

ONTOGENY, SEASON AND TRADE-OFFS: VERTICAL DISTRIBUTION OF THE MESOPELAGIC FISH *MAUROLICUS MUELLERI*

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To investigate the validity of static optimization models, the vertical distributions of two age groups of *Maurolicus muelleri* is compared to the optimal annual ontogenetic growth rate : mortality risk trade-offs as determined from generation-time based life-history equations. Calculations indicate that juvenile feeding rate was near the maximum for efficient conversion to growth, and at times constrained by digestion rate. Feeding rate of adults seems not to have been high enough to sustain body mass. Juveniles seem to follow the static ontogenetic trade-off between growth and survival, while adults in winter emphasize feeding far less than predicted from static optimization. Static trade-offs are thus inadequate in predicting their distributions, and models accounting for time- and state-dependencies are required. The difference between the two age groups with respect to following the annual trade-off, is explained by their different feeding-to-fitness functions: the relation between adult feeding and fecundity is continuous, while the relationship between juvenile feeding and generation time is discrete, with a considerable fitness cost for extension of the juvenile period.

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INTRODUCTION

Over the last decade, several models of optimal spatial distribution of animals have been developed. The methods can coarsely be divided into two main categories, termed static and dynamic optimizations. (By dynamic optimizations we include all models where some aspect of animal state and a time-dependency is incorporated, not only models based on the dynamic programming equation.) Both categories are usually linked to fitness by maximization of net reproductive rate. By static optimization, WERNER & GILLIAM (1984) developed a general equation for the optimal trade-off between mortality risk (μ) and growth (g) opportunities for juvenile fishes, showing that they should stay where the ratio between mortality and growth was at a minimum ('minimize μ/g '). Later, this rule has been supported by both experimental and field studies. GILLIAM & FRASER (1987) found juvenile minnows to choose habitat in an aquarium according to this theory, and GOTCEITAS (1990) found the same in laboratory experiments with juvenile bluegill sunfish. In a field experiment, NONACS & DILL (1990) found ants to trade-off feeding rate and mortality risk according to the μ/g rule, as did BOWERS (1990) for kangaroo rats. However, several field observations indicate that this simple rule do not always

apply. METCALFE & FURNESS (1984), studying feeding of birds of passage, found reduced vigilance in the pre-migratory period, to compensate for lack of feeding opportunities during the oceanic crossing. Pelagic animals do not experience such extreme situations, but seasonal variation in growth patterns are common for boreal animals. A winter check to growth is found for krill and several mesopelagic fishes (MAUCLINE 1991). This might reflect a seasonally reduced growth opportunity, but may also be due to a seasonal change in trade-off. POWER (1984) observed such changed priority for armored catfish, which seemed to experience a constant mortality risk and a growth rate dependent on resource availability. Thus, when growth opportunities were lower than average, the fishes did not adjust their distribution to maintain the same trade-off.

By dynamic methods, like statistical decision theory (STEPHENS 1981) and dynamic programming (HOUSTON & al. 1988; MANGEL & CLARK 1988; LUDWIG & ROWE 1990), it has been shown that optimal solutions may differ on short and long time scales and also be state dependent. LEONARDSSON (1991) claims that static and dynamic methods give the same solutions. If so, the much more time consuming dynamic optimizations can be avoided.

However, LUDWIG & ROWE (1990) state that a solution which does not incorporate the time dimension cannot be optimal, thus disregarding static optimizations.

AKSNES & GISKE (1990) developed static equations for optimal habitat selection of animals with different life histories. Used ontogenetically, these equations can predict optimal distributions for juvenile and adult fishes. In this investigation we apply these equations on the distribution of a mesopelagic fish in winter. The pelagic habitat is very suitable for this purpose, as it over hundred meters offers huge differences in feeding rates and mortality risks. The winter is a good season to look for deviations from static optimization, as feeding opportunities are at its minimum (GISKE & al. 1991). The species chosen is a visual feeder and forms distinct age-specific layers which can easily be traced by acoustic equipment. By this method, we can study actual trade-offs in a natural system, where all aspects influencing the behaviour of these fishes are present and thus examine whether static optimizations can account for natural distributions.

