Life-history approach to habitat shifts for coastal cod, *Gadus morhua* L.

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Abstract. A general ecological approach to habitat shifts of juvenile coastal cod is provided. The aim is to show that optimal timing of juvenile releases in extensive cod mariculture can be investigated by adopting a theoretical framework based on evolutionary and ecological relationships. In order to illustrate what can be achieved from the use of this theory, we have utilized available data sets for cod, *Gadus morhua* L. These data sets are from four habitat types: (a) the natural pelagic habitat, (b) a pond used to rear juveniles, (c) net pens used to raise juveniles and (d) the shallow benthic habitat in a west Norwegian fjord (Masfjorden) where a large-scale extensive cod mariculture experiment is under way. For the four habitat types, the time-dependent instantaneous growth rates (g_t) and mortality rates (z_t) are estimated. Theoretically, the fish should at any time stay in the habitat that provides the lowest mortality rate per growth rate. For individuals it would be favourable to shift from habitat A to B at the time t when the increasing z_{tA}/g_{tA} intersects with the decreasing z_{tB}/g_{tB}. The prediction of cod's natural habitat shift from pelagic to benthic (i.e. settlement) is consistent with field observations, and the intuitively realistic outcome that net pens are better habitats for cod than both the pond and the benthic fjord habitat from June/July, indicates a validation of the life-history approach. The results from our analysis point in the direction that optimal timing of release will generally be after cod have reached a size at which they settle to the benthic fjord habitat. The previous releases of larval cod in Norway from the turn of the century until the 1970s are discussed in view of these results.

Introduction

During their first year of life, wild Atlantic cod, *Gadus morhua* L., in western Norway undergo a morphological change during the pelagic larval period, metamorphosis (Pedersen & Falk-Petersen 1992), approximately 40–45 days after hatching (Blom, Otterå, Svåsand, Kristiansen & Serigstad 1991). Subsequently, the cod 'settle' to the nearshore benthic habitat at 0–20 m (e.g. Godø, Gjøsæter, Sunnanå & Dragesund 1989; Svåsand & Kristiansen 1990). As pelagic larvae, cod feed on zooplankton (e.g. Blom *et al.* 1991), but switch to feed on gobies and benthic crustaceans after settlement (Salvanes 1991b). Mortality on pelagic larvae is mainly due to predation from large crustaceans, fish and jellyfish (Hunter 1984), whereas mortality on settled cod is due to predation from larger gadids (in Masfjorden primarily from large cod and pollack, *Pollachius pollachius* (L.): Salvanes

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1991b). In the pelagic habitat there is no shelter for the larvae, while macroalgae serves as shelter for juveniles within the shallow nearshore habitats of the fjords.

Since the turn of the century millions of newly hatched yolk-sac larvae have been released in the US, Great Britain and Norway (Shelbourne 1964). These releases were intended to stabilize recruitment to the populations and the catches in coastal fisheries. However, 20 years ago it was realized that larval releases did not contribute to the cod populations (Tveite 1971). Presently, early juveniles (11–17 cm length: Nordeide 1993) have been released in large-scale enhancement experiments in western Norway (Smedstad 1991). The current release strategy is to rear cod larvae in a predator-free production pond (Blom *et al.* 1991) during the period when fish larvae in natural environments are very vulnerable to predation. The reared juveniles are then released into coastal areas of western Norway to increase local cod production and yield. The timing of these releases has been an ad hoc approach, and formalized analyses of optimal timing of releases (OTR) in an ecological framework are still lacking. Such an analysis will be beneficial because field investigations (Peterman, Bradford, Lo & Methot 1988) and simulation studies (Bollens, Frost, Schwaninger, Davis, Way & Landsteiner 1992) have indicated that predation and food limitation during the late larval and early juvenile periods largely influence year class survival.

