.

Extensive aquaculture or culture-based fisheries

In extensive aquaculture or culture-based fisheries, hatchery-produced aquatic animals are stocked into ponds or larger water bodies where they utilize natural biological productivity before being recaptured. Examples include the stocking of major carp in Asian reservoirs, coastal shellfish culture, and salmonid stocking for recapture in recreational fisheries. Stock enhancement, where cultured fish are stocked into self-recruiting populations of the same species is discussed in the next section. See Welcomme & Bartley (1998), Lorenzen et al. (2001) and Caddy & Defeo (2003) for reviews of fisheries enhancements.

In extensive aquaculture, population management in the form of stocking and harvesting is the main, if not the only form of management. Hence population dynamics is central to management decision making. The key population processes governing the outcomes of stocking in the absence of natural reproduction are density dependence in body growth and size dependence in mortality. In combination, these processes result in density-dependent mortality. The density-dependent growth and size-dependent mortality models can be used to evaluate stocking density and size as well as harvesting regimes in extensive culture (Lorenzen, 1995; Lorenzen *et al.*, 1997). Direct density-dependent mortality (other than modulated by growth) may be important where early juvenile stages are used for stocking.

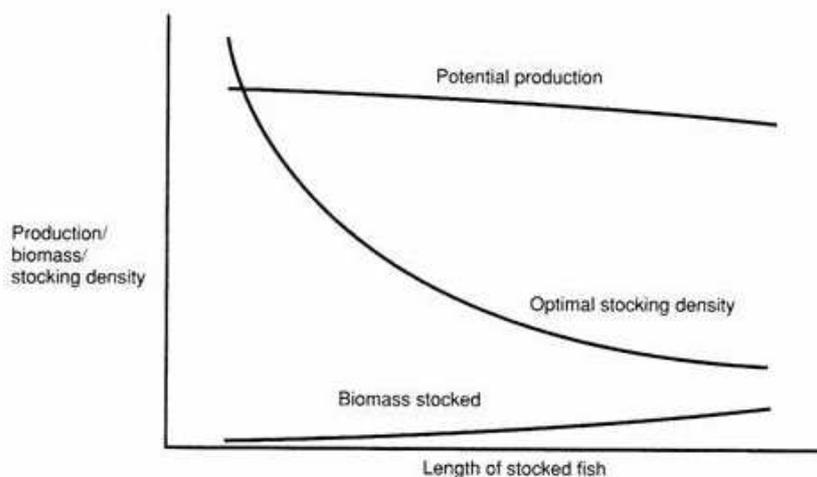


Fig. 6. Schematic relationship between potential production, optimal stocking density and biomass stocked in an extensive aquaculture system or culture-based fishery (modified from Lorenzen 1995).

Lorenzen (1995) provides an overview of the dynamics of stocked populations where dynamics are dominated by size-dependent mortality and density-dependent growth. This is likely to apply in many extensive culture systems for fish and shellfish where organisms are released at size where direct density dependence in mortality is not strong. A wide range of different stocking sizes can be used to achieve similar levels of production, but the numbers that need to be stocked decrease in a non-linear way as size increases (Fig. 6). This is a consequence of the allometric mortality-size relationship, and the fact that larger seed fish require less time to reach a harvestable size. The biomass of seed that needs to be stocked to achieve a given level of yield increases with increasing seed size (and so does the cost of producing each seed organism). Lorenzen (2000) provides quantitative survival models for released fish, based on a generalized mortality-size relationship. The models can be used to assess alternative release sizes given an estimate of mortality at reference length, to facilitate comparative studies, and to aid the design of release experiments.

