

## Why Pelagic Planktivores should be Unselective Feeders

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Diet width theory is a branch of optimal foraging theory, used to predict which fractions of the potential food encountered should be pursued. For pelagic fish, it is generally assumed that light is the dominant stimulus for both prey encounter rate and mortality risk. In order to achieve encounter rates allowing selective feeding, the pelagic predator exposes itself to enhanced predation risk for a prolonged time. The gain in growth obtained by diet selection may seldom outweigh the fitness cost of increased mortality risk. More generally, pelagic feeders will have a higher reproductive rate by searching the depth where feeding will be encounter-limited, and hence be opportunistic feeders. Literature reports of pelagic diet selection either fail to distinguish between the catchability of the prey in a gear and the encounter rate with its predator or neglects the vertical structure in pelagic prey distribution that may give differences in diets for unselective predators operating at different depths. The principal differences between the pelagic habitat and habitats where diet selection will be expected will include one or both of the following: (i) the continuous and steep local (i.e. vertical) gradients in mortality risk and (ii) the lack of local shelter where a newly ingested meal may safely be digested.

### 1. Introduction

Optimal diet width theory was put forward to find the number of prey types an optimal predator should pursue. Under the assumption that the optimal foragers maximize net energetic gain rate, prey types could be ranked according to their net energetic gain ( $E/H$ ; energy per handling time) obtained for each prey type. A diet including  $m - 1$  prey types should not be expanded to also include the  $m$ -th ranked item if the average gain rate from the  $m - 1$  prey types would be higher than the gain rate from the  $m$  prey types:

$$E_m/H_m \leq \sum_{j=1}^{m-1} \lambda_j (E_j - E_m H_j / H_m) \quad (1)$$

(Schoener, 1971; Charnov, 1976; Townsend & Winfield, 1985) where  $\lambda_j$ ,  $E_j$  and  $H_j$  are encounter rate, energy content and handling time of prey type  $j$ , respectively. (All symbols used in all equations are explained in Table 1.) Handling time is “the time

needed to pursue, handle and swallow a single item” (Schoener, 1987: 12). Time elapsed due to digestion constraints are thus not incorporated in  $H$ .

There is no emphasis of spatial differences in prey distributions in equation (1)—they are eventually reflected in the  $\lambda_j$ s. A selective diet implies that the predator encounters potential prey organisms which it does not chase. The fundamental parameter is the predator-prey encounter rate  $\lambda_j$ . (Often diet selection is claimed on basis of prey abundance indices instead of encounter rates. Only when one can ascertain that the predator and the scientist or the sampling tool has equal prey encounter rates, can abundance indices be used. This is seldom the case in an aquatic environment.)

As eqn (1) was developed in the early stages of optimal foraging theory (c.f. Schoener, 1987), the influence of predation risk was not mentioned in these diet selection models. Townsend & Winfield (1985) concluded that doing so “would be a significant step forward”. Gilliam (1990) combined the optimal diet

width equation with the "static optimization" equation for optimal habitat choice under predation risk (Werner & Gilliam, 1984) and developed a model for the influence of mortality risk on diet selection. His variables included mortality risk while searching and handling in addition to those in eqn (1). He linked mortality risk to prey type, so that  $E_j/H_j$  is the energy gain and  $M_jH_j$  is the mortality risk while handling prey  $j$ . Turner & Mittelbach (1990) used optimal diet width to calculate growth in bluegill sunfish in different habitats, and predicted the optimal habitat under the assumption that they prefer the habitat where mortality risk per growth rate is minimal.

The investigations of Werner, Mittelbach and colleagues (e.g. Werner *et al.*, 1983a, b; Mittelbach, 1983, 1988; Werner & Hall, 1988; Osenberg & Mittelbach, 1989; Turner & Mittelbach, 1990) are typical for a situation where diet selection is expected and important. They studied shallow-water freshwater fish living in or near the vegetation. In this environment, light intensity and prey encounter rate is high, and the feeding rate of the fish during daytime will be limited by digestion rate and not by encounter rate. Also, in many lakes, adult bluegill sunfish are not vulnerable to predation. This is the situation optimal foraging theoreticians had in mind (e.g. Schoener, 1987). They imagined food occurring in food patches, where the feeders search for these, feed there at maximum rate, and then seek shelter while the ingested food is digested. Then, for a foraging animal, they assumed a proportionality between feeding rate and fitness (Emlen, 1966) and developed optimal diet models containing the energetic gain from a prey and the handling time to ingest it. Gilliam's (1990) proportionality between handling time and mortality risk is reasonable for this situation.