One way to investigate the optimal timing of release is to utilize the theory of optimal habitat shift (Gilliam 1982; Werner & Gilliam 1984; Aksnes & Giske 1990). Werner & Gilliam (1984) showed that juvenile fish maximize their fitness in a non-reproductive season by staying in the habitat where mortality risk (z) per growth rate (g) is minimal. Also Mittelbach (1983) has shown that a switch to piscivory as the fish grows in size results in an accelerated growth rate because consumption of larger prey is more cost-effective. An increase in body size also reduces the risk of mortality because there are fewer potential predators (Werner 1986). Experiments by Gilliam & Fraser (1987) and Gotceitas (1990) have shown that fish are capable to trade-off between mortality risk and growth potential on the instantaneous time scale. Werner & Gilliam (1984) and Werner (1986) have shown that this trade-off also applies to the ontogenetic time scale. A habitat shift would be favourable when the function describing z_{tA}/g_{tA} in habitat A intersects the function describing z_{tB}/g_{tB} in the alternative habitat B (where t refers to time and indirectly to size) (Werner & Gilliam 1984). The z/g rule is supported by observations for a wide range of organisms, including insects (Nonacs & Dill 1990), amphibians (Skelly & Werner 1990) and mammals (Bowers 1990). In this paper we show that optimal timing of cod 'settling' (shift from pelagic to benthic) and of juvenile releases in extensive cod mariculture can be investigated utilizing this life-history theory. In order to illustrate the application, we have estimated mortality rates and growth rates from available data sets in four habitat types: (a) the natural pelagic habitat, (b) a pond used to rear juveniles in 1987 and 1988, (c) net pens used to raise juveniles and (d) the shallow benthic habitat in a west Norwegian fjord (Masfjorden, where a large-scale extensive cod mariculture experiment is under way), using data for 1987 and 1988. Published estimates of z and g are used for the pelagic larval period and for the production pond, whereas z and g are estimated from data for the benthic habitat of Masfjorden and for the net pen.

Theory of optimal habitat shifts

Fitness of a phenotype is the differential rate of reproduction of the individual relative to the population it belongs to. An individual can increase its fitness by increasing its reproductive rate r (Giske, Aksnes & Førland 1993). For a semelparous fish the following equation is valid:

$$r = \frac{\ln(bS)}{T} \tag{1}$$

where b is fecundity, S is offspring survival and T is the generation time. Note that all symbols used refer to values for each individual, and not for the population as a whole. For a semelparous life history the survival probability over the generation time can be expressed as a function of the average instantaneous mortality rate z:

$$S = e^{-zT} \tag{2}$$

A combination of Equations 1 and 2 illustrates that individuals can maximize their fitness by maximizing the inequality:

$$\frac{\ln b}{T} > z \tag{3}$$

Assuming that adult ontogenetic period is determined by a minimum size rather than a minimum age (Werner & Gilliam 1984), generation time can be expressed as a function of the average juvenile growth rate (g) from birth (w_0) to minimum adult mass (w_A):

$$w_A = w_0 e^{gT} \tag{4}$$

Then Inequality 3 becomes:

$$\frac{z}{g} < \frac{\ln b}{\ln \left(\frac{w_A}{w_0}\right)} \tag{5}$$

where for a juvenile individual, all variables at the right-hand side may be regarded as constants: minimum adult weight w_A is assumed constant, w_0 is the egg mass (or current juvenile weight) and is hence fixed, and a newly settling juvenile cod may on a short time scale not influence its fecundity in the distant future. On the left-hand side are two environmental variables z and g, and optimal behaviour under Inequality 5 becomes to minimize z/g. Optimal timing of habitat shifts is found at the intersection of time-dependent z/g curves for the available habitats (Werner & Gilliam 1984; Werner 1986).

In this study we use field data on cod from the four habitats mentioned earlier. For these habitats, the time-dependent instantaneous growth rate (g_t) and mortality rate (z_t) are estimated. The functions of z_t/g_t are obtained and presented graphically.

Mortality and growth rates

The daily instantaneous mortality rate z for a year class in a time interval may be estimated by solving the general equation:

$$\frac{U_{t_2}}{U_{t_1}} = e^{-z(t_2 - t_1)} \tag{6}$$

This assumes that the number of deaths at any time during the time interval between t_1 and t_2 is proportional to the number of individuals present in a year class (here U_{t_1} and U_{t_2} refer to indices of the numbers present of the year class at t_1 and t_2, respectively), that the year class investigated is nearly stationary and that the fraction of the cod year classes recruiting after t_1 is small. Equation 6 is used on beach seine samples of cod from the 0–5 m depth taken during the period late June to early October in the benthic habitat, but also on samples from the net pen. If a fraction of cod settle subsequent to t_1, the mortality rate will be under-estimated. Regarding the assumption that the year class is nearly stationary, this is realistic for cod within the 0–20 m depth of Masfjorden as judged by field studies and tagging experiments (Nordeide & Salvanes 1988; Salvanes & Ulltang 1992). This is also consistent with other field and tagging studies on coastal cod in Norway (Løversen 1946; Godø 1984; Svåsand & Kristiansen 1990). However, we cannot strictly neglect the possibility that some juveniles may have dispersed from 0–5 m (beach seine sampling depth range) to the 5–20 m depth range of the general cod habitat within the sampling periods. The effect of such a dispersion would be over-estimated mortality rates because a migration rate will always be included in mortality rates. Hence, this source of error would counteract that caused by inappropriate settlement by t_1. Both these potential errors will be taken into account in a sensitivity testing of the model predictions.

