

Growth and maturation dynamics

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INTRODUCTION

Fish populations consist of individuals, which differ in several life history traits. Among the most important ones are those related with growth and maturation, the key topics to be dealt with in the present review. While the fish is sexually immature, assimilated energy is fully allocated for survival and on-growth, but once maturation starts, a part of the energy is required for gamete production and reproductive behaviour. The amount of energy allocated to growth and reproduction will depend on a number of factors, some of them intrinsic (genetic, physiological) while others are environmentally driven (temperature and feeding). Thus, a compromise on balancing the energy must exist, reflected in specific growth and reproduction dynamics in the lifetime of an individual fish. Interacting with this dynamic is the fact that marine ecosystems are fluctuating environments, and the feeding opportunities vary considerably in both short and long terms. Fish populations include individuals of different ages, sizes, conditions and stages of maturation and therefore, growth and reproduction dynamics must, at least from a fisheries assessment point of view, be explored from a population (demographic) perspective. Fisheries remove individuals at various trophic levels in the ecosystem affecting the distribution of energy and hence the amount of energy available for a particular fish. In this way man is influencing fish growth and maturation dynamics.

Quantitative knowledge about growth and maturation processes is of vital importance for any kind of resource assessment, single species as well as ecosystem approaches. This review focuses on these processes and discusses how fish allocate energy to growth and reproduction, and how these two concepts evolve together along the life history of the fish,

interacting with the environment. We concentrate on short-term variation, as this is what most data support. Further, as growth and maturation are heritable characters we also discuss potential long-term evolutionary aspects.

BIOENERGETICS

Natural selection aims at maximizing the survival opportunities of the offspring until it reaches sexual maturity and reproduces successfully. Logically, there is always a trade off between number of reproductive events and reproductive outputs (e.g. fecundity and egg size); reproduction has a cost in terms of energy, which may be very high. To afford it, some requirements must be met, and this is first of all achieved by growing, which also has an energetic cost. Several reviews are available on fish bioenergetics (Brett and Groves, 1979; Tyler and Calow, 1985; Jobling, 1994), but a brief introduction is given here.

Energy flow

The obtained energy is firstly committed to body maintenance costs, and other processes devoted to survive. Surplus energy is allocated to growth and reproduction. The energetic budget for an individual fish can be expressed as:

$$C = E + R + P \quad (1)$$

where C is the energy content of food, E the loss in waste products, R is the energy invested in metabolism and P the energy allocated to production, i.e. growth and reproduction. The assimilated energy, i.e., $C - E$, as modelled by Warren and Davies (1967), will depend on rate of food consumption and rate at which food is assimilated and metabolised (Krohn et al., 1997). Rate of food consumption varies with a number of factors, such as prey availability, foraging competition, the risk of predation, the satiation level, temperature and body weight (Pandian and Vivekanandan, 1985; Wootton, 1990; Walters and Juanes, 1993; Munk, 1995). Nevertheless, there is a maximum ration per intake (Brett, 1979). Daily ration depends on both maximum ration and food density (Ivlev, 1961), while maximum ration is again determined by several factors, e.g. temperature (Brett et al., 1969). Assimilation rate is mainly a function of temperature (Brett and Groves, 1979), and known to be the main factor regulating metabolism (Fry, 1971).

To summarise, fish allocate the assimilated energy following rules determined by its physiological state, and balance the budget between maintenance, growth and reproduction. In total this defines the energy flow (Figure 1).

Trade-offs and feedback mechanisms

The energy required for survival (maintenance) varies as the fish grow and changes after each reproductive episode. Species that reproduce only once (semelparous life history), e.g. some salmonids, invest all the energy in reproduction before dying. Those with repeated reproduction (iteroparous life history) save some energy for survival and possible further growth. Most fish species show indeterminate growth, i.e. individual growth continues after the onset of maturation, and continues throughout life span (Box 1). Energy for gamete

production and reproductive behaviour, however, reduces somatic growth (Roff, 1983). The factors forcing indeterminate growth are discussed elsewhere (Heino and Kaitala, 1996). There may exist important feedback mechanisms among energy invested in survival behaviour, growth and reproduction (Calow, 1985; Roff, 1992) (Figure 1). For example, if priority is given to growth, increased body size will likely reduce the risk of being predated and also improve feeding opportunities. This is reflected in size-dependent survival (Beverton and Holt, 1959; Pauly, 1980; Pepin, 1991). On the other hand, reproduction reduces growth and hence future body weight, which can decrease future fecundity (Roff, 1992). A trade-off between survival, growth and reproduction is, however, possible because fish are able to compensate negative energy balances, through growth, by metabolic or activity compensation (Van Winkle, 1997), e.g. a lower growth rate can delay maturation (see Section 3.4 below). Likewise, fish with limited food supply may partly or fully sacrifice egg production to preserve body condition, while others, may maintain investment in reproduction at the expense of body reserves (Roff, 1982). Skipped spawning is often considered as mass atresia (resorption of oocytes) and may occur in population under various types of considerable stress (see Marshall et al., 1998; Rideout et al., 2000, and references therein).

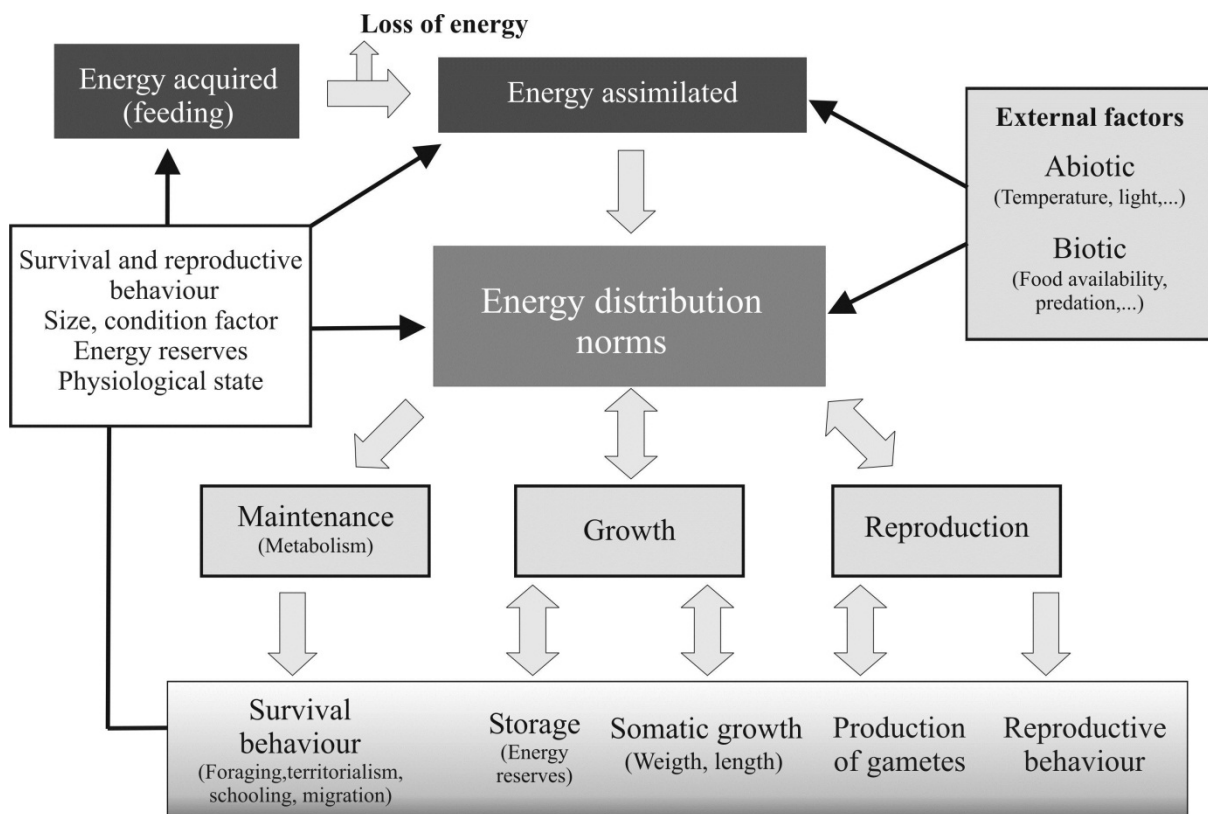
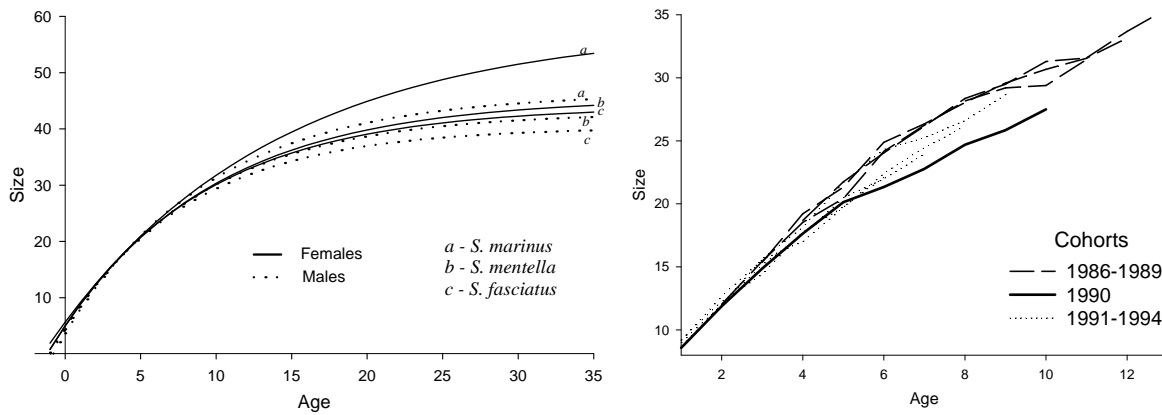


Figure 1. Schematic representation of energy flow allocation norms. Open arrows represent energy routes while solid arrows represent factors affecting energy allocation. Energy allocated for maintenance, growth and reproduction is partitioned between survival (including survival behaviour), storage of energy reserves, somatic growth, production of gametes and reproductive activity, all which may affect energy acquisition, assimilation and distribution through feedback regulating systems. External factors influence the level of energy intake and allocation patterns. Energy invested in growth and reproduction can be reallocated to other locations (by e.g. reduction in reserves, loss of somatic weight, yolk absorption). (Based on van Winkle et al., 1997).