Müller's pearlside *Maurolicus muelleri* GMELIN (Gonostomatidae) has a global oceanic and shelf water distribution (GJØSÆTER & KAWAGUCHI 1980), feeding mainly on copepods and euphausiids (SAMYSHEV & SHETINKIN 1971; GJØSÆTER 1981b). Life-history and ecology of *M. muelleri* in western Norwegian fjords have been studied by GJØSÆTER (1981b). He found length at maturity to be ≥ 40 mm and age at maturity to be one year. Adult mortality in western Norwegian fjords average 50 % year⁻¹. Average clutch size was 300 eggs, with an observed range of 200 – 500. Predation and mortality was studied in Masfjorden in January by GISKE & al. (1990). Large pelagic fishes (blue whiting *Micromesistius poutassou* and saithe *Pollachius virens*) ate predominantly *M. muelleri*, and risk of predation mortality was estimated to be seven times higher for the juveniles than for the adults.

M. muelleri has often been a major contributor to the scatter from sound scattering layers (SSLs) (e.g. SAMYSHEV & SHETINKIN 1971; GJØSÆTER 1986; BERGSTAD 1990). GISKE & al. (1990) found *M. muelleri* in Masfjorden in winter to be concentrated in two SSLs. The two layers were separated by approximately 20 m almost void of mesopelagic fish. The upper SSL, with a day depth of 50–100 m, consisted of juveniles, while the adults were found in a layer below (100–150 m). The juveniles performed a diel vertical migration with midnight sinking while the adults performed a weaker dusk ascent and dawn descent, and remained in the same depth range day and night. During the day, both layers

responded immediately and in parallel to changes in surface light intensity. During the night, juveniles stayed in the depth (40–60 m) of maximum temperature (1.5 °C warmer than below and 3 °C warmer than at the surface). Both juveniles and adults were day-time copepod feeders.

Feeding opportunities for visual-feeding planktivores in Masfjorden is poorer in winter than during the rest of the year, for two reasons: zooplankton biomass is at its annual minimum (GISKE & al. 1991), and due to hibernation (HIRSCHE 1983) in deep and dark basins (own unpubl. obs.), most individuals of the dominant copepod *Calanus finmarchicus* are inaccessible to visual predators. On the other hand, the beginning of the spawning season is just two months ahead, putting a premium on growing for the juveniles and on gonad tissue production for the adults.

Here we will examine this difference in vertical distribution of juveniles and adults by relating the observed vertical distributions to the different fitness values of feeding. A mechanistic model of visual feeding accounting for changes in ambient light, prey size and prey density was developed by AKSNES & GISKE (in press). Feeding rate calculations from this model are used to study feeding regime and growth conditions for juvenile and adult *M. muelleri* in winter, and the results will be compared with the optimal trade-offs of mortality risk versus feeding rate as predicted from the life-history models of AKSNES & GISKE (1990). Field data are based on GISKE & al. (1990), with the supplement of stomach analyses. The Result section therefore mainly contains simulated feeding and growth rates.

MATERIAL

The distributions of *M. muelleri* and their zooplankton prey in Masfjorden are taken from GISKE & al. (1990). Sampling was performed by IKMT (Isaac Kidd Midwater Trawl) and Harstad trawls (NEDREAAS & SMEDSTAD 1987), while vertical distributions were continuously recorded by 120 and 38 kHz Simrad echo sounders (EK 120A and EK 38). Stomach filling of juveniles and adults from the same cruise is determined from IKMT and Harstad trawl catches, respectively. The stomachs are classified as empty, some content, half full, more than half full, or full.

MODELS

Optimal trade-offs

Following WERNER & GILLIAM (1984), AKSNES & GISKE (1990) developed a general life-history model relating generation time, mortality risk, clutch size and offspring sex ratio to fitness through Net Reproductive Rate R_0 . In this model, an individual will increase its fitness by increasing the inequality

$$\mu T / \ln(b/s) \leq 1 \quad (1)$$

(For deduction of this and the two equations to follow, see AKSNES & GISKE 1990. All symbols used are explained in Table 1.) A simple inspection of the equation shows that environmental factors influencing mortality risk and generation time have a larger potential impact on fitness than have factors operating on clutch size and offspring sex ratio. AKSNES & GISKE (1990) termed animals able to influence their generation time *time manipulators* and those who could not *clutch manipulators*. If generation time depends on the time needed to grow to a minimum adult size, as for juvenile *M. muelleri* (GJØSÆTER 1981b), and this growth is linearly related to feeding rate, the general equation is transformed to

$$\mu f \leq k \ln(b/s) / \ln(W_A/W_0) \quad (2)$$

Adult *M. muelleri* spawn annually, and increased feeding can only be canalized to increased clutch size. Then

$$\mu / \ln(afT/s) \leq T^{-1} \quad (3)$$

applies.