The daily instantaneous growth rate g in a time interval is estimated using the general equation (e.g. Bagenal 1978):

$$g_t = \frac{\ln w_2 - \ln w_1}{t_2 - t_1} \tag{7}$$

where w_1 and w_2 are gutted weights at t_1 and t_2, respectively.

If several estimates of z/g ratios were obtained (as done for cod in the pond), a regression analysis (Draper & Smith 1981) was used to fit a continuous function through the points. If only two or three points estimates of z or g could be obtained from the data, a straight line was drawn, and the equation for this line was used as an approximation for the function of mortality or growth rates versus time (indirectly size).

Application to data

Pelagic larval period

Mortality rates used for this habitat originate from data for the North-east Arctic cod as similar estimates are not available for coastal cod off western Norway. Sundby, Bjørke, Soldal & Olsen (1989) report that z decreases with age, having values of 0·115 per day (or 42 per year in terms of per-year rate) as average for ages 60–120 days after hatching, and 0·022 per day (or 8 per year) as average for ages 121–180 days after hatching (assumed to be 1 April). Because some 0-group North-east Arctic cod settle earlier than previously thought (Olsen & Soldal 1989), it could be argued that the $z = 0·022$ per day from Sundby *et al.* (1989) is an over-estimate. However, as the fraction of the year class settling early seems small compared with the fraction remaining in the pelagic habitat 121–180 days

after hatching, this mortality rate is expected to be only slightly over-estimated. The equation for the mortality function between the midpoints of the time periods given in Sundby *et al.* (1989) (i.e. *t* in the range 90−150 days after hatching) becomes $z = 0.2550 - 0.0016 \cdot t$.

Although experimental studies exist (Solberg & Tilseth 1984; Øiestad 1984; Øiestad, Kvenseth & Folkvord 1985), specific growth rates in terms of weight for the pelagic larval period are lacking for cod in natural environments.* The specific growth rates used for the pelagic habitat are therefore from Blom *et al.* (1991). They are estimated for newly hatched cod released into a saltwater pond in 1987, where they could feed on natural zooplankton until 60 days after hatching. From Blom *et al.* (1991) we found specific growth rates (g) for each fifth day within the period 11−60 days after hatching. Then we calculated the instantaneous mortality rates from the equation derived from Sundby *et al.* (1989) for corresponding days. Next we divided the obtained z values with corresponding g values to get the z/g ratios, and fitted a polynomial regression equation (Draper & Smith 1981) through the points of z/g. The use of g values from the pond could result in over-estimated growth rates because of (1) a higher temperature in the production pond due to restricted supply of cooler coastal water from tidewater exchange (G. Blom, personal communication), (2) size-dependent cannibalism (Folkvord 1991), (3) size-dependent growth (Otterå 1992), or (4) density-dependent effects of rearing cod at high density in a pond. The first three arguments indicate that these specific growth rates are over-estimates of the growth in the pelagic habitat of coastal areas of western Norway. Concerning the fourth argument, Blom *et al.* (1991) conclude that growth rate was density independent in the pond. Although the larval density was higher in the pond than in coastal water masses, this factor did not affect the growth rate negatively. Hence, the values of g for 'wild' cod larvae may be over-estimated, leading to under-estimated z_1/g_1 ratios as given by the equation of Table 1.

Production pond and net pen

Functions for the ratios of z/g in the production pond are estimated for 1987 (z_2/g_2; Table 1) and 1988 (z_3/g_3; Table 1) using the z and g values that Blom *et al.* (1991) provide for cod for ages 11−80 days after hatching when the individuals primarily feed on zooplankton. In 1987 cod were kept within the pond also for a longer time period than 80 days after hatching, and 50% of the reared juveniles were still in the pond at age 125 days (i.e. in early September) (G. Blom, personal communication). The z_4 and g_4 (Table 1) refer to the functions for mortality rate and growth rate estimated for this period.[†] In 1988 the cod were transferred from the pond to net pens at an age of about 90 days (i.e. in early July), and about 90% of them were released into Masfjorden a month later (on 6 August). The remaining 10% were kept in net pens for a longer period (z_5, g_5; Table 1).

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* If growth rates for larval fish are provided for cod or other fish species, they are generally given in terms of length (e.g. review by Pepin 1991 and Pepin & Myers 1991).

[†] One function describing the growth during the entire period could not be found as the points of g and t did not give a good fit by regression analysis. Therefore five equations for growth rates for subsequent age periods are provided in Table 1.