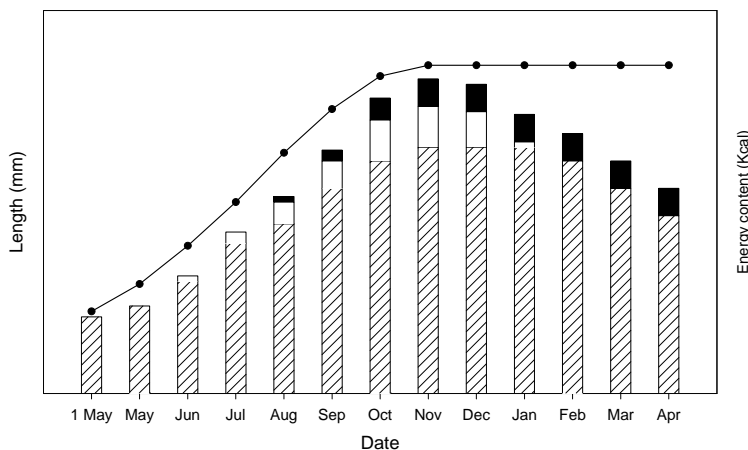
Box 1. Growth patterns

Fish show a great variety in growth patterns. When measuring lifetime growth, the pattern is usually smooth, with substantial differences among populations and, within a population, among sexes or cohorts. Growth pattern is usually asymptotic (see illustration), but may appear linear when measured in shorter periods as shown for cod in the Northeast Arctic (Jørgensen, 1992) or at Flemish Cap (Saborido-Rey and Junquera, 1999a).



Redfish (*Sebastes* spp) at Flemish Cap display different growth patterns both among species and between sexes. For *S. mentella*, differences were also observed among cohorts. The 1990 year-class showed a density-dependent growth pattern and note that at age 5-6 there is a sudden shift in growth rate, probably related with a switch to a non-optimal food resource. Source: Saborido-Rey *et al.* (2004).

At short term the growth curve will reflect variations in food supply, temperature or other environmental factors, as fish live in a seasonal environment, implying periods of fast and slow (or zero) growth. Growth in weight can also reflect an annual reproductive cycle. Gonad size (more correctly gonadosomatic index) usually increases with fish weight with successive weight losses towards the completion of spawning. Temperate and cold-water species, experiencing periods of food depletion, store parts of the assimilated energy for later use when food supply is limited (Bagenal, 1969) (see illustration below). The cyclic pattern in weight for such species needs to be considered as part of the growth dynamics as the energy reserves are of special importance for the onset of maturation as well as the seasonal variation in gonad development (Eliassen and Vahl, 1982; Rowe *et al.*, 1991; van Winkle, 1997).



Simulated values for energy content of the soma (tilted), storage (open), and gonad (solid) and for length (line) of a female rainbow trout during one annual reproductive cycle. Source: van Winkle *et al.* (1997).

GROWTH

Growth is normally considered a necessity to complete reproductive costs. The ecological niche a species occupies imposes a constraint to the maximum body size, but within this limit larger individuals often show a lower risk to be predated and a higher reproductive success. Fast growth not only improves food availability, but also, and more important, facilitates earlier reproduction. As shown in previous section, somatic growth is the result of the energetic balance between assimilated and consumed energy and several physiological mechanisms play important roles in this balance. Both biotic and abiotic factors can modify considerably fish growth.

Growth physiology

Generally speaking, growth is gain in energy content over a defined time period reflected in changes in somatic growth and/or energy storages (Note that growth can be both positive and negative). Growth efficiency, the relationship between growth and food ingested (Brett, 1979), will depend on several physiological processes that control metabolic rates, such as digestion rates and osmoregulation, and ultimately survival.

Conversion efficiency of energy assimilated into growth varies enormously both within and among populations (Boisclair and Leggett, 1989). Fish growth is sensitive to small variations in metabolic rates (Kitchell et al., 1977). Thus, Trudel et al. (2001) have shown that dwarf fish of lake whitefish, *Coregonus clupeaformis*, display a lower growth rate than fish of normal size or sympatric fish in spite of higher feeding rates due to higher metabolism. Metabolic costs tend to be higher in sexually mature than in juvenile/immature fish, which seems to be related to reproductive efforts (van Rooij et al., 1995; Rowan and Rasmussen, 1996). The

chemical composition of food and associated digestion rates are also highly relevant for growth performance (Pandian and Vivekanandan, 1985; Weatherley and Gill, 1987; Mommsen, 1998; Carter et al., 2001; de la Higuera, 2001).

Physiologically there is always a maximum ration (food consumed for a given period) that a fish can assimilate and an optimum ration at which growth efficiency is maximized (Brett, 1979; Houlihan et al., 2001) (Figure 2). The relation between growth rate and ration is usually curvilinear (Figure 2) (Brett et al., 1969; Williams and Caldwell, 1978; Russell et al., 1996), although there are some exceptions (Soofiani and Hawkins, 1985). This relation defines

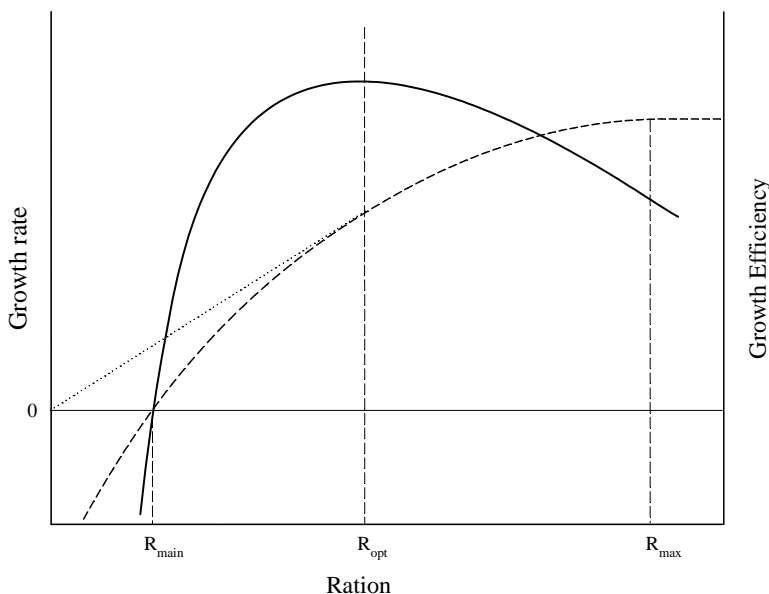


Figure 2. Schematic diagram of relationship between food ration, growth rate (dashed line) and growth efficiency (solid line). Growth is zero at maintenance ration (R_{main}), growth efficiency is maximized at optimum ration (R_{opt}), while growth rate reaches a maximum at maximum ration (R_{max}). The tangent to growth rate curve from origin (dotted line) identify R_{opt} . (Based on Brett et al., 1969)

also a ration below which growth rate will be negative (maintenance ration). However, it should be noted that maximum growth rate does not coincide with maximum growth efficiency (Wootton, 1990). Observations indicate that in natural populations fish forage at a rate that maximizes their growth rate (Ware, 1975a).

Although growth is the result of an energetic balance, it is usually expressed in terms of length or weight changes because these properties are easily measured and more intuitive to interpret and model (see Box 2). Growth in length is always positive or zero (the solid backbone and head prevent negative length development) even though an energetic deficit could occur (see Box 2), which can lead to a major overall loss of weight.

Box 2. Modelling fish growth

Growth models should be based on physiological principles, where growth represents the difference between anabolism (constructive biochemical processes) and catabolism (deconstructive biochemical processes). Influential variables on metabolism such as rations, body size, temperature etc. need consideration, an approach used by von Bertalanffy (1957), Paloheimo and Dickie (1965, 1966a, 1966b), Ursin (1967), Kitchell *et al.* (1974), Pauly (1981) and others. Ursin (1967) proposed a growth model based on the energy balance equation:

$$dW/dt = e_f dR/dt - Q$$

where dW/dt is the growth rate, dR/dt is rate of food consumption, Q is the total metabolic rate, and e_f is the efficiency of food utilization. Jensen (1998) further developed these models taking into account reproductive expenses to simulate relationships among fish life history parameters.