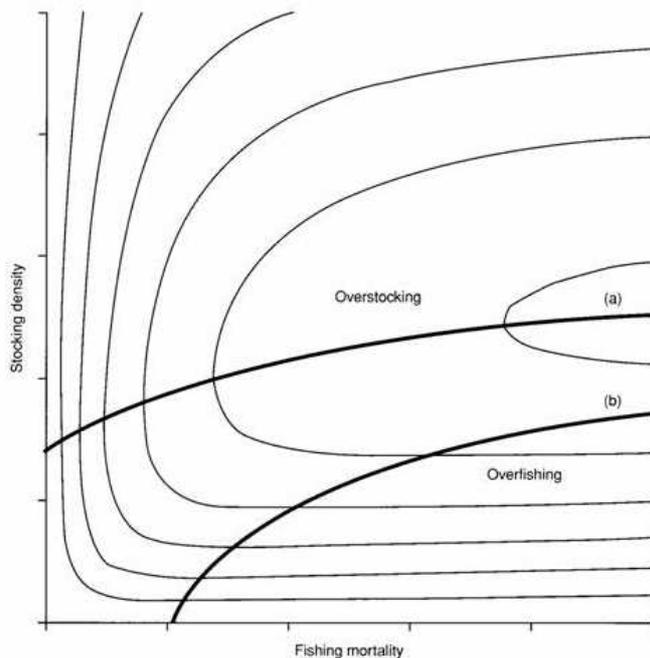


Fig. 7. Schematic relationship between production, fishing mortality and stocking density in an extensive aquaculture system or culture-based fishery (modified from Lorenzen 1995).

Due to the action of density-dependent growth, the optimal stocking and harvesting regimes in extensive culture systems are not independent. This is illustrated schematically in Fig. 7, where production is shown as a function of stocking density and fishing mortality (the rate at which organisms are removed by fishing). High fishing mortality calls for high stocking densities and vice versa. High stocking densities combined with low fishing mortality lead to overstocking, with low production due to slow growth and low survival from stocking to harvest. Conversely, low stocking rates combined with high fishing mortality lead to overfishing. Note that both overstocking and overfishing can be alleviated by changes in either stocking density or fishing mortality.

Potential production from stocked fisheries is inversely related to the size at which fish are harvested. Hence, in combination with the overall biological productivity of the environment, the minimum size at which fish are marketable effectively limits the production that can be achieved from stocking. Where large fish are desired, as in certain sport fisheries, stocking densities should be low and overall production will also be low. Where small fish are marketable, high production levels are achieved when stocking densities are high and fish are harvested at the smallest marketable size. Where fish are marketable below their normal size at maturity, culture fisheries can achieve higher levels of production from a given environment than wild stocks of the same species, because large and somatically unproductive spawners can be replaced by a large number of small and somatically productive fish.

The principles described above apply in a similar way to the culture of bivalve mollusks, except where self-thinning is a dominant process (Frechette et al 1996;

Frechette & Bacher 1998). For examples of application of population dynamics to bivalve culture see Pelot (1999), Penney & Mills (2000) and Gagnery et al. (2004).

Practical assessment of population management options in extensive culture systems can be carried out at three levels. Prior to the start of operation, the potential of an extensive culture system can be assessed using comparative information on population processes and parameters (see above). If projections look promising and it is decided to proceed to pilot operation, stocking and harvesting data allow the estimation of growth parameters, and natural and fishing mortality rates. This allows a much more reliable assessment of potential, but parameters of density-dependent relationships are likely to remain uncertain until full scale operation commences and data become available for different levels of stocking density and fishing mortality. For a worked example of assessing a large-scale extensive culture system see (Lorenzen et al. 1997).

Stock enhancement

Stock enhancement is the release of cultured fish into populations of naturally recruiting conspecifics, with the aim of enhancing yields and/or rebuilding populations. The population dynamics of fisheries stock enhancement, and its potential for generating benefits over and above those obtainable from optimal exploitation of wild stocks alone are poorly understood and highly controversial. Key questions concern the performance of cultured fish in the wild and, most importantly, ecological and genetic interactions between the released (cultured) and wild fish.

Building on the population processes discussed above and previous studies (Botsford & Hobbs 1984, Byrne et al. 1992 and Cuenco 1994), Lorenzen (2005) develops and analyses a population dynamics model for stock enhancement that accounts for ecological interactions as well as implications of genetically based fitness differences and introgression. Enhancement through release of recruits or advanced juveniles is predicted to increase total yield and stock abundance, but reduce abundance of the naturally recruited stock component through compensatory responses or overfishing. Release of genetically maladapted fish reduces the effectiveness of enhancement, and is most detrimental overall if fitness of hatchery fish is only moderately compromised. As a temporary measure for rebuilding of depleted stocks, enhancement can not substitute for effort limitation, and is advantageous as an auxiliary measure only if the population has been reduced to a very low proportion of its unexploited biomass. Economic feasibility of enhancement is subject to strong constraints, including tradeoffs between the costs of fishing and hatchery releases. Costs of hatchery fish strongly influence optimal policy, which may range from no enhancement at high cost to high levels of stocking and fishing effort at low cost.