Thus we have two separate – still very general – special case equations relating environmental mortality risk and feeding rate to fitness for juveniles and adults. The two equations differ in the fitness value of feeding, and the optimal trade-off when increased feeding also results in increased mortality risk. The optimal (fitness maximizing) depth is here given by the depth resulting in the smallest left-hand side of Eqs 2–3. The difference in predicted vertical distribution for *time manipulators* (Eq. 2: maximize f/μ) and *clutch manipulators* (Eq. 3: maximize $\ln(fT/s)/\mu$) is exemplified in Fig. 1. This ontogenetic approach to habitat profitability shows that the fitness value of feeding is higher for juvenile time

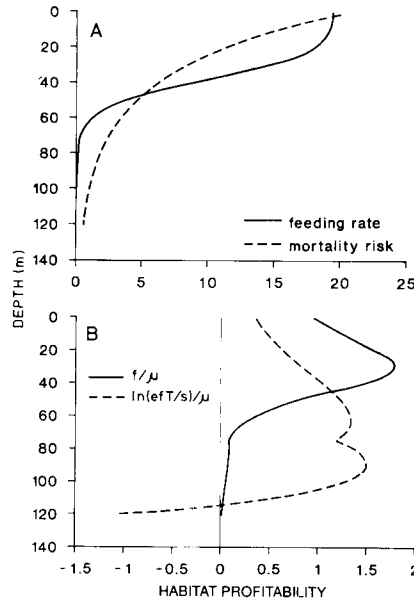


Fig. 1. Examples of optimal habitat choice. Vertical distribution of mortality risk and feeding rate (A), and the corresponding habitat profitability values for time manipulators (maximize f/μ) and clutch manipulators (maximize $\ln(afT/s)/\mu$) (B). Feeding rate is assumed to be constrained by digestion in upper layers, while predation risk is assumed to be a function of the predator's visual range.

manipulators, which accordingly should take higher mortality risks in order to gain increased feeding rates than should adult clutch manipulators.

Feeding, growth and mortality

The linear relationship between feeding rate and growth rate ($g = kf$) assumed in Eqs 2–3 is valid only for a restricted range of feeding rates. North Sea herring larvae have a linear relationship in the feeding rate range of $0.03 - 0.2 \text{ g g}^{-1} \text{ day}^{-1}$ (KJØRBOE & al. 1987, fig. 2). Below this range, feeding is not sufficient for growth, and above $0.2 \text{ g g}^{-1} \text{ day}^{-1}$ the conversion efficiency drops. Feeding rate dependent assimilation efficiency and specified temperature-dependent metabolic costs changes the linear feeding-to-growth assumption to

$$g = \alpha(1 - e^{-\beta f}) - m \quad (4)$$

where $\alpha - m$ is the maximum growth rate (KJØRBOE & al. 1987).

When feeding rate depends on encounter rate, and attacks are assumed to be successful, vision-based maximal feeding rate ($\text{prey ind} (\text{predator ind})^{-1} \text{ s}^{-1}$) may be modelled by the mechanical equation

Table 1. Definition of life-history parameters used in Eqs 1–3.

Symbol	Description	Unit
μ	Mortality risk	day^{-1}
a	Conversion efficiency from feeding to fecundity	dim. less.
b	Fecundity	eggs
f	Feeding rate	$\text{g g}^{-1} \text{ day}^{-1}$
k	Food-to-growth conversion efficiency	dim. less
s	Average number of eggs necessary to give birth to one female offspring	dim. less
T	Generation time	days
W_0	Mass at start-feeding	g
W_A	Minimum adult mass	g

$$f_N = \frac{h^{-1} N}{(h \pi (r \sin \Theta)^2 v)^{-1} + N} \quad (5)$$

(CLARK & LEVY 1988; AKSNES & GISKE in press; symbols used in the Eqs 5–11 are explained and defined in Table 2). In the life-history equations (Eqs 2–3) feeding is measured in prey mass (predator mass)⁻¹ time⁻¹, and the corresponding feeding rate equation is