In fisheries research growth is frequently described using the von Bertalanffy growth model:

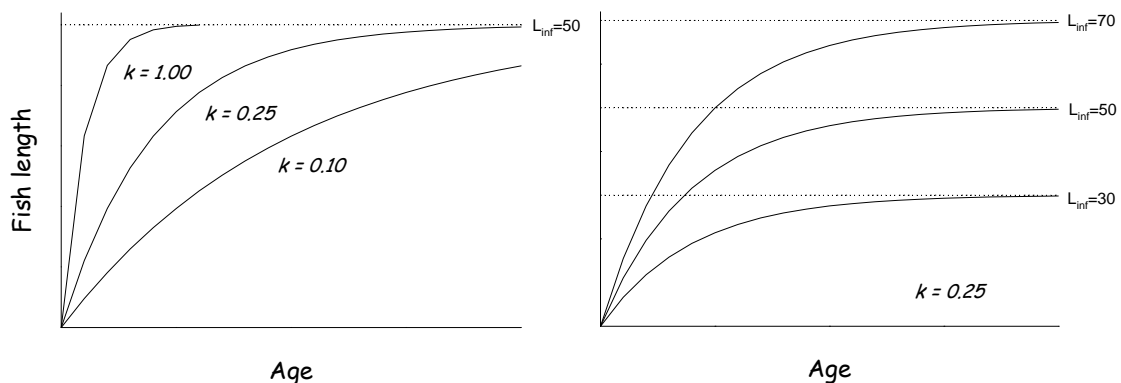
$$L_t = L_\infty (1 - e^{-k(t-t_0)})$$

where L_t is the length at age t , L_∞ is the asymptotic length (theoretical length at which growth rate is null), k defines the rate at which the curve approaches the asymptote and t_0 is the hypothetical time at which the length is zero in the model. Similarly, the von Bertalanffy weight growth curve is expressed as:

$$W_t = W_\infty (1 - e^{-k(t-t_0)})^b$$

where b is the exponent of the length-weight relationship. The k has the same meaning as above but shows a different value.

While k and L_∞ (or W_∞) define growth trajectory, t_0 shifts the curve to the left or right along the x-axis. Although subjected to important controversy, L_∞ and k can be interpreted as the result of different life history strategies. How differences in L_∞ and k influence growth curves are illustrated in the figure below (based on Jobling, 1995).



During lifetime sudden changes in growth rate are commonly observed at specific times (Ricker, 1979). Such changes may for instance be related to larval metamorphosis, physiological changes (as salmon migrating from salt- to freshwater) or to maturation (Alm, 1959; Balon, 1984; Fuiman and Higgs, 1997). When growth is compared among populations of the same species, and even within the same population, very different patterns of growth have been reported, both in short and long terms (Present and Conover, 1992; ICES, 2000). The plasticity of fish growth, i.e. the phenotypic response to a changing environment, including fishing pressure (Summerfelt and Hall, 1987; Radtke and Fey, 1996) is an important ecological feature of fish. Due to its influence on fish population dynamics, the sources of variation in fish growth will be described below.

Factors affecting growth

Feeding conditions are normally considered the main environmental factor causing variations in fish growth. More specifically, food availability, which is a function of relative abundance and dispersal of prey, is believed to be most important. While prey dispersal is independent of predator density, relative prey abundance depends on the absolute quantity of prey in the ecosystem, i.e. prey density (Ringler and Brodowski, 1983; Pepin et al., 2000; Laurel et al., 2001), as well on the density of predators, including both the target species involved in the growth analysis and competitors. Thus, competition plays an important role in feeding success (Łomnicki, 1988; Harwood et al., 2001) and hence for growth and future abundance (Wang, 1999).

Foraging theory predicts that animals maximize their net rate of energy return when selecting prey (Stephens and Krebs, 1986). Thus, fish have been found to be highly selective in terms of prey size (Greene, 1986; Sih and Moore, 1990; Kaiser and Hughes, 1993; Juanes, 1994). Although predators have a tendency to eat the largest prey available (Pandian and Vivekanandan, 1985), the observed diet composition shows a significantly smaller average prey size (Blaxter, 1965; Juanes, 1994). This is believed to be due to the fact that the energy spent on predation increases with prey size. Thus, for the predator there exists an optimal prey-size range that maximizes the relation between the energy obtained and the energy used to catch the prey (Wotton, 1990). Both the mean and the range of prey sizes selected tend to increase with fish size (Figure 3) (Persson, 1990; Juanes, 1994; Scharf et al., 2000), and many species also switch to other prey types (Werner and Gilliam, 1984), as for example salmonids changing from invertebrate eaters to piscivorous as they grow (Keeley and Grant, 2001).

Growth may fall due to a deficit of the preferred preys (Mittelbach, 1983), but in such situation some species may shift to alternative preys, with lower energetic content. Non-optimal preys in the diet may negatively affect growth rate of the predator. The importance of prey quality is demonstrated by the direct effect of capelin abundance on growth and condition of Northern cod (Lilly, 1987) and Northeast Arctic cod (Bogstad and Mehl, 1997). Clearly, below the maintenance ration, fish do not grow in length and lose weight (Figure 2). The timing of foraging during the day (Boujard and Leatherland, 1992; Sanchez-Vázquez and Madrid, 2001) as well as in relation to demanding processes like migration and maturation may also have a profound effect on growth (Jobling, 1994). This is exemplified most clearly in Norwegian spring-spawning herring (*Clupea harengus*), a capital breeder (Stearns, 1992), feeding only during summer time (Slotte, 1999).

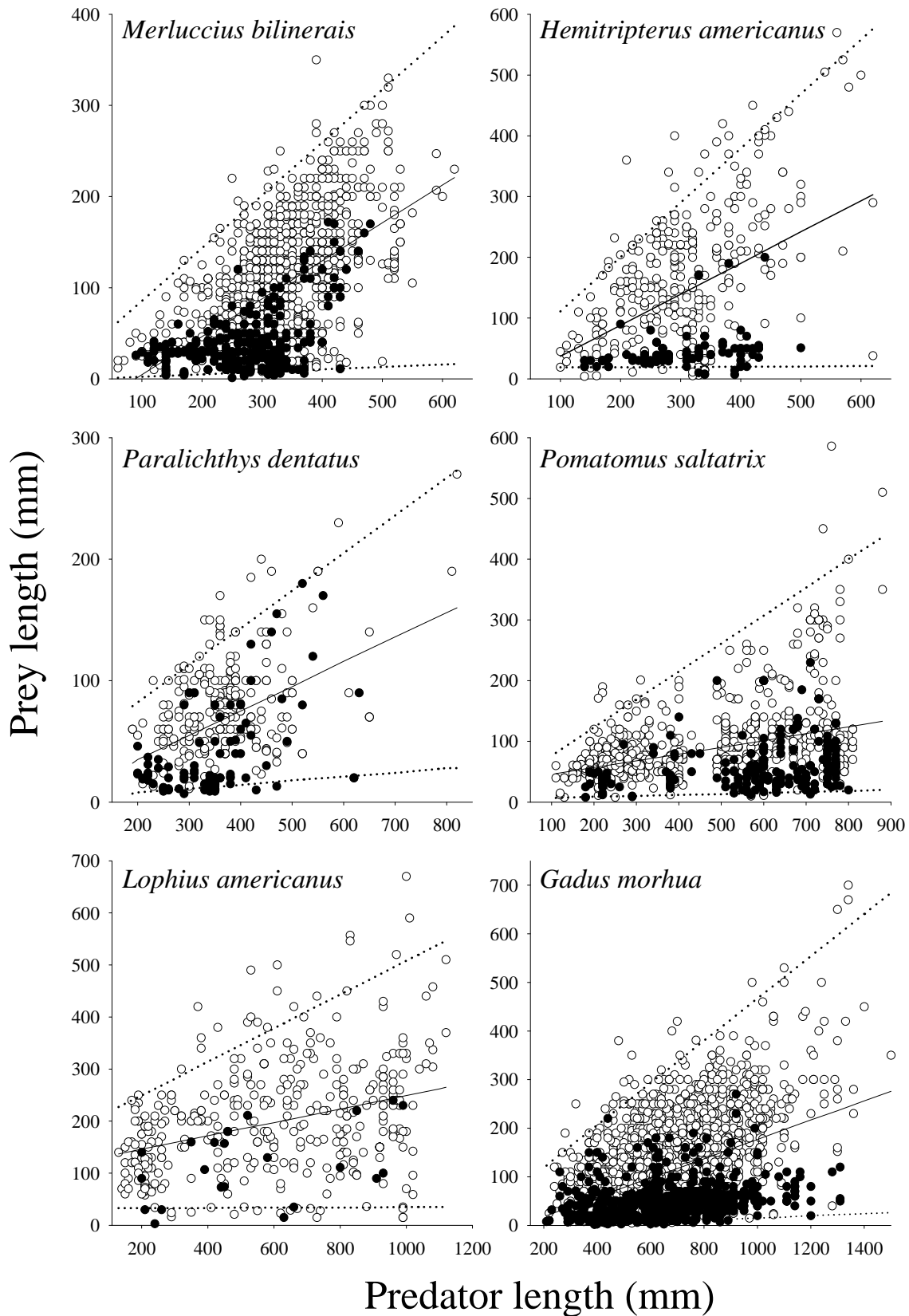


Figure 3. Predator size *versus* prey size diagrams for marine predatory fishes from the northeast shelf of USA. Each symbol represents a single prey consumed by a predator. Open circle: fish prey; black circles: invertebrate prey. Regression lines show ontogenetic changes in prey sizes consumed with increasing predator size for all prey combined. Dashed lines: minimum and maximum prey sizes; continuous lines: mean prey sizes. Source: Scharf et al. (2000).