Practical assessment of management options for stock enhancements and their overall feasibility must integrate wild and cultured fish dynamics. The model developed in Lorenzen (2005) can be used and where necessary adapted for a wide range of enhancement systems. Prior Information on all key population processes is

available from comparative studies, see above. Lorenzen (2005) also provides an approach to unpacking an observed stock-recruitment relationship in to size-specific density-dependent mortalities. Hilborn (2004) and Walters & Martell (2004) consider the management of stock enhancements in the face of temporal variation, and design criteria for management experiments.

Disease epidemiology and control

Infectious diseases are among the most important sources of mortality in aquaculture, and may also affect growth and product quality. Infectious diseases are caused by parasites, but host and environmental factors also play a role in their occurrence. The term “parasites” is used for both “microparasites” such as viruses or bacteria, and “macroparasites” such as worms or crustacea. Understanding and modelling the population dynamics of host-parasite interactions has become an important tool for the evaluation of control options in human, animal and plant populations (Thrusfield 1997). Application to aquaculture has as yet been very limited, but the field is developing rapidly.

To illustrate the application of population dynamics to disease epidemiology and control, consider the example of a directly transmitted bacterial (microparasitic) disease introduced into a cohort of farmed fish. It is clearly difficult to consider the dynamics of bacterial populations within fish explicitly. Instead, one can divide the host population into classes by disease status. If fish do not recover but either remain chronically diseased or die, there are only two classes: susceptible and infected. Such a simple model is illustrated in Figure 8. Susceptible fish (class X) may either die from causes other than disease (at a rate m), or become infected and thus move into class Y. The rate at which this happens depends on the transmission coefficient of the disease (β) and the rate of contact between susceptible and infected fish, which is assumed to be proportional to the product of X and Y. Infected fish may die from the disease (at rate d), or from other causes (at rate m). This conceptual model can be translated into a simple mathematical model (see des Clers 1991) to analyse the impact of the disease on cohort abundance over time, and the prevalence of the disease (the proportion of live fish that are infected).

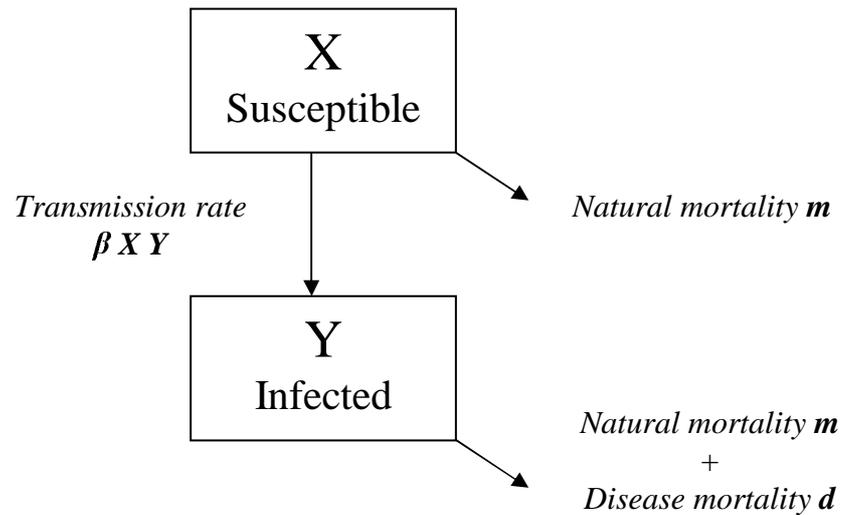


Fig. 8. Conceptual model for the population dynamics of a microparasitic infection in a cohort of farmed fish.

Model predictions are shown in Figure 9 for three different levels of disease-induced mortality d . If disease mortality is very low, cohort abundance declines only due to non-disease mortality, but all fish become infected. At a medium level of disease mortality, there is an epidemic during which the majority of fish become infected and die, but prevalence drops after the epidemic as too few individual are left to sustain the parasite population. At very high disease mortality, infected fish die too quickly for an epidemic to develop so that both mortality and prevalence remain low and the disease disappears from the cohort. An important management implication in this hypothetical example would be that a parasite of medium pathogenicity would require better surveillance and possibly culling of the infected cohort than a parasite of high pathogenicity. For further exploration of such theoretical issues see Reno 1999. There has been as yet only limited application of disease population models in aquaculture, but Lorenzen et al. (1991), Patterson (1996) and Murray et al. 2003 provide applications to exploited wild fish stocks.