The pelagic habitat is not like this. It is a three-dimensional transparent landscape, without local shelter adjacent to the feeding areas. True pelagic organisms cannot feed efficiently in a food patch and then seek cover nearby while digesting. What comes closest to a cover is vertical migration or shoaling. Both these strategies may involve costs and benefits (Clark & Mangel, 1986; Pitcher & Parrish, 1993) and, due to their complexity, a thorough discussion is beyond the scope of this paper.

In this paper, we discuss whether pelagic planktivores may have higher reproductive rate by feeding unselectively upon encounter with potential prey than by a restricted diet. Our argument is based on the assumption that the predator of the planktivore will find its prey by visual stimuli. Although long-distance searching must rely on other cues, and other sensory systems will eventually replace vision at large depths

(Montgomery, 1987; Jumper & Baird, 1991; Janssen & Corcoran, 1993; Montgomery & Milton, 1993), in depths where prey encounter rate is sufficient for selective feeding, vision will be the dominant cue for prey perception (e.g. Vinyard & O'Brien, 1976; Munz & McFarland, 1977; Confer *et al.*, 1978; Howick & O'Brien, 1983; Nicol, 1989). The model does not apply to surface predators. Neither does it apply to aquatic birds, nor rarely to marine mammals, as they depend on regular surface encounters and are probably forced to feed in depths where diet selection may pay.

In Section 2.1 we first outline life-history models to show that feeding rate can be linked to fitness either by a reduction in generation time or by an increase in fecundity. This is used to illustrate static optimization trade-offs between feeding and mortality risk for different life histories and age groups. The fitness-gain of feeding is highest when increased feeding may lead to reduction in generation time (c.f. Werner & Gilliam, 1984: "minimize mortality risk per feeding rate"). In Section 2.2 we show that environmental variability in mortality risk will be proportional to the visual range of a predator. The mortality risk will thus depend on the vertical attenuation of light. Section 2.3 concerns feeding limitations; feeding rate may be limited by handling time, encounter rate and digestion rate. Environmental variability in encounter rate may span many orders of magnitude due to differences in light intensity, while there is low vertical variation in digestion rate and handling time. In Section 2.4 we argue that if the food concentrations are high enough to allow for selective feeding at a particular depth in the water column, there must also exist a depth range below this zone where planktivores are encounter-limited. By combining environmental gradients in mortality risk with maximum potential environmental impact on digestion rate, we finally show in Section 3 that if the planktivore enters this depth range where diet selection is possible, it may hardly achieve a fitness premium.

## 2. Models and Data

### 2.1. FITNESS TRANSLATION OF FEEDING AND MORTALITY RISK

In the original optimal foraging theory, a direct link between feeding rate maximization and fitness was assumed (Emlen, 1966): by feeding at maximum efficiency, time was saved for other fitness-related activities. During the last decade, other aspects of fitness have become explicit, and Mangel & Clark (1986) expressed in dynamic programming terms, a

framework for which several aspects of fitness could be included simultaneously. By a life-history approach, direct relationships between behaviour and adaptive traits can be revealed. Following Giske *et al.* (1993) we express fitness as the difference between reproductive rate of an individual  $\rho$  and that of its population  $r$

$$\Phi = \rho - r. \quad (2)$$

The reproductive rate of an individual can be expressed as

$$\rho = \ln(bS)/G, \quad (3a)$$

where  $b$  is fecundity,  $S$  is juvenile survival probability and  $G$  is generation time. By assuming constant

mortality risk from a given day over the rest of the juvenile period, so that juvenile survival over the remaining generation time may be expressed  $S = e^{-MG}$ , we obtain

$$\rho = \ln b/G - M. \quad (3b)$$

Equation (3b) expresses the average importance of fecundity, generation time and mortality for the reproductive rate. Due to the assumption of constant mortality risk, eqn (3b) does not apply to the initial egg and larval period with high and decreasing mortality rate (Chen & Watanabe, 1989; Roff, 1992: 107–110). The behaviour that will lead to a maximization of  $\rho$  will depend on the life history pattern of the organism, especially on the fitness value of feeding. Feeding has another impact on fitness if it influences