Table 1. Functions for mortality and growth rates [z (i/day) and g (g/day), respectively] for cod in the pelagic larval period, in a juvenile production pond, in net pens and in the benthic habitat of Masfjorden. Age refers to the period of days from hatching (assumed to be 1 April) for which the functions are estimated. Source refers to authors providing estimates of z and g or data to estimate functions for z and g or z/g

Growth and mortality equations	Age (days)	Source
Pelagic larval period		
		Sundby *et al.* (1989),
$z_1/g_1 = 9\cdot8851 - 0\cdot3159\cdot t + 0\cdot0028\cdot t^2$; $R^2 = 0\cdot995^*$	11−60	Blom *et al.* (1991)
Production pond		
For 1987: $z_2/g_2 = 1\cdot4998 - 0\cdot0379\cdot t + 0\cdot0003\cdot t^2$; $R^2 = 0\cdot99^†$	11−80	Blom *et al.* (1991)
For 1988: $z_3/g_3 = 1\cdot1220 - 0\cdot0322\cdot t + 0\cdot0002\cdot t^2$; $R^2 = 0\cdot88^†$	11−80	Blom *et al.* (1991)
For 1987: $z_4 = 0\cdot0643 - 0\cdot0003\cdot t^‡$	71−150	Blom (personal communication)
For 1987: $g_{4i} = -2\cdot2099 + 0\cdot0311\cdot t^§$	75−83	Blom (personal communication)
For 1987: $g_{4ii} = 2\cdot16863 - 0\cdot0214\cdot t^§$	84−98	Blom (personal communication)
For 1987: $g_{4iii} = -0\cdot6261 + 0\cdot0069\cdot t^§$	99−105	Blom (personal communication)
For 1987: $g_{4iv} = 0\cdot5498 - 0\cdot0043\cdot t^§$	106−127	Blom (personal communication)
For 1987: $g_{4v} = -0\cdot8729 + 0\cdot0069\cdot t^§$	128−150	Blom (personal communication)
Net pen		
For 1988: $z_5 = 0\cdot0162 - 0\cdot0001\cdot t^‡$	90−126	Blom (personal communication)
For 1988: $g_5 = 0\cdot1070 - 0\cdot0005\cdot t^§$	75−185	Blom (personal communication)
Benthic habitat of Masfjorden		
For 1987: $z_{6i} = 0\cdot2306 - 0\cdot0017\cdot t^‡$	87−122	Fosså (personal communication)
For 1987: $z_{6ii} = 0\cdot0433 - 0\cdot0002\cdot t^‡$	123−161	Fosså (personal communication)
For 1988: $z_{7i} = 0\cdot2805 - 0\cdot0020\cdot t^‡$	94−131	Fosså (personal communication)
For 1988: $z_{7ii} = 0\cdot0275 - 0\cdot0001\cdot t^‡$	132−173	Fosså (personal communication)
For 1987: $g_6 = 0\cdot0138 - 0\cdot000037\cdot t^§$	195−270	Own data
For 1988: $g_{7i} = 0\cdot1394 - 0\cdot0007\cdot t^§$	126−195	Own data

* Function fitted to estimates of z/g by polynomial regression (Draper & Smith 1981). Values of g are stratified by 5-day intervals and are obtained from Blom *et al.* (1991), and values of z are from Sundby *et al.* (1989).
† Function fitted to estimates of z/g by polynomial regression (Draper & Smith 1981). The ratios for z/g are stratified by 5-day intervals and are obtained from Blom *et al.* (1991).
‡ Estimated from Equation 6.
§ Estimated from Equation 7.

Benthic habitat of Masfjorden

Estimates of daily instantaneous mortality rates (z) for the benthic habitat are provided for Masfjorden for the years 1987 (z_6; Table 1) and 1988 (z_7; Table 1). These estimates are based on abundance indices (U_i) originating from a total of 42 standardized beach seine samples in mid June to early October 1987 and 1988 (in 1987 $U_{t1} = 49\cdot5$, $n = 8$ at 10 June; $U_{t2} = 3\cdot6$, $n = 6$ at 13 July; $U_{t3} = 1\cdot8$, $n = 3$ at 20 August; $U_{t4} = 1\cdot2$, $n = 5$ at 1 October and for 1988 $U_{t1} = 136\cdot8$, $n = 6$ at 16 June; $U_{t2} = 5\cdot8$, $n = 3$ at 20 July; $U_{t3} = 3\cdot2$, $n = 8$ at 30 August; $U_{t4} = 2\cdot0$, $n = 3$ at 13 October; J.H. Fosså, personal communication). The beach seine samples seem to reflect the trend in the year class development of settled 0-group cod because (1) the sampling was done in the cod habitats, (2) the abundance index for each month is the average of several hauls and (3) the sampling was standardized so that each haul sampled a similar volume of water from shoreline sections of similar length.