$$f_w = f_N w/W \quad (6)$$

Stomach capacity imposes an upper limit on ingestion rate, and a well fed fish cannot ingest faster than its stomach content is evacuated. Stomach evacuation is often simply described as an exponential process (JOBLING 1981; MACPHERSON & al. 1989). Feeding in a period cannot exceed the difference of maximal stomach capacity and the non-digested remains of previous meals at the end of the period:

$$D = D_{\max} - D_r = D_{\max} - D_s e^{-(td)} \quad (7)$$

Maximum actual feeding in a period of length *t* is finally obtained by combining Eqs 6–7

$$f t = \min (f_w t, D) \quad (8)$$

Reactive distance *r* in Eq. 5 is a non-linear function of light regime, eye morphology and prey characteristics and may be expressed mechanistically by

$$r^2 e^{(zK+cr)} = \rho E_0 | C_0 | A S_e^{-1} \quad (9)$$

(AKSNES & GISKE in press), resembling case III of Eggers (1977).

Being hunted by visual piscivores, the mortality risk function of *M. muelleri* will resemble Eq. 5, adjusted for density of predators and individual dilution among alternative prey. However, both predators and prey are highly mobile in the vertical axis, and an environmental mortality risk could rather be proportional to *r*², since prey encounter

Table 2. Parameters for calculation of visual range and feeding rates for juvenile and adult *M. muelleri* (Eqs 4–11)

Symbol	Description	Water	Juvs	Adults	Unit
α	Assimilation efficiency parameter ⁽⁸⁾		0.12	0.12	g g ⁻¹ day ⁻¹
β	Feeding-to-growth rate parameter ⁽⁸⁾		7.6	7.6	day
ρ	Fraction of irradiance lost through air-sea interface				dim.less
Φ	Reactive field angle ⁽¹⁾		30	30	degrees
<i>A</i>	Visible area of prey	Eq. 10			m ²
<i>C</i> ₀	Inherent contrast of prey		0.5	0.5	dim.less
<i>c</i>	Beam attenuation coefficient	0.3			m ⁻¹
<i>D</i>	Stomach capacity available for feeding				g AFDW
<i>D</i> _{max}	Maximum stomach capacity				g AFDW
<i>D</i> _r	Non-digested remains of <i>D</i> _s at end of period				g AFDW
<i>D</i> _s	Stomach content in beginning of period				g AFDW
<i>d</i>	Digestion rate ⁽²⁾		1.9·10 ⁻⁴	1.9·10 ⁻⁴	s ⁻¹
<i>E</i> ₀	Irradiance in the air at the sea surface ⁽⁵⁾				μE m ⁻² s ⁻¹
<i>f</i>	Potential vision and stomach limited feeding rate				g g ⁻¹ s ⁻¹
<i>f</i> _l	Focal length of eye lens ⁽³⁾		0.0013	0.0026	m
<i>f</i> _N	Potential instantaneous vision limited feeding rate				ind ind ⁻¹ s ⁻¹
<i>f</i> _w	Potential instantaneous vision limited feeding rate				g g ⁻¹ s ⁻¹
<i>g</i>	Potential instantaneous daily growth rate		Eq. 4	Eq. 4	g g ⁻¹ day ⁻¹
<i>h</i>	Handling time ⁽⁴⁾		2	2	s
<i>K</i>	Vertical attenuation coefficient for irradiance ⁽⁵⁾	0.12			m ⁻¹
<i>k</i>	Ratio between radiances at retina and lens				dim.less
<i>m</i>	Metabolic rate parameter		0.029	0.029	g g ⁻¹ day ⁻¹
<i>N</i>	Prey density ⁽⁵⁾	Fig. 2			ind m ⁻³
<i>r</i>	Visual range				m
<i>S</i> _c	Eye sensitivity threshold for detection of changes in irradiance ⁽⁶⁾		2.8·10 ⁻⁴	7.0·10 ⁻⁵	μE m ⁻² s ⁻¹
<i>S</i> _r	Retinal sensitivity detection threshold of radiant flux changes ⁽⁶⁾				μE s ⁻¹
<i>t</i>	Time				s
<i>v</i>	Fish swimming speed ⁽⁷⁾		0.02	0.04	m s ⁻¹
<i>W</i>	Fish mass ⁽⁵⁾		0.02	0.13	g AFDW
<i>w</i>	Prey mass ⁽⁵⁾	Fig. 2			g AFDW
<i>z</i>	Depth				m