Temperature affects growth in fishes through metabolic rates and assimilation (Brett, 1979). There is a difference between the energy in the food consumed and the energy finally assimilated, which in turn depends on food quality and two positive temperature depending factors: absorption efficiency and metabolism (Wootton, 1990). Variations in these two factors will affect consumption rates (Colgan, 1973), which are especially critical at early stages of development. Physiological processes accelerate with temperature (except at very high temperatures), which are supported by increasing catabolism, demanding higher food consumption to maintain body mass (Sogard and Olla, 2001). As a consequence, the optimal temperature for growth decreases as food availability decreases (Brett et al., 1969; Crowder and Magnuson, 1983) and conversion efficiency is generally highest at temperatures slightly below those supporting the fastest growth (Brett et al., 1969; Woiwode and Adelman, 1991; Jobling, 1996; Björnsson et al., 2001) (Figure 4 and Figure 5). In a heterogeneous thermal environment, fish can reduce their metabolic costs by moving into colder temperatures as food availability decreases (Stuntz and Magnuson, 1976; Mac, 1985; Morgan, 1993; Sogard and Olla, 1996). This fact can partly explain latitudinal and geographic variation in growth rates among populations (Brander, 1995; Jonassen et al., 2000), and interannual variation in growth in populations (ICES, 2000). It should be remembered, however, that the effect of temperature on growth depends on fish size (Björnsson et al., 2001) (Figure 4) and, likewise, that the growth rate increases with temperature up to a maximum at some intermediate optimum temperature (Brett, 1979; Jonassen et al., 2000) (Figure 5). To mention only, temperature is not the only abiotic factor that should be considered in growth studies; other relevant ones include, among others, oxygen (Taylor and Miller, 2001) and salinity (Lambert *et al.*, 1994). Also, adaptations to maintain growth under suboptimal conditions are still not fully understood. For example, cod feeding at polar fronts on fatty food like capelin may remain in cold water (<2°C) over substantial periods during the main growing season (K. Michalsen, Institute of Marine Research, Bergen, Norway, unpubl. data).

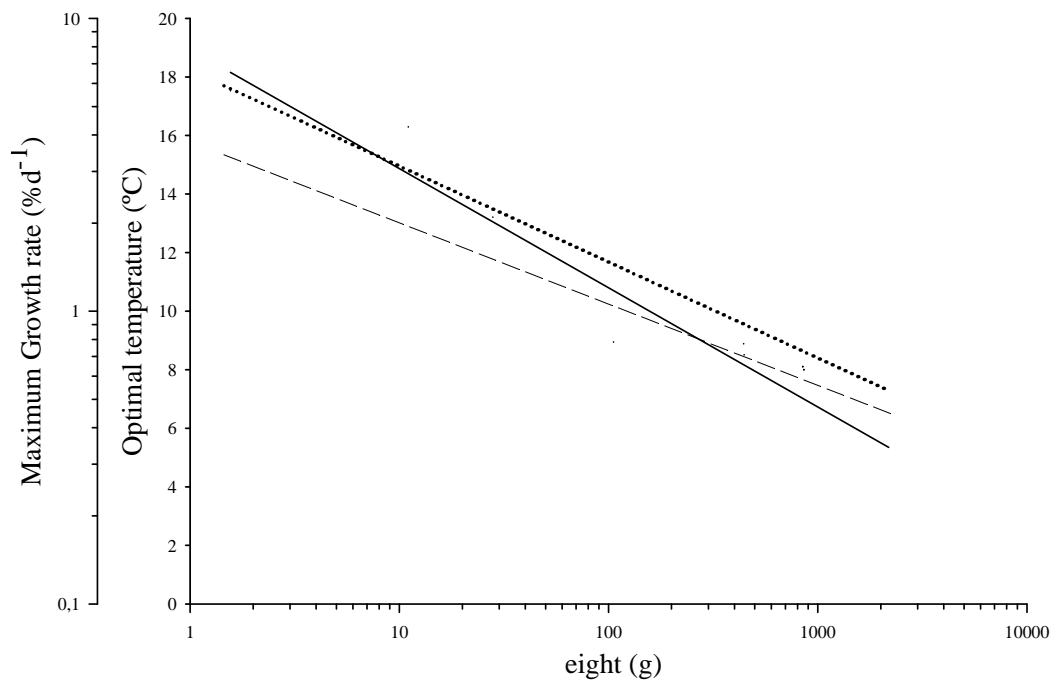


Figure 4. Relationship between fish weight and optimal temperature for growth rate (solid line), optimal temperature for feed conversion (dashed line) and maximum growth rate (dotted line), i.e., growth rate at optimal temperature, in cod (*Gadus morhua*). Source: Björnsson et al. (2001).

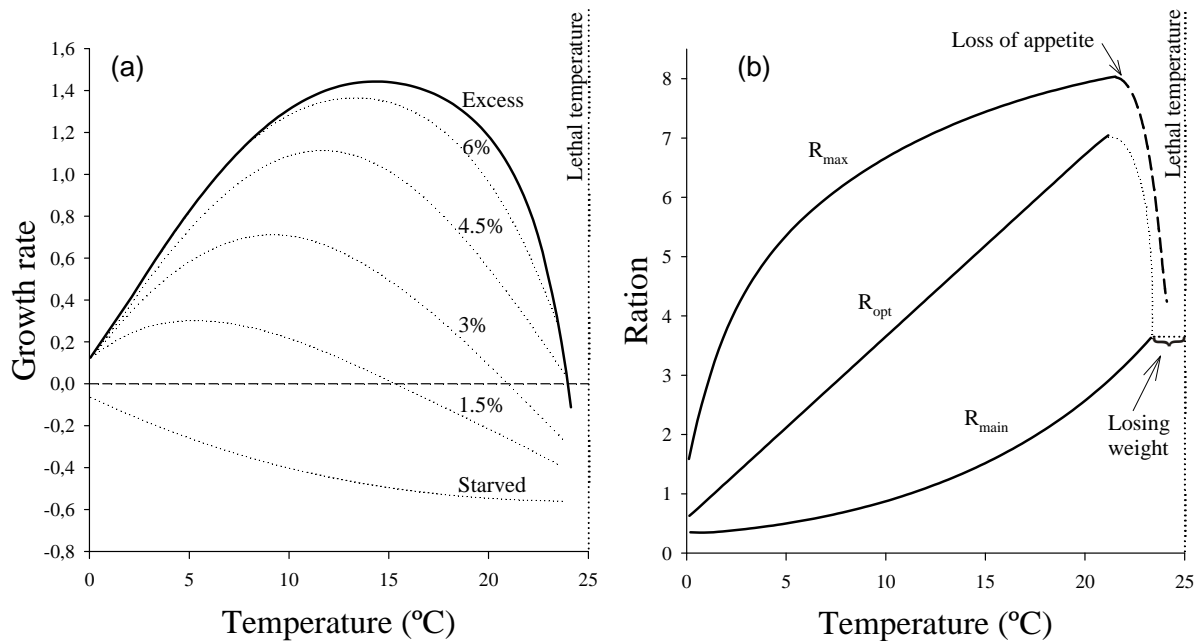


Figure 5. Relationship between temperature and (a) growth rate at different levels of ration and (b) different levels of ration, in fingerling sockeye salmon, *Oncorhynchus nerka*. Source: Brett et al. (1969).

MATURATION

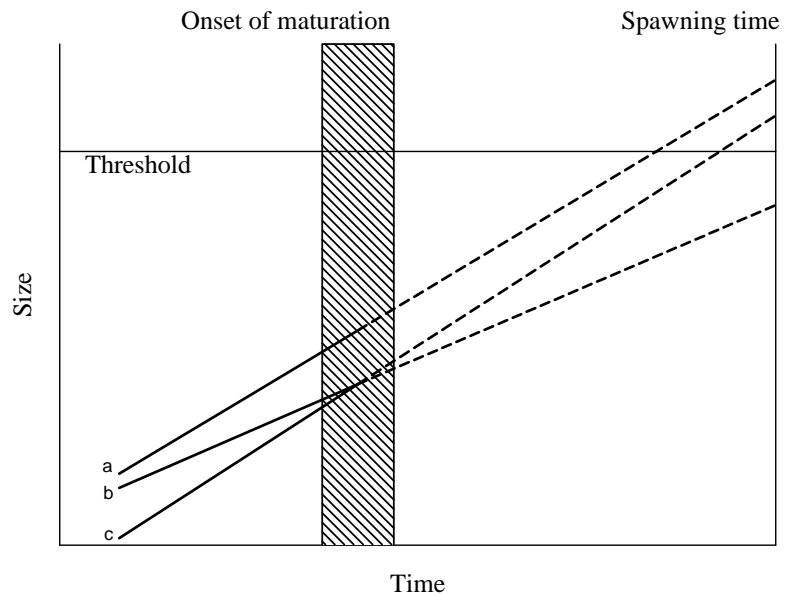
According to Pianka (2000), the biological success of an individual should be defined as the number of progeny produced in its lifetime that reach sexual maturity compared to the similar number produced by the whole population during the same time period. Maximizing the lifetime production of viable offspring demands a decision on timing of maturation in order to optimize the age schedule of reproduction (Roff, 1992). Roff (1992) divided this schedule in two components: age at first reproduction and reproductive effort. In this section we deal with a) physiological principles of maturation, b) relationships between age or size and initiation of maturation, and c) variation in reproductive effort throughout life.