TABLE I  
*Explanations of variables used in the equations*

Symbol	Description	Unit
$\Delta S$	Eye sensitivity threshold for detection of changes in irradiance	$\mu\text{mol m}^{-2}\text{sec}^{-1}$
$\epsilon$	Total number of predator-prey encounters over a time period	$\text{ind}^2\text{m}^{-3}$
$\Theta$	Reactive field angle	degrees
$\lambda$	Predator-prey encounter rate	$\text{ind ind}^{-1}\text{day}^{-1}$
$\rho$	Individual reproductive rate	$\text{day}^{-1}$
$\Phi$	Fitness (relative reproductive rate)	$\text{ind ind}^{-1}\text{day}^{-1}$
$a$	Visible area of prey	$\text{m}^2$
$A$	Prey detection area	$\text{m}^2$
$b$	Fecundity (eggs per mother)	$\text{ind ind}^{-1}$
$B$	Temperature scaling factor for digestion	$^{\circ}\text{C}^{-1}$
$c$	Beam attenuation coefficient	$\text{m}^{-1}$
$C_0$	Inherent contrast of prey	dimensionless
$d$	Digestion rate	$\text{day}^{-1}$
$D$	Stomach capacity (fraction of body mass)	$\text{g g}^{-1}$
$e$	Predator prey encounter rate	$\text{g g}^{-1}\text{day}^{-1}$
$E$	Energy content of prey	J
$E_0$	Irradiance in the air at the sea surface	$\mu\text{mol m}^{-2}\text{sec}^{-1}$
$f$	Daily feeding rate	$\text{g g}^{-1}\text{day}^{-1}$
$f_D$	Daily digestion-limited feeding rate	$\text{g g}^{-1}\text{day}^{-1}$
$f_E$	Daily encounter-limited feeding rate	$\text{g g}^{-1}\text{day}^{-1}$
$f_H$	Daily handling-limited feeding rate	$\text{g g}^{-1}\text{day}^{-1}$
$g$	Daily growth rate	$\text{g g}^{-1}\text{day}^{-1}$
$G$	Generation time	days
$H$	Individual prey handling time	days
$i$	Fraction of the irradiance lost through the air-sea interface	dimensionless
$k_1-k_4$	Conversion factors	dimensionless
$K$	Vertical attenuation coefficient for irradiance	$\text{m}^{-1}$
$M$	Mortality risk	$\text{day}^{-1}$
$N$	Prey density	$\text{ind m}^{-3}$
$p$	Diet scaling factor for digestion rate	$\text{day}^{-1}$
$P$	Predator density	$\text{ind m}^{-3}$
$r$	Population reproductive rate	$\text{day}^{-1}$
$R$	Visual range	m
$S$	Survival probability	dimensionless
$t$	Time	days
$T$	Temperature	$^{\circ}\text{C}$
$v$	Water volume in which densities of predators and prey is found	$\text{m}^3$
$V$	Predator swimming speed	$\text{m day}^{-1}$
$W_{\text{pred}}$	Predator body mass	g
$W_{\text{prey}}$	Prey body mass	g
$W_d$	Minimum adult body mass	g
$W_j$	Current juvenile body mass	g
$x, y$	Two particular depths, $x$ shallower than $y$	m
$z$	Depth (positive number)	m

generation time rather than fecundity [eqn 3(b)]. Werner & Gilliam (1984) showed that for a juvenile fish with size-dependent onset of reproduction, the remaining generation time could be found from the equation for growth until minimum adult size