AFDW: ash-free dry weight. (1) From LUECKE & O'BRIEN (1981: bluegill sunfish) and DUNBRACK & DILL (1984: juvenile coho salmon). (2) Comparable to data in WINDELL (1978). (3) Calculated from lens diameter. (4) From EGGERS (1976: 6 cm 'planktivore') and CLARK & LEVY (1988: juvenile sockeye salmon). (5) From GISKE & al. (1990). (6) See text for explanation. (7) Assumed to be one body length per second (PRIEDE 1985; CLARK & LEVY 1988). (8) KJØRBOE & al. (1987)

rate for visual predators is proportional to r^2 [$e = \pi(r \sin\Theta)^2 vN$; AKSNES & GISKE in press]. Here, we only assume that mortality risk is strongly light dependent, and thus reduced with increasing depth. GISKE & al. (1990) estimated individual predation death rate for juveniles to be seven times higher than for adults in January, which they ascribed to the different vertical distributions.

Parameter values

Mass of adults and juveniles, surface irradiance, diffuse attenuation coefficient and vertical profiles of prey density and mass were measured by GISKE & al. (1990). Prey area is calculated from prey mass assuming cube/circle relationship on wet weight basis

$$A = \pi(0.75w/\pi)^{2/3}; 1 \text{ g wet weight} = 1 \text{ cm}^3 \quad (10)$$

Values of N and w for each meter depth are calculated as the depth-weighted mean between centers of the sampling intervals (Fig. 2). Other characteristics of *M. muelleri* are based on measurements carried out on other species. This is unfortunate, but has probably little impact on the general conclusions, as will be shown in the Discussion.

The predator's sensitivity threshold for detection of changes in irradiance is the only of the variables in Eq. 9 that may be difficult to measure. However, if the values of the other variables are known, S_e can be back-calculated using Eqs 5-9 and focal length relationships. The focal length of the fish eye is a measure of the difference in sensitivity of retina and the lens. S_e can be expressed as a function of f_l by

$$S_e = S_r k^{-1} f_l^{-2} \quad (11)$$

(AKSNES & GISKE in press), and we assume S_r and k to be equal for juvenile and adult *M. muelleri*. CHARMAN & TUCKER (1973) found the focal length to be $1.18 \times$ lens diameter. Therefore, eye lens diameters was measured, and the relationship between fish length (L , mm) and lens diameter (D , mm) was found to be $D = 0.26 + 0.04 \times L$ ($L = 18-60$ mm, $N = 114$, $r^2 = 0.88$). For average sized fish of 21

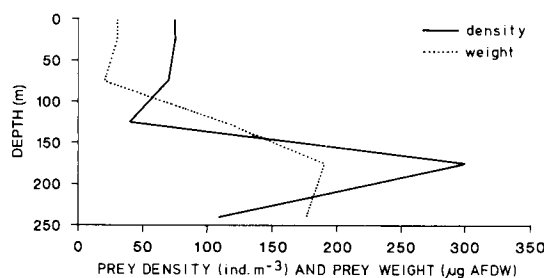


Fig. 2. Vertical distribution of prey density (N) and mass (w) to be used in Eqs 5, 6 and 9. Data of N and w are from GISKE & al. (1990). Values used are linear approximations between the centers of the sampling intervals.

and 47 mm, this implies focal lengths of 1.3 and 2.6 mm, respectively. Stomach analyses of adults (Table 3) show that adult feeding rate was not limited by stomach fullness, a necessary condition for estimating S_e from Eqs 5-11. S_e for adults is then calculated under the following assumptions: (1) parameters of Eqs 5-11 as given in Table 2 and in Fig. 2, (2) average intake is five copepods per day for adults in lower SSL, i.e. 3-4 times the average stomach content at dawn. The sensitivity of the results to the accuracy of S_e is discussed later. The calculations are performed by combining ambient depth location, light intensities, prey densities and sizes (GISKE & al. 1990, figs 6 and 7; Fig. 2) for each 30 minute interval of daylight. This results in a computed sensitivity threshold for adults of $7.0 \cdot 10^{-5} \mu E m^{-2} s^{-1}$. According to Eq. 11 S_e for juveniles is then $2.8 \cdot 10^{-4} \mu E m^{-2} s^{-1}$.