Physiology of maturation

Initiation of maturation may to some extent depend on the attainment of a critical size (Le Bail, 1988; Roff, 1991). For each individual there seems to exist an optimum body size when to enter maturation; most fish species sexually mature when reaching 65-80% of their final maximum size (Beverton and Holt, 1959; Beverton, 1963). The onset of maturation involves several endocrine and metabolic changes to mobilize and reallocate both material and energy (Jobling, 1995; Evans, 1998). Female and male fish have to produce and develop sex cells, in both cases often at extremely high numbers, at least for the males. Body growth and accumulation of energy stores are likely to act as early triggering signals for determining the onset of puberty (Rowe et al., 1991; Hutchings and Jones, 1998; Dufour et al., 2000). The threshold value needed for an individual to enter sexual maturity has been found to refer to the time of first reproduction (Metcalf, 1998). In other, this suggests that maturation is only triggered if the individual is on course to surpass the threshold state by the time of spawning

(Roff, 1996) (Figure 6). These thresholds are genetically predetermined (Thorpe and Metcalfe, 1998), while many of the triggering factors are environmentally controlled. Thus, the process of maturation is significantly influenced by the environment (Thorpe et al., 1998) (to be discussed later).

Figure 6. The concept of threshold determining maturation. The sexual maturation is only triggered if the state of the fish (e.g. its body resources) at a given time is such that the projected trajectory (in this case growth trajectory) will exceed the relevant threshold by the time of spawning. The future state of the fish is presumably estimated from a combination of its current state and the rate at which such a state has been changing. In this example only fish a and c will mature. Source: Metcalfe (1998).



Age and size at maturation

Size (length, L) at maturation, L_{mat} , is defined as the size as which an individual becomes sexually mature, the equivalent term for age (A) being A_{mat} . In fish, i.e., in species showing indeterminate growth (see definition above), size and age are not necessarily coupled. Fish populations consist of individuals of different ages and sizes, and with different growth trajectories. In the particular case of semelparous species (see Box 4), as the Pacific salmon (*Oncorhynchus* spp), age at maturation determines life span. In some other species, the proportion of adults surviving the first breeding season is very low, as in the genus *Salmo*. However, in most of the exploited species, mortality is not expected to increase drastically following maturation, though maturation does, as mentioned above, negatively affect growth. In term of individual size at maturity this typically varies significantly among members of the same population, an exception being short-lived species, such as sardines, where all individuals become sexually mature within a short size interval. Thus, in a given population the proportion of mature individuals changes with size (and age). A frequently used variable to reflect this phenomenon is size and age at 50% maturity, or L_{50} and A_{50} respectively (see Box 3).

Between species A_{50} ranges from a few weeks in some cyprinodonts (Wootton, 1990) to more than 30 years in orange roughy (*Hoplostethus atlanticus*) (Horn et al., 1998). Populations of a single species also differ in their A_{50} and L_{50} (Figure 7), usually in response to latitude (temperature, light), food supply and intrinsic growth rate (Trippel, 1995). Examples of this are plentiful in the literature (Ni and Sandeman, 1984; Bowering and Brodie, 1991; Jennings and Beverton, 1991; Trippel, 1995; Brodziak and Mikus, 2000; Yamaguchi et al., 2000).

Within a population, A_{50} and L_{50} are known to be highly plastic parameters (Stearns and Crandall, 1984), varying both in short and long term under external pressure, but in particular at major changes in population abundance (i.e. density-dependent responses) (Adams, 1980;

Gunderson, 1980). Environmentally induced changes in growth produce variation in the phenotypic expressions of size and age at maturation traits, known as “phenotypic plasticity” (Roff, 1992). If a phenotype varies as a function of the variation in the environment, then the phenotypic plasticity determines the reaction norm (Stearns, 1989) (Figure 8). Ecologically speaking, the optimal reaction norm is the one that maximizes population fitness. Shifts in age and size at 50% maturity are well documented in many fish stocks (Pitt, 1975; Haug and Tjemsland, 1986; Jørgensen, 1990; Morgan and Brattey, 1997; Trippel, 1995; Rijnsdorp and Vethaak, 1997), even in very short terms (Figure 9).

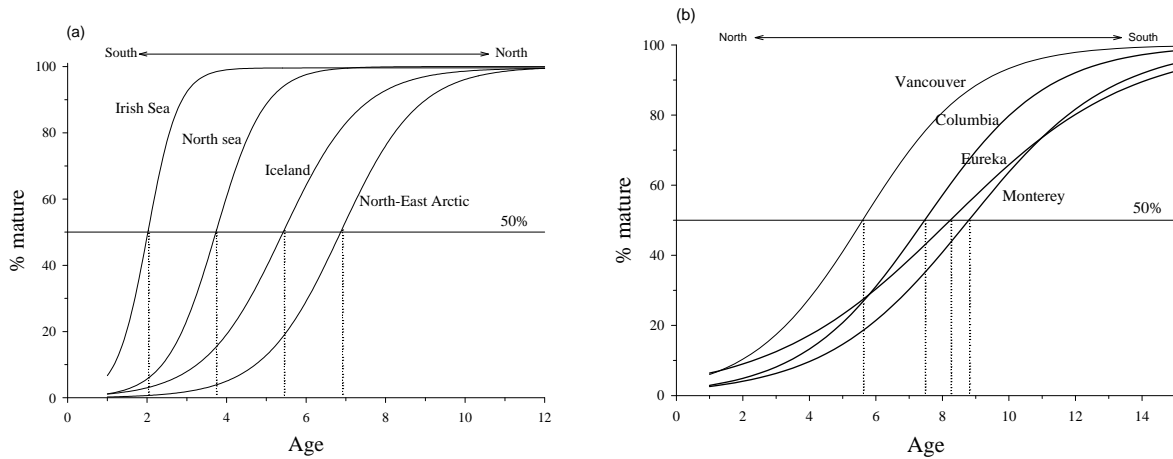


Figure 7. Geographic variation in age at 50% maturity in four populations of (a) cod (*Gadus morhua*) in 2001 and (b) Dover sole (*Microstomus pacificus*) in the early 1990's. Note that latitudinal clines are opposite in cod and Dover sole. Sources: Brodziak and Mikus (2000); ICES (2001a,b,c,d).

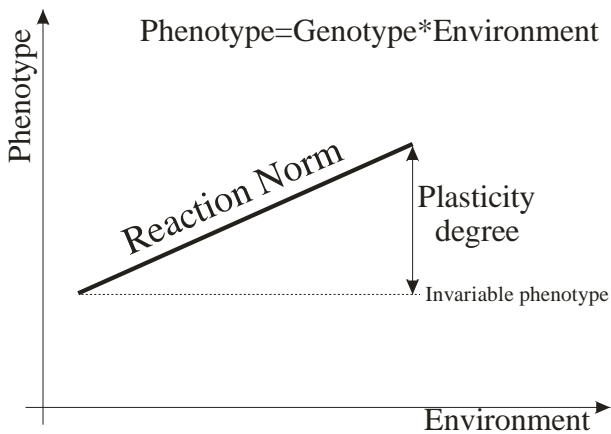


Figure 8. Schematic representation of a reaction norm. Phenotype is the result of the interaction of genotype and environment. If the environment has no effect on the genotypic expression, then phenotype remains invariable for this genotype. If the phenotype changes with the environment a reaction norm is produced.

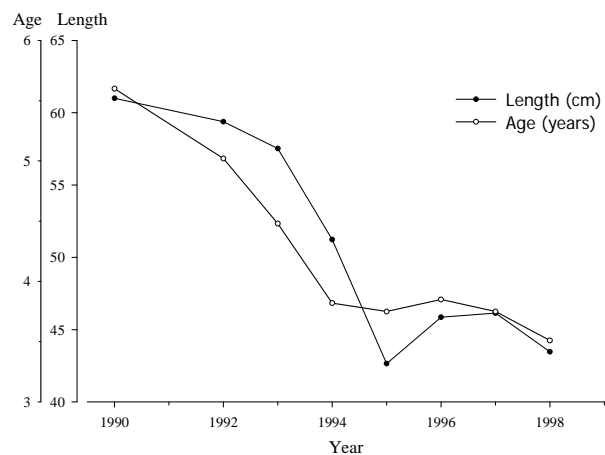


Figure 9. Variation in size and age at 50% maturity in Flemish Cap cod (*Gadus morhua*) from 1990 to 1998. Sources: Saborido-Rey and Junquera (1999a,b).