$$W_A = W_J e^{gG}, \quad (4a)$$

where  $g$  is somatic growth rate and  $W_J$  is current juvenile size. Equation (4a) may be rearranged to substitute for  $G$  in eqn (3b). In this life history  $W_A$  is fixed, and  $W_J$  is a current value, so that  $G = \ln(W_A/W_J)/g = k_1/g$ , by definition of  $k_1$ . If we further assume a proportionality between feeding and growth,  $g = k_2 f$ , we obtain an expression for the potential fitness value of feeding

$$\rho = f \ln b/k_3 - M, \quad (4b)$$

where  $k_3$  is the conversion efficiency (including  $k_2$ ) from feeding to generation time. The rôle of feeding is overexaggerated in eqn (4b), since (i) metabolic demands ( $m$ ) are neglected from feeding to growth (a more proper relationship would be  $g = k_2 f - m$  to show that growth is not proportional to feeding, and will be negative at low feeding rates) and (ii) growth can hardly be constant exponential for a long time. Thus, eqn (4b) expresses the maximum fitness gain from feeding. For an individual to obtain higher fitness than average of the population,  $\rho > r$ , we may write

$$\rho = f \ln b/k_3 - M > r \leftrightarrow f/(r + M) > k_3/\ln b. \quad (4c)$$

For this life history, where increased feeding rate may shorten generation time,  $\rho$  is proportional to feeding rate, and is maximized when  $f/(M + r)$  is maximized. Under the special situation where population size is stable ( $r = 0$ ),  $f/M$  is to be maximized. For simplicity of calculation we will let  $r = 0$  and study vertical profiles of  $f$  and  $M$ . For a life history with fixed reproductive pattern, i.e. in a highly seasonal environment, Aksnes & Giske (1990) showed that fitness gain of growth was moved to a maximization of fecundity. Then, according to eqn (3b), the fitness gain of feeding and growth is reduced by the ln-operator. Let  $b = k_4 f$ , and eqn (3b) can be rearranged to

$$\ln(k_4 f)/(r + M) > G. \quad (4d)$$

Giske & Aksnes (1992) showed similarly that the fitness gain of feeding was higher for a juvenile who could impact its age at maturity [eqn (4c)] than for an adult who could increase fecundity [eqn (4d)]. Juveniles who can feed to shorten their generation time [eqn (4c)] thus have higher fitness-value of feeding than juveniles with a fixed age at maturity [eqn (4d)] and adults with a fixed seasonal reproduc-

tive pattern [eqn (4d)]. By adopting the terms in eqn (4c), we give feeding a maximum fitness value relative to mortality risk. Then we may show that not even under the best conditions will improved feeding by diet selection be beneficial to the pelagic planktivores.

## 2.2. MORTALITY RISK

We assume the pelagic planktivores and their predators to be randomly distributed on the local horizontal scale. The total number of encounters between predators and their prey over a time period  $t$  is then a function of local densities of predators  $P$  and prey  $N$ , their relative encounter speed  $V$  and the ability of the predators to detect their prey (here interpreted as a prey detection area  $A$ ; Giske *et al.*, 1994):

$$\epsilon = tNPV. \quad (5a)$$

In the water column, the local rate of encounters ( $\epsilon/t$ ) is strongly influenced by depth distribution of predators and prey. However, as both planktivores and piscivores are mobile and can take any position in the vertical, a static description of predation risk with focus on current location of predators is of little value. Rather, the density-independent aspect of predator-prey contact rates is of fundamental importance, as it describes the objective (i.e. environmental) aspect of predation risk:

$$\lambda = \epsilon/(tNPv) = AV/v, \quad (5b)$$

where  $v$  is the total water volume in where the densities  $N$  and  $P$  are assessed. For a visual predator, the prey detection area  $A$  is determined by ambient light (depth), predator eye sensitivity, prey size and contrast, and the speed  $V$  is the predator's swimming speed (or, if both predator and prey move, by their average encounter speed—Gerritsen & Strickler, 1977). The physical variables underlying  $A$  will be crucial for the vertical variation in objective predation risk. Gerritsen & Strickler (1977) and Gerritsen (1980) have shown how the effect of both predator and prey movements can be combined in the search rate variable, but we will here assume that the speed of the predator outweighs the speed of its prey so the latter may be ignored.