Disease population models can be integrated into decision analysis tools that are widely used in veterinary epidemiology to assess the economic consequences of diseases and alternative control measures. For an overview see Thrusfield 1997.

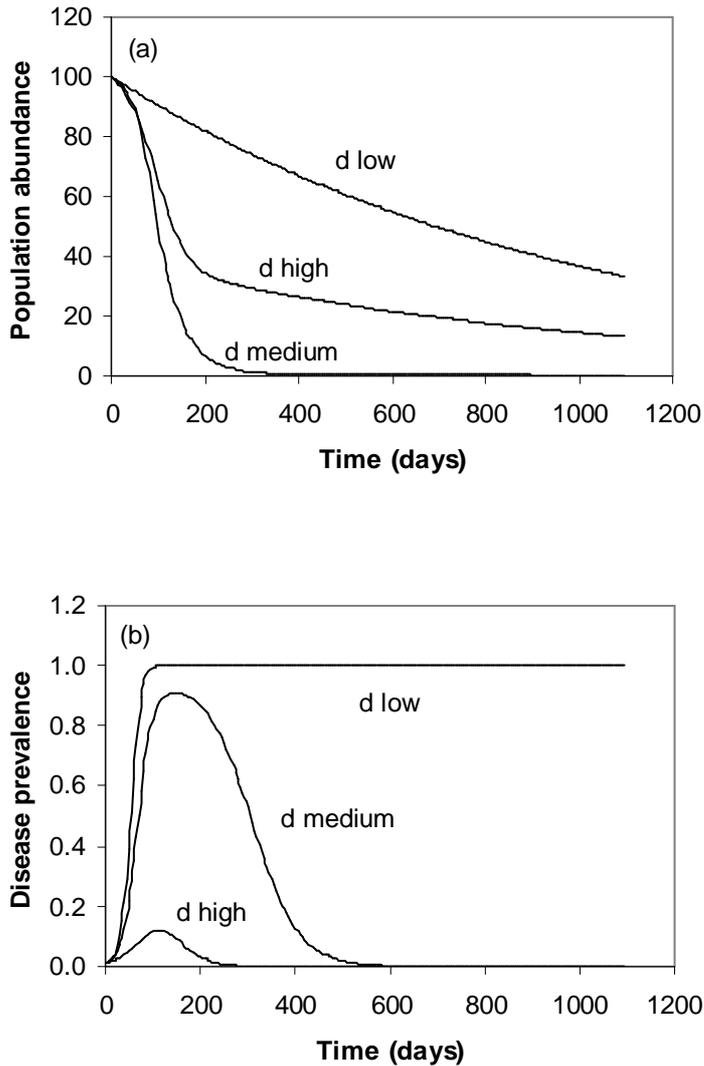


Fig. 9. Simulated population dynamics of a microparasitic infection in a cohort of farmed fish for different levels of the disease-induced mortality rate d : (a) population numbers and (b) prevalence (proportion of infected individuals among all fish alive).

Building and using population model in aquaculture

Population models can be used in a variety of ways: to help structure a management problem and explore the behaviour of populations under different assumptions, to test hypotheses about processes (by confronting alternative process-based models with data), or to make quantitative predictions of the outcomes of alternative management actions. Starfield (1997) and Mangel et al. (2001) discuss approaches to and uses of modelling.

To be useful to management, models need not be mathematically complex or computationally demanding. Relatively simple models implemented in spreadsheet programmes such as Excel can be powerful tools to aid understanding of dynamics and decision making (see Lorenzen et al. 1997 and De Waal & Cook 2001 for applications, and Haddon 2001 for an introduction to spreadsheet based fish population modelling).

Often there will be uncertainty about key process and their best mathematical description. Contrary to a widely held belief, models are particularly useful where such uncertainties exist and their development should not be postponed until all uncertainties are resolved through experiments! The best approach is to develop several models representing alternative assumptions and testing how sensitive predicted management outcomes are to these assumptions. Often, assumptions that seemed critical before model development turn out to be quite irrelevant. Where this is not the case, experiments may be designed to resolve key uncertainties. This will often involve testing how well alternative models describe a given set of data, see Johnson & Omland (2004) for an overview of approaches.

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