Box 3. Age and size at 50% maturity

At the population level, age/size at maturation is often defined as the age/length at 50 % maturity, abbreviated as A_{50} and L_{50} , and representing 50% probability of being mature. To estimate these properties, the proportion of mature individuals at each age or size within the population is needed, i.e., the maturity ogive (often written as ogive).

Maturity ogives are often calculated after a macroscopic observation of the gonads at a time of the year when maturity can be easily determined, usually during spawning or shortly before. Reliability of this method has been questioned, especially for species with a protracted spawning season, and when separating immature fish from recovering/spent fish. The use of histological techniques has proved to be much more precise (West 1990) and advantageous (Saborido-Rey and Junquera, 1998; see recommendations in Anon. 2003) overcoming these problems and has become widespread in recent years.

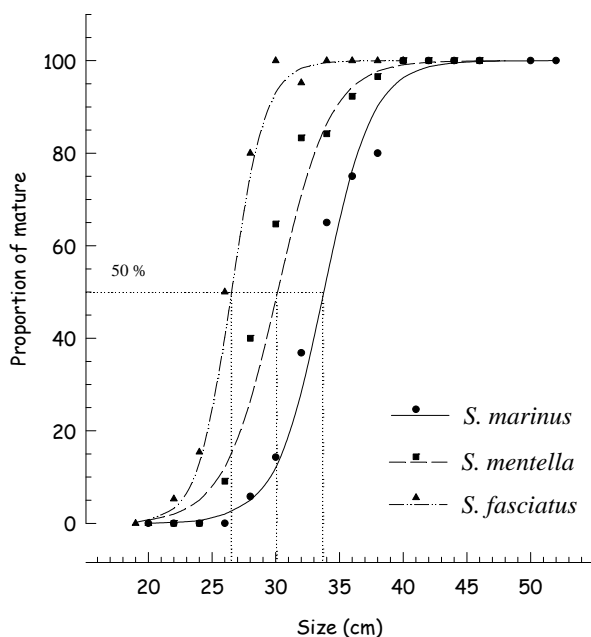
Often maturity is estimated based on samples from commercial catches. Since the fishery normally is selective, biased maturity ogives and, hence A_{50} and L_{50} , are expected. A length-stratified sampling programme is recommended. However, for most species, a given age can include several length classes and the probability of being mature at a given age is influenced by length at that age. Thus a bias in the estimation of length-based maturity ogive can result if the size frequency distribution at age is not considered (Morgan and Hoenig, 1997).

Once the maturity ogive has been calculated, it is fitted to a logistic equation (see illustration), which can have different forms, but classically it is expressed as follows (Ashton, 1972):

$$\hat{P} = \frac{1}{1 + e^{-(\alpha + \beta L)}}$$

where \hat{P} is the expected proportion of mature; α and β are the coefficients of the logistic equation and L is the size (or replaced with A in terms of age). Thus L_{50} is:

$$L_{50} = -\alpha/\beta$$



Maturity ogives and size at maturity for three species of redfish coexisting in Flemish Cap, showing how each species display a different size at maturity, which is also reflected in age (not shown). Source: Saborido-Rey (1994)

Maturation and reproductive success

The size and age at which a fish become sexually mature is postulated to have a profound effect on its reproductive success. Firstly, this success is assumingly closely tied to larger body size (Roff, 1992). Secondly, in iteroparous fish there is an unavoidable trade-off between current and future reproduction: maturation may decrease survival, deplete body reserves, reduce growth and hence reduce the success of future reproductive events (Heino, 1998). Both components are very much related with the reproductive strategy of the fish (Box 3).

Larger and older individuals have different reproductive attributes than smaller and younger individuals (Solemdal, 1997; Trippel et al., 1997). Most of these works have been undertaken on females only, but also some male characteristics, such as spawning (dominant) behaviour, might change with age (see Trippel et al., 1997 and references therein). Maternal physiological status, spawning experience (recruit or repeat spawners) or food ration during gametogenesis are all known to alter fecundity, egg and larval quality (Hislop et al., 1978; Kjesbu et al., 1991; Trippel, 1999; Marteinsdottir and Begg, 2002). Fecundity and relative fecundity (see Box 4 for further explanations of fecundity) generally increase with body size (Figure 10) (Wootton, 1979; Kjesbu et al., 1998). Consequently, at the population level the annual population fecundity (total egg production) will, in addition to number of mature specimens, depend on size (age) structure, but also fish condition (Marshall et al., 1998). Condition factor is, as explained above, a function of relative densities of prey and predator. Females in poor condition may show high levels of atresia significantly reducing realised egg production or even skip spawning altogether (see review of Witthames, 2003). In multiple batch spawners species (Box 4), the duration of the spawning season increases with the size of the fish, mainly because the number of batches produced is larger but also because of the existence of size-specific spawning times; the larger fish are often assumed to spawn first in the year (Kjesbu et al., 1996; Marteinsdottir and Begg, 2002). This reproductive strategy is believed to increase the probability that larvae hatch in a suitable environment, cf. the match-mismatch hypothesis (Lambert and Ware, 1984). In other species such as Atlantic herring, a single batch spawner, repeat spawners shed their eggs earlier in the season than recruit spawners, but in contrast to the situation for recruit spawners their spawning time is independent upon fish size (Slotte et al., 2000). Egg size is positively related to female size (Kjesbu et al., 1996; Murawski et al., 2001; Marteinsdottir and Begg, 2002) (Figure 11). Furthermore, larger females with higher energetic surplus apparently allocate more resources in form of nutrients (yolk-sac) to the egg (Figure 12a). Many larval features will depend on egg size; a bigger egg means a bigger yolk sac. It has been shown that larvae from big eggs are larger, grow faster, and in general their quality, and therefore, their probability to survive, should be higher (Figure 12b) (Ware, 1975b; Solemdal et al., 1995; Marteinsdottir and Steinarsson, 1998; Trippel 1998; Vallin and Nissling, 2000).

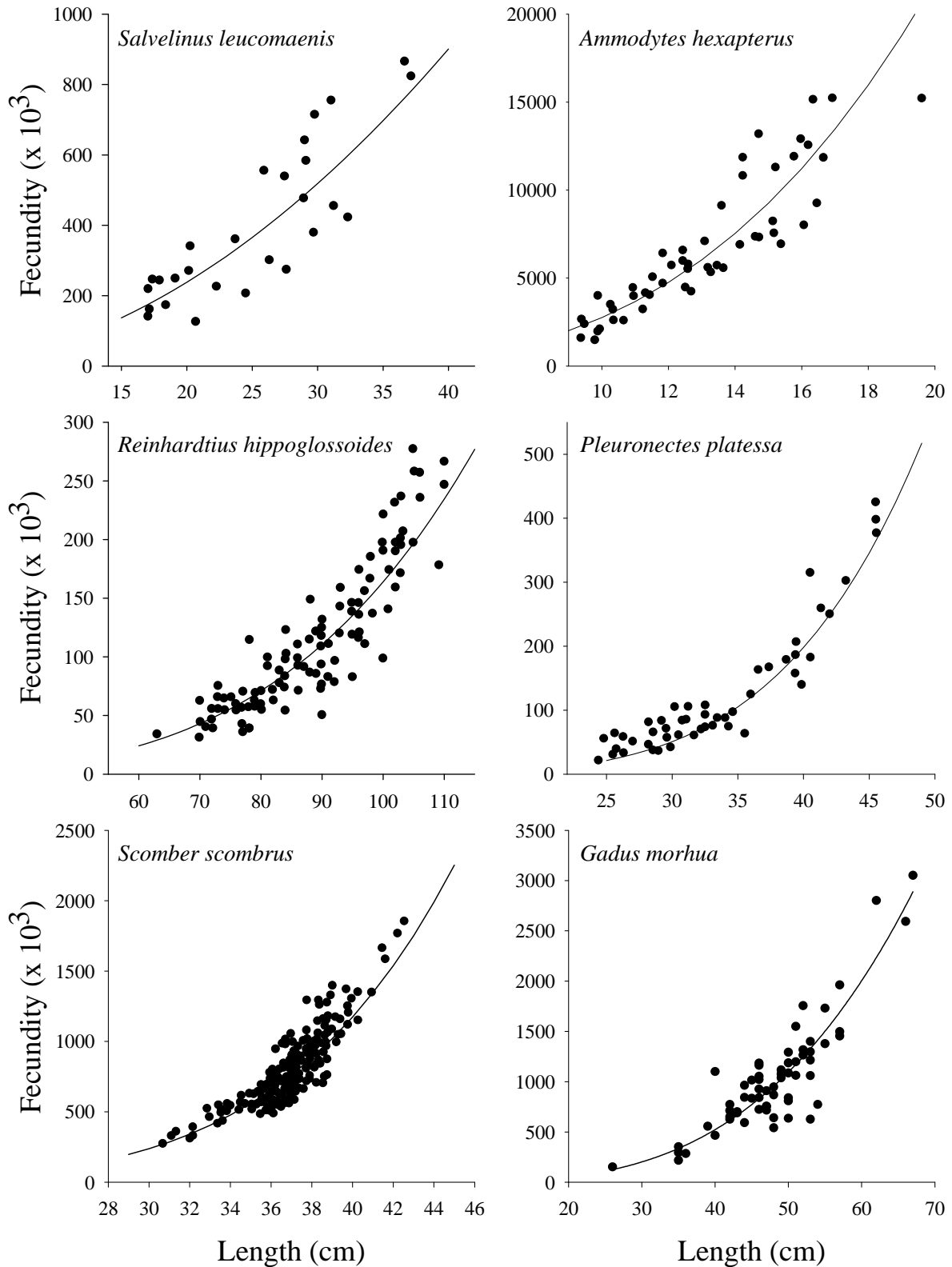


Figure 10. Relationship between potential fecundity and fish length for six species with different reproductive strategies. Sources: Morse (1980); Horwood (1993); Morita and Takashima (1998); Robards et al. (1999); Gundersen et al. (2001); Kraus et al. (2002).