The prey detection area of a swimming visual predator is the cross-sectional area of the cylinder determined by its swimming path, its visual search range  $R$  and the search angle  $\theta$

$$A = \pi (R \sin \theta)^2 \quad (6)$$

(Luecke & O'Brien, 1981; Dunbrack & Dill, 1984; Aksnes & Giske, 1993). Variation in detection area

and encounter rate will be influenced by prey size and predator swimming speed, but of overall importance is the influence of light intensity on the visual range of the predator (Eggers, 1976; Vinyard & O'Brien, 1976; Confer *et al.*, 1978; Schmidt & O'Brien, 1982; Townsend & Rosebrow, 1982; Aksnes & Giske, 1993). Aksnes & Giske (1993) derived a model for how fish visual range  $R$  is influenced by the environment. The visual range depends on depth  $z$ , light regime (air light intensity  $E_0$ , fraction of irradiance lost in the air-water interface  $i$ , diffuse attenuation coefficient  $K$  and beam attenuation coefficient  $c$ ), the predator (sensitivity threshold of the eye for detection of changes in irradiance  $\Delta S$ ) and the prey (surface area  $a$  and contrast  $C_0$ ):

$$R^2 e^{zK+cR} = iE_0 |C_0| a \Delta S^{-1}. \quad (7a)$$

Equation (7a) applies both to piscivores and planktivores. Due to the deformation of an image by scattering and absorption,  $R^2$  will not be proportional to light intensity in shallow water. For fish in deeper water (usually below 30–50 m during the day, shallower at night) we may simplify eqn (7a):

$$R^2 \approx iE_0 e^{-zK} |C_0| a \Delta S^{-1}, \quad (7b)$$

as  $zK \gg cR$  with increasing  $z$  and decreasing  $R$  (Aksnes & Giske, 1993). This expression will overestimate visual range and hence predator-prey encounter rates in shallow water. Mortality risk for a pelagic planktivore from moving visual piscivores is now proportional to the piscivore's prey detection surface, for which the visual range [given by eqns (7a) or (7b)] is the only environmental variable:

$$M \propto \lambda \propto A \propto R^2. \quad (8)$$

The proportionality factors are influenced by overall abundance of predators  $P$  and their swimming speed  $V$ , on the (time or state-dependent) optimal trade-off between survival and other activities [c.f. eqn (3)]. Although eqn (8) is reached through eqn (7b) and not eqn (7a), the error of applying eqn (8) also in shallow (but strictly pelagic) water is generally not large (c.f. Aksnes & Giske, 1993). Assessments of feeding of mesopelagic planktivores based on eqns (6–7) have been performed by Giske & Aksnes (1992) and Rosland & Giske (1994). We will focus here on risk assessment for the pelagic planktivore after eqns (7–8). For a piscivore, only the term  $e^{-zK}$  will show vertical variation, so that change in mortality risk with depth may be expressed

$$\lambda_x / \lambda_y = e^{K(y-x)}, \quad (9)$$

where  $x$  is shallower than  $y$  and hence  $y > x$  (depth is positive). [Recall that differences in densities of

predators and prey are excluded from this analysis. However, with exponential decay of light intensity, changes in  $N$  or  $P$  in eqn (5) cannot counteract the effect of  $R$  on pelagic predator-prey encounter rates. A numerical illustration is given in Aksnes & Giske (1993, their table 2). Giske & Aksnes (1992) calculated vision-based feeding rate for the mesopelagic fish *Maurolicus muelleri* to decrease by a factor of 15 over a 50 m depth range, while prey concentration increased by a factor of 7 and individual prey mass by a factor of 2.]

In the clearest oceanic water, where vertical gradients in visual mortality risk are minimal,  $K = 0.04 \text{ m}^{-1}$ . There, change in mortality risk by vertical migration is  $e^{0.04}$  or 4% per meter, after eqn (9). In more typical coastal waters with  $K = 0.2 \text{ m}^{-1}$  the change in mortality risk is 22% per meter.