RESULTS

Observations

Juveniles in upper SSL had higher stomach content than the adults below (Table 3). At midday, 85 % of the juveniles had at least half full stomachs, while only 13 % of the adults reached this level. Stomach fullness during night does not indicate feeding in darkness.

Table 3. Stomach contents of juvenile and adult *M. muelleri* from Masfjorden 8 January 1989.

	Juvs	Juvs	Adults	Adults	Adults	Adults	Adults	Adults
Time caught (h)	0830	1100	0700	0900	1400	1700	2230	0400
Depth interval (m)	0-27	65-92	0-150	0-150	125-150	0-270	50-100	0-270
Number of fish	20	57	40	30	31	21	22	22
Empty stomachs	12	2	21	10	12	15	15	20
Some content	8	6	17	9	15	6	6	2
Half full	0	14	1	8	0	0	1	0
More than half full	0	5	1	2	2	0	0	0
Full	0	30	0	1	2	0	0	0

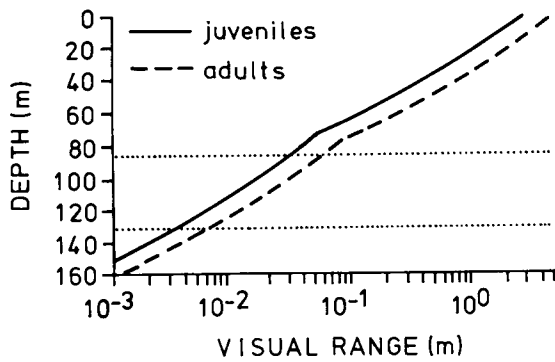


Fig. 3. Calculated visual ranges (Eq. 9) for juveniles (line) and adults (dotted) in Masfjorden at daytime in January 1989. Irradiance $E_0 = 21 \mu\text{E m}^{-2} \text{s}^{-1}$. Centers of upper and lower SSL indicated with dotted lines.

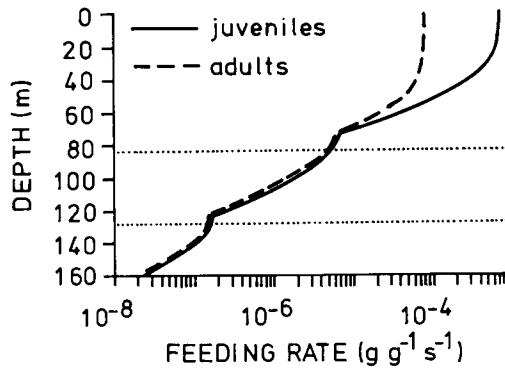


Fig. 4. Calculated vision-restricted feeding rates (f_w , Eq. 6) for juveniles and adults in Masfjorden at daytime in January 1989. Irradiance $E_0 = 21 \mu\text{E m}^{-2} \text{s}^{-1}$. Centers of upper and lower SSL indicated with dotted lines.

Model calculations

Due to a change in zooplankton size below 100 m, the decrease in visual range (Fig. 3) with depth deviated slightly from the exponential decline given by light intensity. The calculated potential feeding rate (Eq. 6, Fig. 4) reached an upper limit in near-surface waters, restricted by handling time. Potential feeding rates also decreased with depth, except between 125–150 m, due to increases in both prey abundance and size (Fig. 2).

Based on the assumed cumulative adult feeding of five copepods per day in lower SSL, juveniles in upper layer could potentially eat 135 copepods per day, restricted by both vision and stomach capacity (Table 4). These feeding rates correspond to 0.2 and 0.003 $\text{g g}^{-1} \text{day}^{-1}$ for juveniles and adults, respectively (Eq. 8), resulting in instantaneous daily growth rate estimates of 0.06 and $-0.026 \text{ g g}^{-1} \text{day}^{-1}$. Table 5 gives feeding and growth rates over a wider range of possible adult daily food intake, showing that the general trends are not sensitive to the assumptions underlying adult feeding rate. The calculated feeding patterns (Fig. 5) indicate that juveniles fed most actively near dusk and dawn, and their high food intake in the first period of the day is due to empty stomachs. Juvenile feeding rate seems to have been limited by digestion rate in the morning and evening (Fig. 6) and by vision at mid-day.