However, we may of course not eliminate the chance that some juveniles may have dispersed from 0−5 m (beach seine sampling depth range) to the 5−20 m depth range of the general cod habitat within this period. The effect of such a dispersion would be over-estimated mortality rates as the emigration rate will always be included in mortality rates. The average weight of cod caught by the beach seine increased through the sampling period (for 1987 $w_1 = 0.5$; $w_2 = 3.7$; $w_3 = 5.1$; $w_4 = 5.8$, and for 1988 $w_1 = 1.6$; $w_2 = 2.5$; $w_3 = 6.4$; all values in grams) suggesting that this source of error may not be severe. However, if present, this error would result in over-estimated mortality rates. The possibility of this bias is included in the sensitivity testing.
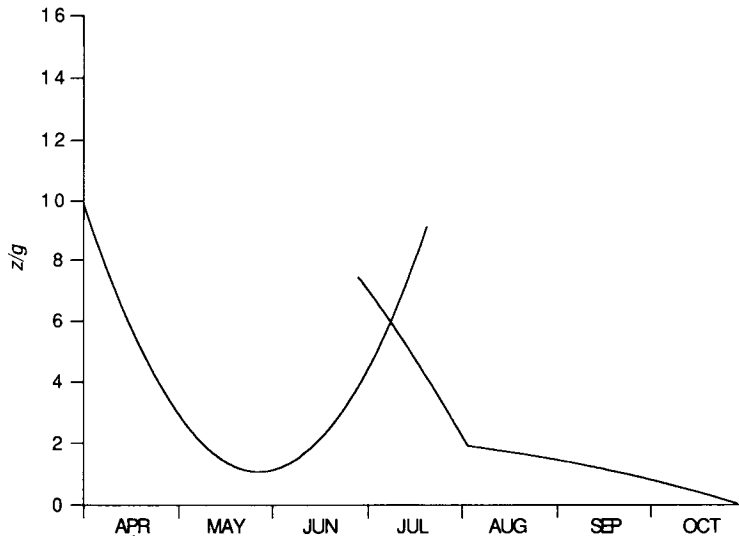
Daily instantaneous growth rates are estimated for cod in the benthic habitat of Masfjorden based on experimental net group samples for 1987 (g_6) and 1988 (g_7).[‡] (Sampling strategy is described in Salvanes 1991a.) For both years, we estimated the average g for two time intervals from average gutted weights w from 15 September (in 1987 $w = 42.7$ g, SE = 0.09, $n = 24$; in 1988 $w = 53.0$ g, SE = 2.7, $n = 28$) to 15 November (in 1987 $w = 63.5$ g, SE = 0.03, $n = 89$; in 1988 $w = 58.7$ g, SE = 2.0, $n = 86$) and from 15 November to 15 February the following year (in 1988 $w = 89.3$ g, SE = 4.0, $n = 189$; in 1989 $w = 70.6$ g, SE = 3.2, $n = 73$). A standardized sampling strategy was used during the entire sampling period: three net types with different mesh sizes (including trammel nets) made up an experimental net group, and 40 such net groups were set each month. Although 0-group cod may be sampled selectively by the experimental net groups, 1-group and older cod are sampled non-selectivity (Salvanes 1991b). Due to selectivity we expect that the samples of 0-group cod early in the fall were dominated by a larger fraction of faster-growing individuals than later in the fall of 1987 and 1988, but that this fraction becomes negligible around the turn of the year when the new cod recruits become non-selectively sampled by the net groups (Salvanes 1991a). Within years the slope of g_6 and g_7 (Table 1), and the z/g ratios early in the fall, may therefore be slightly over-estimated, while differences between years may reflect actual differences in the fjord.

Results

Shift from pelagic to benthic habitat

Due to initial high mortality rate (z) and low growth rate (g), the ratio between mortality and growth rate for pelagic cod larvae is high immediately after hatching in wild environments (Fig. 1). With increasing age, until about 40 days (early May), the z_1/g_1 ratio decreases; it becomes almost constant at 40−70 days (early May−early June) and increases thereafter (Table 1 and Fig. 1). Note that the right-hand side of the bell shape in Fig. 1 is an extrapolation of data. However, this curve could be constructed on general ecological relationships: a rising z/g with increased age must be true, as (1) the initial extremely high mortality rate is a decreasing function of time in the Sundby *et al.* (1989) data set − this strong reduction in the instantaneous mortality rate must stop long before $z < 0$, and will

[‡] For 1988 we also used growth data for cod including those released into Masfjorden on 6 August (about 82 500). As mean length of wild and released 0-group cod was considered similar, similar growth pattern for the two groups (Nordeide unpubl.) was assumed. The growth rate was obtained by transforming from length (11.6 cm) to weight (15.6 g) according to the estimated weight−length relationship for cod in this fjord given in Salvanes & Ulltang (1992).