### 2.3. FEEDING LIMITATIONS

The feeding rate may be limited by rate of encounter with prey organisms, by handling time of prey (capture and ingestion) or by digestive processes, in addition to motivation. The latter will not be discussed here and as diet choice implies that encounter rate must exceed ingestion rate, we will analyze digestion, handling and encounter. Neither of these are constants, but their expected variations in the vertical are quite different.

#### 2.3.1. Encounter-limited feeding

The individual-based encounter rate  $\lambda$  cannot directly be compared with the weight-based digestion rate. We therefore define the maximum encounter-limited per body mass feeding rate as

$$f_E = \lambda W_{\text{prey}} W_{\text{pred}}^{-1}, \quad (10a)$$

where  $W_{\text{prey}}$  and  $W_{\text{pred}}$  are prey and predator body mass, respectively. The encounter rate  $\lambda$  between the planktivore and its prey is expressed similar to the encounter with its predator [eqs (5–7)], so that maximum encounter-limited feeding rate at a depth  $z$  is

$$f_E \propto e^{-Kz}. \quad (10b)$$

#### 2.3.2. Digestion limited feeding

Studies of digestion and gastric evacuation of fish have generally been to fit empirical models to experimental data, and various models have been used (Jobling, 1986, 1987; Persson, 1986; Dos Santos & Jobling, 1991; Bromley, 1994). An exponential model often fits best when applied to small and easily digested prey, whereas a linear model often provides better fit if the prey is a large fish (Jobling, 1987). In the

absence of a general theoretical model for gastric evacuation, and since in this paper we consider pelagic planktivores, we assume an exponential pattern for gastric emptying. By empirical regression analysis Elliott (1972) described stomach evacuation of small meals of amphipods fed to brown trout as dependent on time  $t$ , stomach capacity  $D$  (fraction of fish weight;  $\text{g g}^{-1}$ ) and evacuation rate  $d$  ( $\text{g prey digested per gram stomach contents per day}$ ). (Use of symbols and dimensions differ from his notation.) The prolonged maximum feeding rate [ $\text{g ingested (g fish weight)}^{-1} \text{ day}^{-1}$ ] that balances evacuation in his model is

$$f_D = D(1 - e^{-dt})/t, \quad (11a)$$

where the evacuation rate  $d$  is described by a rate constant  $p$  related to prey type, temperature  $T$  and a temperature constant  $B$

$$d = pe^{BT}. \quad (11b)$$

Elliott (1972) reported values for  $p$  between 0.5 and  $1.3 \text{ day}^{-1}$  for brown trout feeding on invertebrate prey. (He reported hourly values.) Estimates of  $B$  range from 0.08 (Bromley, 1994) to  $0.17^\circ\text{C}^{-1}$  (Smith *et al.*, 1989). Using these estimates to generate a maximum estimate of variation in digestion-limited feeding rate due to different prey digestibility suggests

$$f_{Dmax} \approx 2f_{Dmin}, \quad (12)$$

for a fixed temperature  $T = 2^\circ\text{C}$ . At higher temperatures the effect of prey digestibility is far less.

Daily maximum ingestion rate  $f_D$  from eqn (11a) will also vary with stomach capacity  $D$ . This is an individual constant and not an environmental variable, but it is useful as a set of the maximum range of digestion-limited feeding rates. By assuming  $D = 5\%$  of body mass in a slow evacuation set ( $p = 0.5$ ,  $B = 0.1$  and  $T = 2^\circ\text{C}$ ) and  $D = 20\%$  for the fast digesters ( $p = 1.5$ ,  $B = 0.2$  and  $T = 25^\circ\text{C}$ ), we obtain  $0.03 < f_D < 0.2 \text{ g g}^{-1} \text{ day}^{-1}$  as range for digestion-limited maximum feeding rate. The same total range in digestion-limited feeding rate can be obtained by recalculating data in Windell (1978, his table 3). He reports "half-life parameters" defined as the time taken to empty 50% of food from stomach for 10 species at six temperatures. The average digestion rate increased from  $d = 1.4 \text{ day}^{-1}$  at  $5^\circ\text{C}$  to  $d = 3.8 \text{ day}^{-1}$  at  $20^\circ\text{C}$  with a range in the average feeding rate over the temperature interval of  $0.04 < f_D < 0.2 \text{ g g}^{-1} \text{ day}^{-1}$ . This upper limit of daily ingestion at 20% of body mass due to digestion is also

reflected in the Kiørboe *et al.* (1987) regression model of herring larvae ingestion.