DISCUSSION

Reliability

Within a range of low feeding rates, estimates of S_c will be inversely proportional to number of prey eaten. In the range of 1–20 copepods eaten by the

Table 4. Calculated daily potential feeding of juveniles and adults

	Juvs in upper SSL	Adults in lower SSL	Unit
Number of prey items eaten	135.6	5.0	ind. day^{-1}
Average feeding rate	0.20	0.003	$\text{g g}^{-1} \text{day}^{-1}$
Not ing. due to stomach limitation	1.1	0	$\text{g g}^{-1} \text{day}^{-1}$
Average growth rate	0.07	-0.03	$\text{g g}^{-1} \text{day}^{-1}$

adults, the predicted growth rates (Eq. 4) of juveniles and adults do not differ greatly from those predicted at feeding rate of 5 copepods day^{-1} (Table 5). In all these simulations, adult growth rate was negative, and juvenile growth rate 5–7 % per day. For adults to have a positive net growth rate, a minimum of 54 copepods must be ingested. This is incompatible with the stomach analyses (Table 3). The main results of the simulations are thus not sensitive to the uncertainty in the parameter estimations.

Our estimates indicate that the juveniles might maximally ingest at a rate of 20 % day^{-1} , which, according Eq. 4 would imply a growth rate of 7 % day^{-1} . Spawning season for *M. muelleri* in Norwegian fjords lasts at least from March to September (LOPES 1979; GJØSÆTER 1981b), with an estimated maximum in May (LOPES 1979). Following this growth rate, the juveniles would reach the mass of adults in 35 days, i.e. in middle of February ($T = \ln(W_A/W_{juv})/g$). But food availability in February and March is generally lower than in January (Giske & al. 1991), and taking into account

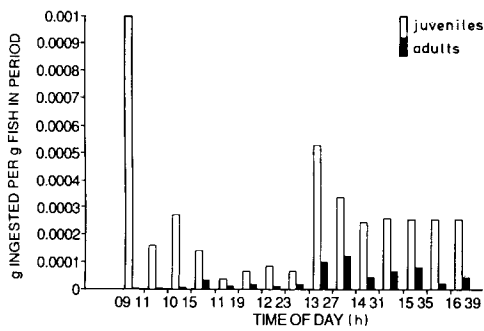


Fig. 5. Calculated time-distribution of feeding for juveniles in upper SSL and adults in lower SSL during 32-minutes intervals at daytime (after Eq. 8). Time along x-axis is center of intervals.

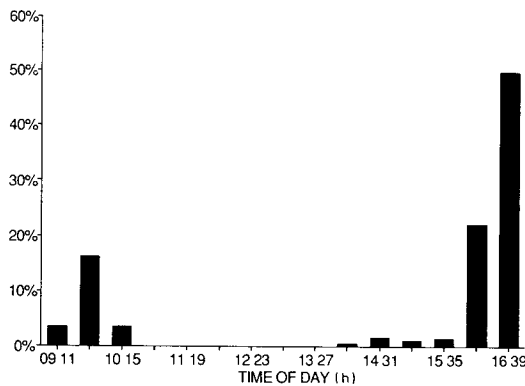


Fig. 6. Calculated time-distribution of proportion of food encountered which could not be eaten due to stomach limitation for juveniles in upper SSL (Eqs 6–8). Time along x-axis is center of intervals.

that they also need time to build up gonad tissue before spawning, our growth rate estimate of juveniles seems reasonable.

Due to digestive limitations, only 16 % of the food encountered (Eq. 6) by the juveniles could be eaten (Eq. 8). This does not imply that they might have obtained the same feeding rate at a deeper location, since almost all of this uneaten food was encountered in the afternoon, i.e. before a long night without feeding. Rather, we may have underestimated feeding at dawn due to a misjudgment of their stomach capacity. The night time distribution of the juveniles at the temperature maximum (GISKE & al. 1990) also indicates that they were feeding at a high rate. Similarly, WURTZBAUGH & NEVERMANN (1988) found juvenile sculpins to congregate at the temperature maximum during night, and therefore concluded that growth was restricted by digestion rather than prey encounter.