Figure 1. The ratio of mortality (z) to growth rates (g) for cod in different habitats of western Norway as a function of age (calculated from hatching 1 April). The pelagic habitat (z_1/g_1; Table 1) is represented by the curve to the left. The benthic habitat is the curve to the right (z_6/g_6).
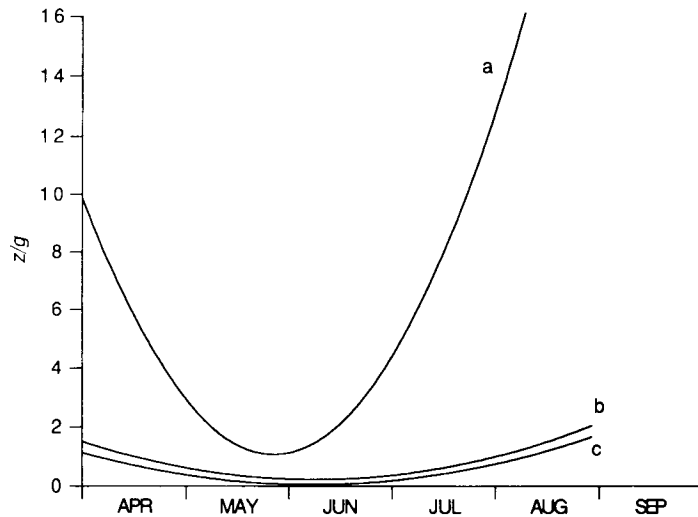
probably settle at a more stable level; and (2) the per-biomass growth rate may not continue to increase as the fish mass increases, and growth rate for living animals will therefore decrease with time (for cod, see Braaten 1984; Blom *et al.* 1991). Both these effects will lead to an increase in z/g, and a bell shape is to be expected. However, because it is an extrapolation, one should be careful not put too much attention to the actual values predicted by this curve although its shape seems realistic.

The right ascend of the curve intersects in early July with the curve for 1987 representing the benthic habitat of Masfjorden. Subsequently the curve for the benthic habitat decreases while the curve for the pelagic habitat ascends further. Hence, individuals would do better if they settled in the benthic fjord habitat rather than remained in the pelagic habitat where the balance between survivorship and growth would be less favourable. This predicted settling is consistent with field observations of shifts from pelagic to benthic habitats which are reported to occur from mid-June to early August in west Norwegian coastal areas (Godø *et al.* 1989; Svåsand & Kristiansen 1990).

The pelagic, the production pond and the net pen as cod habitats

The z_1/g_1 ratios for the wild pelagic habitat are much higher than the curves for the production pond, both for 1987 (z_2/g_2) and 1988 (z_3/g_3) (Fig. 2). The much lower mortality rate in the production pond was due to the removal of other predators before cod larvae were put into the pond. The difference may in fact be even larger than Fig. 2 depicts because z_1/g_1 may be under-estimated, as mentioned earlier. Later than 70 days after hatching (early June), when the z_1/g_1 curve for the pelagic habitat increases sharply, the z_2/g_2 and z_3/g_3 curves for cod in the pond still remain relatively flat (Fig. 2).

Figure 2. The ratio of mortality (z) to growth rates (g) for cod in different habitats of western Norway as a function of age (calculated from hatching 1 April). Curve (a), the pelagic habitat $(z_1/g_1$; Table 1); (b), the production pond in 1987 $(z_2/g_2$; Table 1); (c), the production pond in 1988 $(z_3/g_3$; Table 1).

For 1988, the curves for the production pond, and the net-pen habitat intersect about 80 days after hatching (Fig. 3). Subsequently the estimated mortality per growth rate ratios are lower in the net pen than in both the production pond and in the benthic fjord habitat. This suggests that individual cod would do best in net pens after this intersection. This is no surprise, as cod in net pens do not have to use much energy to obtain food, and the mortality rate is low because other predators are absent.

Shift from production pond to benthic fjord habitat

While comparing the estimated z/g curves for the production pond with those for the benthic fjord habitat for 1987 (Fig. 4a) and for 1988 (Fig. 4b) the following pattern became apparent. From about 70 days after hatching (early June) in 1987 the z_2/g_2 ratio for the production pond increased slightly. At mid-August it intersected with the decreasing z_6/g_6 curve for the benthic fjord habitat (Fig. 4a). Beyond this period, the z_6/g_6 ratio for the benthic habitat was reduced further, whereas the z_2/g_2 ratio increased, suggesting that cod in the fjord had the best prospects. A similar habitat shift is indicated for 1988 (Fig. 4b). In that year, the z_3/g_3 curve for the production pond intersected with the z_7/g_7 curve for the benthic fjord habitat in late July.