One can argue that the food utilized in Elliott's investigation, and perhaps also in the data from Windell (1978), does not represent a full range of potential prey organisms, and that wider ranges in  $d$  and  $f_D$  are to be expected in the marine pelagic habitat. An experiment by Bromley (1991) indicates, however, that large crustaceans are digested as fast as fish: digestion rate of cod that were fed sprat (at  $12.9^\circ\text{C}$ ) was  $1.76\% \text{ h}^{-1}$  of initial meal size, as compared to  $1.59\% \text{ h}^{-1}$  for cod given Norway lobster (at  $8.8^\circ\text{C}$ ). Crustaceans with as hard an exoskeleton as the lobster are not pelagic.

### 2.3.3. Handling limited feeding

When handling time  $H$  limits feeding, the maximum feeding rate is the inverse of handling time,  $1/H$ . Maximum feeding rate (in  $\text{g g}^{-1} \text{ day}^{-1}$ ) under handling limitation is

$$f_H = H^{-1} W_{\text{prey}} W_{\text{pred}}^{-1}. \quad (13)$$

Handling time will vary extensively with predator and prey size. Handling time for piscivores will obviously be negligible relative to digestion time, due to the large item size. Prolonged handling time limitation of feeding is only possible if prey size is minute relative to the predator's stomach. Thus, if we assume individual handling time of one second, and daily maximum digestion-limited feeding to be 20% of body weight per day, handling time may dominate ingestion rate of a continuous feeder if individual prey mass is less than 0.0002% of predator body mass. This is unlikely for normal pelagic predator-prey relationships, and lower  $f$  or  $H$  will reduce this ratio further. Ingestion rate will therefore be constrained by digestion long before by handling. Handling limitation is only of importance for short-time feeding (on food patches).

### 2.4. CRITERION FOR BENEFIT OF DIET SELECTION

With an exponential increase in encounter rate with decreasing depth, there will be a depth  $z$  where  $f_E = f_D$ . Above this depth, feeding will be digestion limited, while encounter limited below. If we further assume that there is environmental variation in digestion rate, and that digestion rate will improve above  $z$  ( $f_{Dz} = f_{Dmin}$ ) there is a potential for an increase in growth rate by staying above this depth. Over how short a vertical distance must this potential be realized for a depth allowing diet choice to be optimal? The static optimization rule of Werner & Gilliam (1984), maximizes  $f/M$  [eqn (4c) for  $r = 0$ ] can be restated: depth  $x$  is more profitable than the deeper depth  $y$  when  $f_x/f_y > M_x/M_y$ . As shown in eqn (9), mortality

risk increases by a factor  $e^K$  for each metre upwards, so we may write

$$f_{D_x}/f_{E_y} > M_x/M_y = e^{-Kx}/e^{-Ky} = e^{K\Delta z}. \quad (14)$$

A number of assumptions have been made above that all shall act to maximize the fitness value of high feeding and growth rate, in order to maximize a benefit of selective feeding. The vertical range  $\Delta z$  obtained from eqn (9) must then finally be evaluated against these assumptions to examine the likelihood of an adaptive value of diet selection for pelagic planktivores.