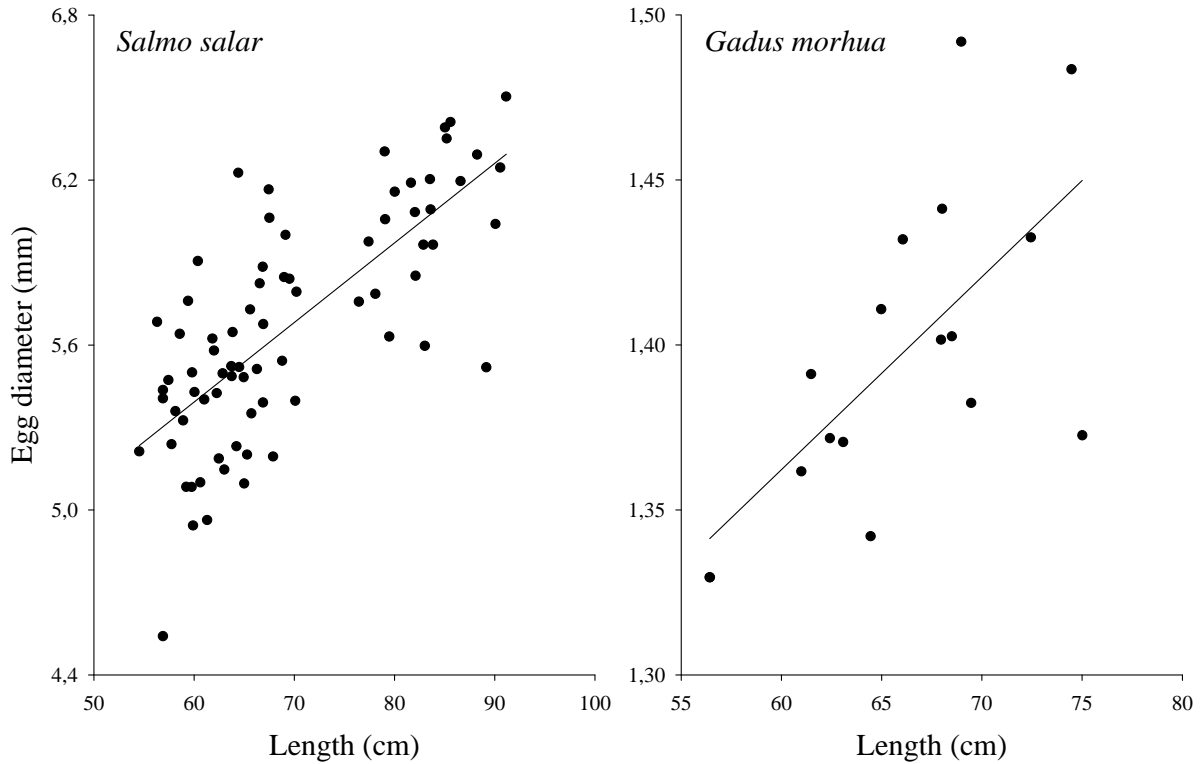


Figure 11. Relationship between maternal size and a) egg diameter of Atlantic salmon (*Salmo salar*) from Scottish waters and b) mean egg diameter of the first batch of Norwegian coastal cod (*Gadus morhua*), and the fitted linear regressions. Sources: Thorpe et al. (1984) and Kjesbu (1989).

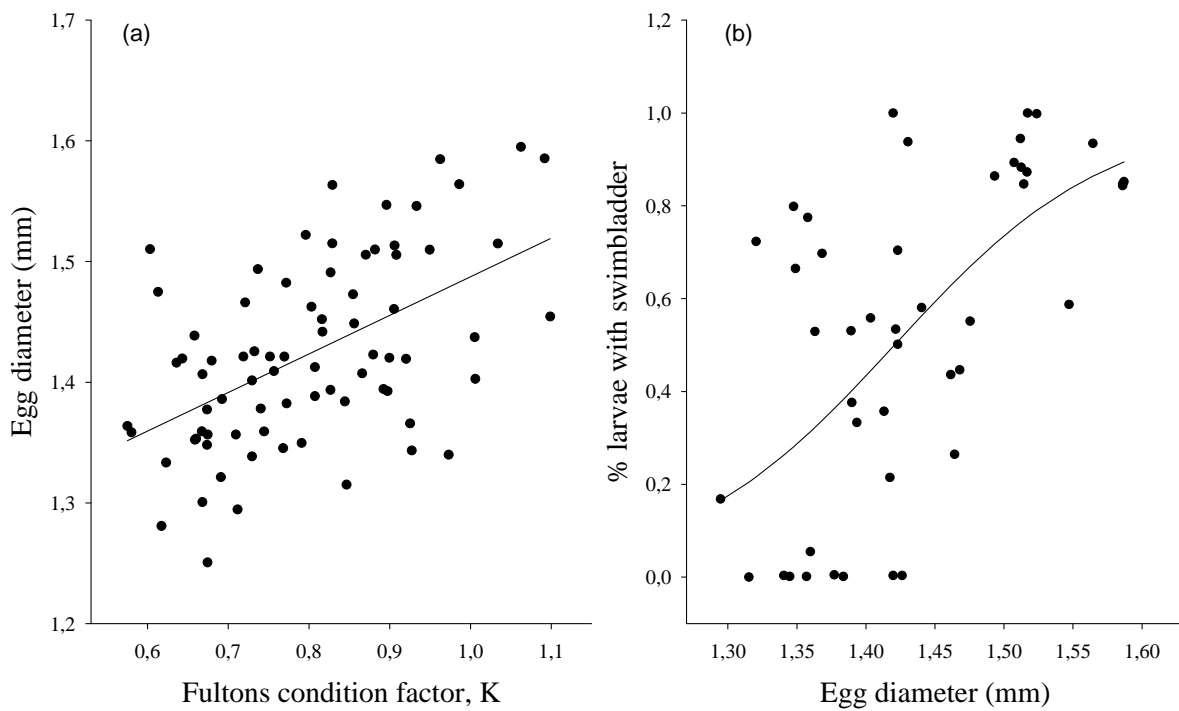


Figure 12. Relationships between a) female condition ($K = 100 \cdot \text{eviscerated weight} \cdot \text{length}^{-3}$) and mean egg size, and b) mean egg size and the proportion of larvae that developed swim bladder by day 10 post-hatch, in cod (*Gadus morhua*) off Iceland. Data are fitted to a linear regression (a) and to a logistic regression (b). Source: Marteinsdottir and Steinarsson (1998).

Box 4. Reproductive strategies and fecundity

Most of the commercially exploited species are oviparous (females release eggs into the water, where fertilization happens), but some important commercial species like rockfishes and sharks are viviparous, i.e., females extrude embryos or larvae (being at different levels of development depending on species) after an internal fertilization.

In the light of population dynamics the most relevant classification of reproductive strategies is based on number of lifetime reproductive efforts and how the eggs develop and are released. Thus, it can in the first instance be distinguished between:

- a) **Semelparity.** Fish spawn once and then die. Individuals invest the whole energy to ensure a high survival of eggs and larvae. Usually there is a very high energetic expenditure in reproductive behaviour, such as migrations, nest building, mating etc. Typical examples are the anadromous *Oncorhynchus* or catadromous eels.
- b) **Iteroparity.** Fish spawn more than once in their lives. Thus, there exists a post-spawning survival. Only parts of the surplus energy is allocated to reproduction while other parts are put aside for survival and further growth. It is the most common reproductive mode in fishes.

Marza (1938) provided a useful classification of ovarian type based on the dynamics of organization of the ovary itself:

- a) **Synchronous:** all oocytes, once formed, grow and ovulate from the ovary in unison; further replenishment of one stage by an earlier stage does not take place. Typical of semelparous species.
- b) **Group-synchronous:** at least two populations of oocytes can be distinguished at some time; a fairly synchronous population of larger oocytes (defined as a “clutch”) and a more heterogeneous population of smaller oocytes from which the clutch is recruitment. The former includes oocytes that are to be spawned during the current breeding season, while the last includes oocytes to be spawned in future breeding seasons. This is by far the most common situation among teleosts.
- c) **Asynchronous:** oocytes of all stages are present without dominance of any populations. The ovary appears to be a random mixture of oocytes in every conceivable stage. Only when hydration occurs there is a clearly separated stock of oocytes regarding oocyte diameter.