Discussion

The early releases of cod larvae were far from optimal for increasing cod production. Accumulated mortality until 120 days after hatching (August) from the equation derived from Sundby *et al.* (1989) indicates that there were only 1—2 survivors from the 33 million
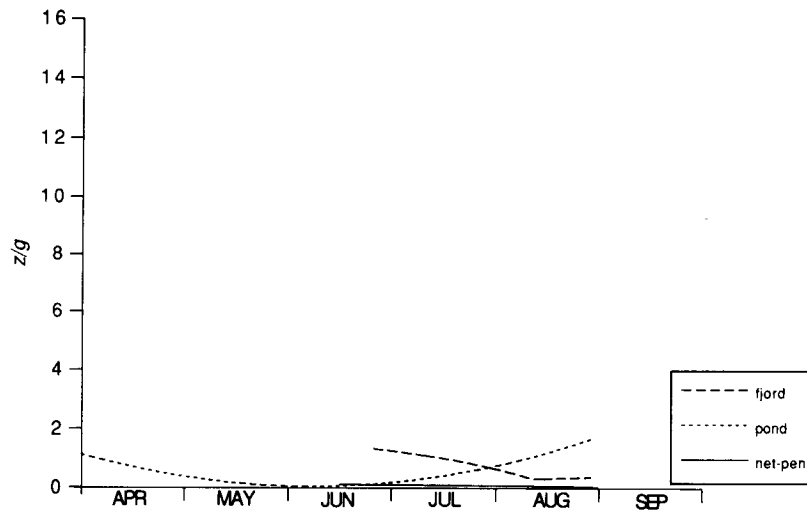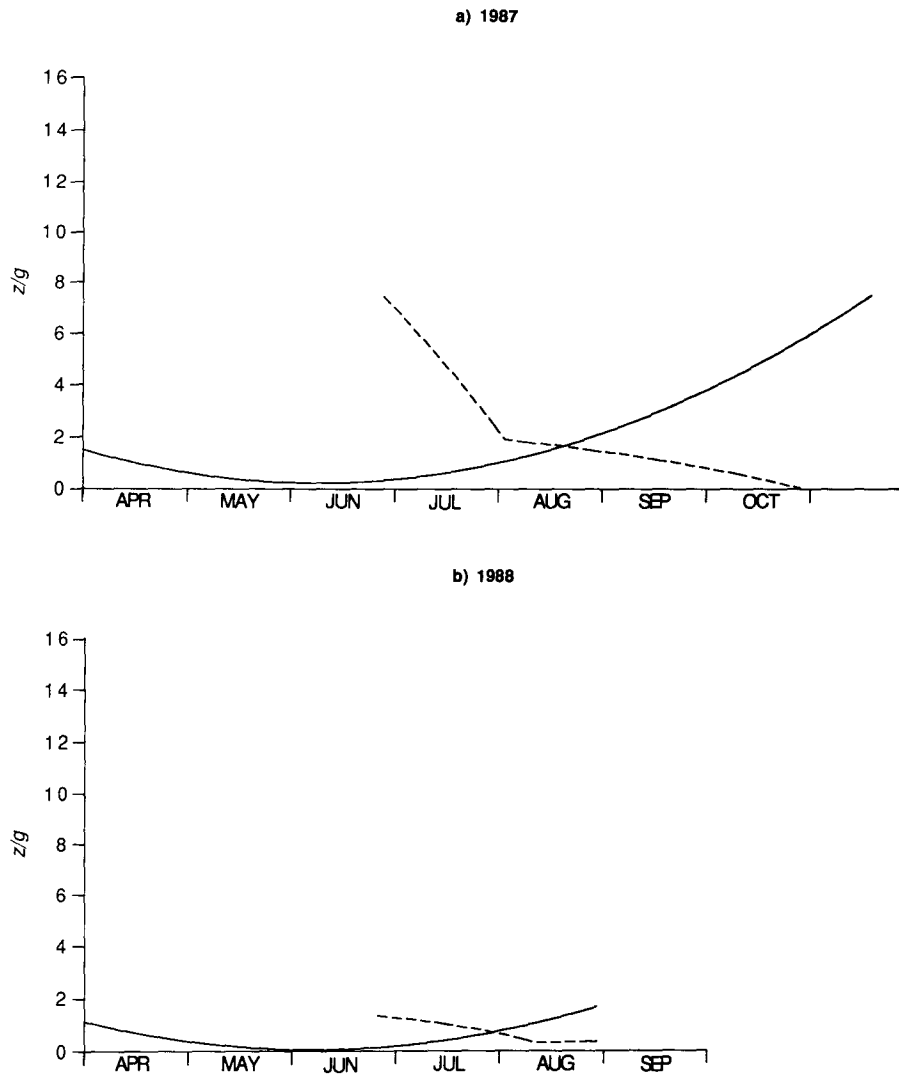
Figure 3. The ratio of mortality (z) to growth rates (g) for cod in the pond, net pen and fjord in western Norway in 1988.

yolk-sac larvae released in Søndeledfjord on the Norwegian Skagerrak coast in 1904 and 1905 (Shelbourne 1964). Even if z is kept constant until August, and we use the mortality rate given in Sundby *et al.* (1989) (0·115 per day), only about 100 individuals would survive until early August. The overall conclusion of our analysis is that cod of a size which normally stays in the pelagic habitat, should not be released to enhance cod stocks due to the high mortality rate there.