Ontogenetic differences

The stomach analyses show that juvenile *M. muelleri* had a higher average feeding rate than the adults, and our calculations indicate that while the juveniles had a feeding rate in the upper range of an

efficient (or constant linear) conversion to growth, the adults did not eat enough to sustain their mass. While juveniles would gain little (if any) increased growth by adopting a shallower (and probably more risky) distribution, adults could dramatically increase their growth. A seasonal variable growth pattern (GJØSÆTER 1981a; MAUCLINE 1991) may thus not be ascribed to lack of opportunity.

Field observations by GISKE & al. (1990) also show that juveniles more than adults emphasize feeding relative to predation avoidance. Juveniles in the upper SSL performed more pronounced dusk and dawn migrations than the adults below, thus prolonging the daylight period of feeding opportunities and risk of visual predation. The estimated seven times higher predation mortality rate of the juveniles relative to the adults (GISKE & al. 1990) itself indicates that adults were more risk-sensitive.

Trade-offs

The life-history models of AKSNES & GISKE (1990) applied to ontogenetic stages (Eqs 2–3) predict different risk-proneness of juveniles and adults, as observed here. The optimal depths do however

Table 5. Sensitivity of feeding rates, growth rates and sensitivity threshold to assumed adult feeding. S_e calculated from daily food intake as described in Parameter values.

Assumed adult daily intake (ind day ⁻¹)	Calculated adult S_e ($\mu\text{E m}^{-2} \text{s}^{-1}$)	Juvenile feeding rate ($\text{g g}^{-1} \text{day}^{-1}$)	Adult feeding rate ($\text{g g}^{-1} \text{day}^{-1}$)	Juvenile growth rate ($\text{g g}^{-1} \text{day}^{-1}$)	Adult growth rate ($\text{g g}^{-1} \text{day}^{-1}$)
1	$3.5 \cdot 10^{-4}$	0.14	0.0007	0.051	-0.029
2.5	$1.4 \cdot 10^{-4}$	0.18	0.002	0.060	-0.027
5	$7.0 \cdot 10^{-5}$	0.20	0.003	0.066	-0.026
10	$3.5 \cdot 10^{-5}$	0.22	0.007	0.068	-0.023
20	$1.75 \cdot 10^{-5}$	0.23	0.014	0.070	-0.017

depend on the depth-dependent mortality risks, which is not assessed here. However, the f/μ and lnf/μ rules are so different (Fig. 1) that contrasted vertical distributions are to be expected for organisms obeying each of the two rules. The precise trade-off for juveniles and adults cannot be assessed as long as mortality risk is unknown, but hints can be given by comparing the calculated growth rates to what could be ontogenetic optimal. The high growth rate of juveniles indicates that they also in January follow close to the static optimum derived from life-history theory (Eq. 2). This was not found for the adults, their growth rate being negative. A lower adult growth rate was expected (Eq. 3 vs Eq. 2), but negative rates are incompatible with a static optimization.

The adults were located at the depths of low zooplankton abundance (GISKE & al. 1990). The abundant, deeper located plankton seems to be almost undetectable by visual perception (Fig. 3), while zooplankton above should allow higher feeding rates and positive growth rate. Food concentrations in late winter are however at the annual minimum (GISKE & al. 1991), and the mortality risk associated with maintaining the annual average growth rate during winter would perhaps imply intolerable high mortality risks.

Why is it that the animals for whom growth has higher fitness value still maintained the annual average trade-off? While fitness-representations of feeding are explicit in Eqs 2–3, the effects of (slight) deviations from the averages are not. While there is a gradual reduction in fecundity with reduced adult feeding, generation time for juveniles has yearly steps. This step function makes the fitness cost of not reaching the adult stage in one year substantial (SIBLY & CALOW 1986; CHARNOV 1989).

The optimal trade-offs derived from life-history theory by WERNER & GILLIAM (1984) and AKSNES & GISKE (1990) are independent of both season and energetic state of the animal. LEONARDSSON (1991) included body size, but argued that static optimization will yield the same result as a time-dependent analysis. The trade-off employed by adult *M. muelleri* in winter is incompatible with a time-independent optimization, and the high growth rate of juveniles is probably related to a strong state-dependency of fitness through generation time. Thus, dynamic optimizations are necessary for understanding actual distributions. The scientific value of static optimization is thus to reveal long-term, or order of magnitude, differences; actual and short-term behaviour cannot be assessed for optimality unless state and time are considered (LUDWIG & ROWE 1990).

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