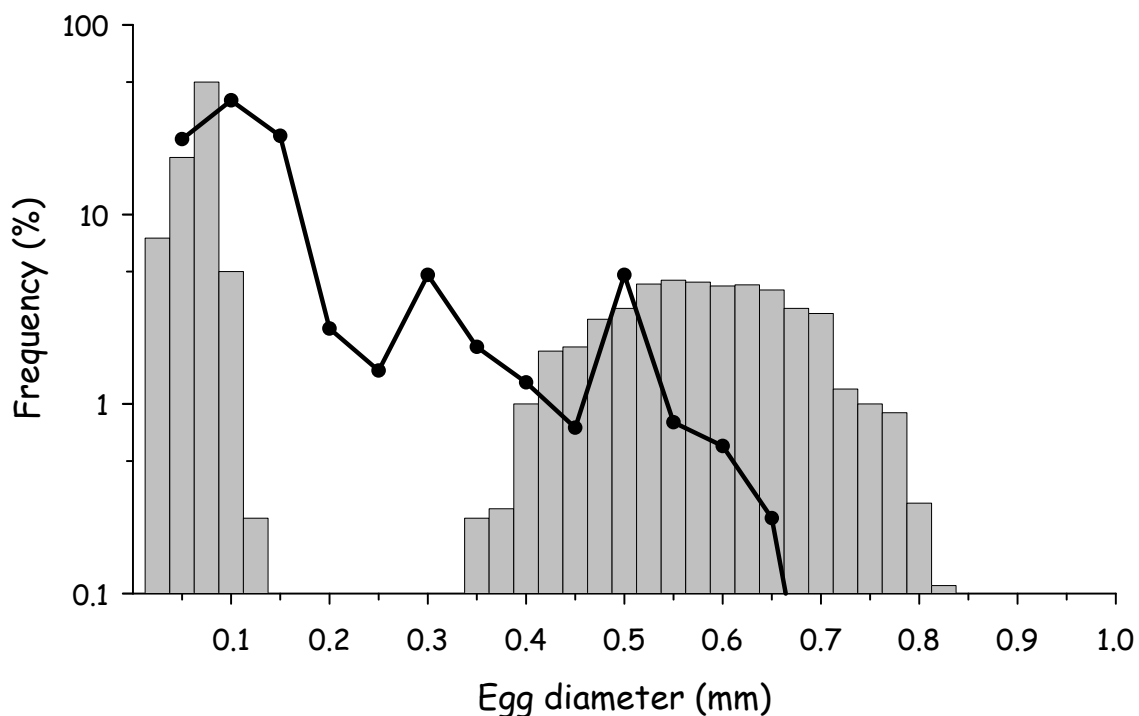
Hunter *et al.* (1985) defined two types of fecundity (principles for oocyte recruitment):

Determinate fecundity: In fishes with determinate fecundity, the standing stock of yolked (vitellogenic) oocytes at spawning is considered to be equivalent to the potential annual fecundity measured prior to spawning (i.e., in maturing females). This applies, however, only if there is no atresia (resorption of vitellogenic oocytes) present. Atresia might, however, be frequent, at least for fish in poor condition (Witthames, 2003). In multiple batch spawners (see below) with a determinate spawning strategy, the numbers of vitellogenic oocytes remaining in the ovary decreases steadily with each spawning event (batch) because the standing stock of vitellogenic oocytes is not refilled during the spawning season (Kjesbu *et al.*, 1990; Hunter *et al.* 1992; see also review in Hunter and Macewicz, 2003).

Box 4. Cont.

Indeterminate fecundity: This term refers to species in which potential annual fecundity is not fixed before the onset of spawning; previtellogenic oocytes recruit to the vitellogenic mode(s) and are subsequently spawned during the spawning season (Hunter *et al.*, 1992). Thus, in such species oocytes contributing to the annual fecundity might appear at any time during the season (*de novo vitellogenesis*) (Hunter and Goldberg, 1980). This seriously complicates fecundity determination, but circumvented normally by counting only fully developed eggs (more correctly hydrated oocytes) instead of vitellogenic oocytes, i.e. the batch fecundity approach (see review in Hunter and Macewicz, 2003). If vitellogenic oocytes are counted, atresia needs to be considered as well as defining a lower threshold value (oocyte diameter) for vitellogenic recruitment (Witthames, 2003).

Within a spawning season some species mature and release eggs in batches over a period that can last days or even months, the so-called **batch spawners**. Other species spawn all the eggs in a single episode and are designated as **total spawners** (which should be held separate from semelparous species, which can be batch or total spawners). Batch spawners are typical in species with indeterminate fecundity, but also a high number of those species with determinate fecundity are batch spawners. It is apparently a strategy to release the eggs over a long period of time to increase the survival probability of the offspring. Besides, in species releasing pelagic eggs, the hydration process in itself drastically increase the egg volume, making it physically impossible to contain all hydrated eggs in the ovary at one time and thereby implies the adoption of a batch spawning approach.



Size distributions of eggs (more correctly oocytes) in anchovy (*Engraulis mordax*) (line) and redfish *S. mentella* (bar). Note that in redfish (group-synchronous, determinate fecundity) there are two groups of oocytes, the bigger ones to be spawned in the current breeding season and the smallest ones to be spawned in the future, while in anchovy there is a continuous distribution (asynchronous, indeterminate fecundity). Anchovy data are from Hunter *et al.* (1985), while the redfish data are taken from the files of the first author.

DISCUSSION

Growth and reproduction are in principle parallel processes competing for the same limited amount of body resources. Growth is affected by a number of factors, some exclusively dependent on the environment, like temperature. Others, such as food supply, can be altered by man. Exploitation may influence the individual growth of fish, both at short and long term, in four different manners: 1) by reducing population abundance (giving rise to density-dependent responses), 2) by altering the density of the different preys (incl. switch to non-optimal feed), 3) by diminishing the abundance of predators/competitors, and 4) by systematic, selective removal of individuals growing at rates deviating from the average for the original population as a whole. Further complexity is added to the prey-predator relationship as more interacting populations are affected by the fishing effort. Logically, if a single species is targeted, individual growth will be improved by reduction in intraspecific competition provided the environmental conditions remain constant. However, in practice several species are exploited, so changes in interspecific relationships may be just as important as the intraspecific ones, creating an extraordinarily complex situation. Excluding here that fishery can induce adaptive changes in the population, the simplest view is that increasing fishing pressure will increase individual growth, due to an improved predator-prey situation. Growth may, however, remain unchanged if a simultaneous reduction in prey availability occurs due to changes in environment or corresponding level of exploitation. While environmental variations produce changes in age at maturation at medium and long term, fisheries, altering population abundance and individual growth rate, can produce a quick response in age at maturation as shown for several fish stock, e.g., as in the case of Flemish Cap cod.

Onset of maturation reflects that certain requirements, either with respect to size or accumulations of energy stores, or both, have been fulfilled at a specific time in life. Thus, a prerequisite for maturation is growth, but when initiated maturation negatively affects further somatic growth as stated by Alm (1959) and demonstrated by Roff (1983). Because fecundity and viability of the offspring are positively related to maternal size, any decreasing growth rate after maturation may have a negative effect on reproductive success of the individual. The phenomenon of atresia and skipped spawning might be seen in light of both survival strategies (at low fish condition) as well as saving resources for further more successful spawnings (i.e. at higher body masses/better environmental conditions). Furthermore, because of the unavoidable energetic trade-off between growth and maturation, changes in growth rate before maturation will often lead to significant changes in age schedule of maturation. If juvenile fish growth is reduced, size at maturation is expected to happen at an older age. Conversely, under accelerated growth, maturation should occur earlier. However, optimum size at maturation is not the same under different ecological or physiological conditions. Fisheries, or more specifically the reduction in population size, are commonly believed to be one of the major causes behind noticed changes in age at maturation (and growth rates). If maturation occurs when a certain body size is achieved, accelerated growth should imply a reduction in age at maturation, but not necessarily in size at maturation. However, the majority of documented shifts in maturation not only refer to age, but also size, as shown in this review. Thus, under these circumstances, the smaller fish have apparently accumulated enough surplus energy to successfully support the cost of reproduction, cf. plasticity and reaction norm for size at maturation. However, age at maturation is also a heritable trait, and the shift to an earlier age and size at maturation becomes a function of changes in genotype frequencies in the population over

time (Trippel, 1995). In a heavily exploited population, characterised among other aspects by excessive removal of larger individuals, fish genotypically programmed to late maturation (at large size) are inevitably much less likely to reproduce before being fished out. Contrarily, those individuals programmed to mature early, and at smaller size, may reproduce at least once. This principle should be reflected, through generations, in a higher relative abundance of fish genotypically predetermined for early, small-size maturation. Such a manipulation at the population level may not only affect the composition of the realised commercial catch but also change the ecological fitness. The long-term effects of this are still uncertain but if happening, may seriously influence productivity of harvested fish stock.

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