That the model-predicted timing of cod settlement (Fig. 1) is consistent with field observations in coastal areas of western Norway (Godø *et al.* 1989; Svåsand & Kristiansen 1990), in addition to the intuitively realistic outcome that net pens are better habitats for cod than both the pond and the benthic fjord habitat from June/July and onwards (Fig. 3), illustrate that the theoretical framework based on evolutionary and ecological relationships may prove useful to study habitat shifts for cod, including also the 'artificial habitat shift' from production ponds to natural habitats in extensive cod mariculture.
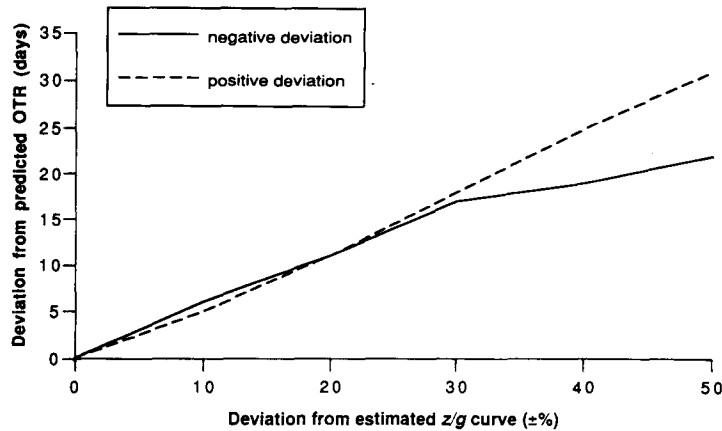
As a habitat shift depends on growth and survival prospects in alternative habitats, we may expect interannual variations due to fluctuations in food availability and predator abundances, but we may also expect uncertainties in predicted habitat shifts because estimates of such rates always suffer from uncertainties connected with the sampling procedure. Field studies have shown that production of gobies fluctuates greatly between years (Fosså 1991) mainly due to variable advection of zooplankton to the fjord (Aksnes, Aure, Kaartvedt, Magnesen & Richards 1989; Giske, Aksnes, Lie & Wakili 1991; Salvanes, Aksnes & Giske 1992). Both because it is difficult to relate food and predator abundance directly to growth and mortality rates, and because it is hardly feasible to calculate the uncertainties of the estimated growth and mortality rates, the effects of such variabilities are illustrated in our study by a sensitivity test of the model predictions of habitat shifts (Fig. 5). Moderate deviations in predicted habitats shift are shown for moderate changes in the z/g curves (e.g. ±20% deviation in the z/g ratios gives only ±10 days in deviation

a) 1987

b) 1988

Figure 4. The ratio of mortality (z) to growth rates (g) for cod in different habitats of western Norway as a function of age (calculated from hatching 1 April). (a) The solid curve refers to z_2/g_2 (Table 1) for the production pond in 1987 and the broken curve refers to z_6/g_6 for the benthic habitat of Masfjorden in 1987. (b) The solid curve refers to z_3/g_3 for the production pond in 1988 and the broken curve refers to z_7/g_7 for the benthic habitat of Masfjorden.

from present predicted habitat shift date). Improved precision on optimal release dates can only be achieved when carefully designed investigations are conducted.

There are strong interannual variations in zooplankton abundance in the fjord (Aksnes *et al.* 1989; Giske *et al.* 1991). These large fluctuations are damped, but still prominent, at the planktivore level (Fosså 1991), probably due to a dynamic coupling of risk-willingness with food concentrations (cf. Equation 3 in Stearns & Crandall 1984). However, the natural interannual fluctuations in food for cod may be reasonably well predicted months

Figure 5. Deviation from predicted optimal timing of release (OTR, days) as a function of changes from estimated z/g curve. The z_2/g_2 curve is changed relative to estimate, showing the dependency of data sets on precision OTR.

in advance of release, as major cod prey, gobies, are relatively long-lived. It may also be possible to estimate the variation in, and actual level of, the mortality risk for newly settled cod by e.g. estimating predation mortality from quantitative dietary studies of large piscivore predators. Because of interannual variations in both mortality risk and growth prospects, the exact optimal timing of cod releases cannot be found for a particular year. Nevertheless, Fig. 5 shows that the unavoidable uncertainties in the estimated range for predicted habitat shifts are well within the range needed for making the life-history approach we propose applicable to extensive mariculture.

Acknowledgments

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