### 3. Results

Digestion-limited feeding rate may vary by a factor of 2 due to diet [eqn (12)]. Over how large a depth range can a gradual improvement in feeding rate—caused by higher digestion rate due to prey selection—still be beneficial to exploit, when also predation risk increases towards the surface? We first consider fish with the highest motivation for feeding: those with a potential of reducing time to maturation by an increased growth rate [eqn (4c)], and assume that the population size is stable, so that  $f/M$  is maximized. If we allow the digestion rate change to occur immediately above the depth where feeding shifts from encounter-limited (below) to digestion-limited (above), so that  $f_{D_x}/f_{E_y} = 2$ , and assume the clearest oceanic water, the total range of environmental variation in digestion rate must be obtained within  $\Delta z = \ln 2/K = 17 \text{ m}$  [eqn (14)] above, where  $f_E = f_D$  if selective feeding is to give a higher fitness than encounter-based ingestion. For other life histories, with less fitness gain of feeding and growth (Aksnes & Giske, 1990; Giske & Aksnes, 1992), or by including metabolic costs in the conversion from feeding to growth, or in more turbid water masses,  $\Delta z$  will be even smaller. So, if  $K = 0.2 \text{ m}^{-1}$ ,  $\Delta z$  is reduced to 3.5 m, all else being equal.

### 4. Discussion

The combination of two important and principal factors distinguishes the pelagic habitat from littoral, benthic and terrestrial habitats: (i) the lack of shelter on the local spatial scale combined with (ii) strong local environmental gradients in mortality risk. The optimal diet models were originally developed for—and tested on—animals that could increase their time in a cover by increasing their feeding rate, i.e. they could improve their survival probability by feeding efficiently over short time intervals. But diet selection is also shown and modelled for more continuously

feeding herbivores with digestive limitations in feeding rate (e.g. Belovsky, 1981; Belovsky *et al.*, 1989). In these situations local and predictive gradients in mortality risk were weak or absent. Diet selection is beneficial if digestion can take place in a refuge or if local spatial mortality gradients are weak; neither of these apply to the pelagic habitat.

In this analysis, we have not shown that diet selection will never be profitable for pelagic planktivores, but we have shown under which circumstances it may be possible. It is unlikely that digestion rate will improve so quickly just above the depth where the fish are no longer encounter-limited. More probably, digestion rate gradients will be very weak unless there is a sharp temperature boundary or a shift in zooplankton species composition. Therefore, it is most likely that fitness will be higher for a slower-growing encounter-limited fish than for its faster-growing diet selective conspecific.

So what have we ignored in this analysis? A basic theorem is that predation risk is light-dependent. There are no assumptions on where in the water column the predators normally reside. Had we (or the fish) made such assumptions, and then distributed shallower than their predators, then the predators could also redistribute, and gain a good meal. As long as they can move, the only objective mortality risk function is the one derived from the sensory capability of the predators (Giske *et al.*, 1994). It is also obvious that other sensory mechanisms than vision are involved in searching for prey. Schools of predators are attracted to prey herds from long distances. Still, the ingestion of the chemically or audibly discovered prey will, in the end, rely mostly on visual contact, whereby the visibility of the prey will be of utmost importance for its predation risk. However, assuming mortality risk to decrease by  $e^{-Kz}$  is the same as to assume that all predators have the same visual capability ( $\Delta S$ ). Rather, a series of predators replace each other in the vertical of the oceans, with gradually bigger eyes with increasing depth. This error may underestimate slightly the depth range  $\Delta z$  over which the improvements of digestion rate must occur. On the other hand, this increase in eye size, which is an indication of the importance of visual stimuli also for fish in deep water, occurs on a far larger vertical scale than needed to influence a shift to a selective diet.

The analysis is also restricted to the transparent pelagic environment. Demersal fish may also be assumed to feed selectively. Although prey encounter rates may be low, there are opportunities for shelter, and the value of exploiting patchily distributed food thus increases (e.g. Mauchline & Gordon, 1986). Also, prey types differ, and handling time (on

crustaceans, molluscs, etc.) may be formidable, as well as diet-dependent differences in digestion rate. We have also neglected the variations in mortality risk associated with prey handling (Gilliam, 1990), as the pelagic handling times are short relative to digestion times, but even more as the vertical aspect of mortality risk will—even on a small scale—outweigh diet-dependent differences.

The title of this paper restricts the model to planktivores. There is a great difference in prey density and prey encounter rate for planktivores and piscivores, and the assumption of digestion-limited feeding in shallow water will not generally hold for before pelagic piscivores (c.f. Clark & Levy, 1988).

The argument that encounter rate will increase towards the surface so that there will be a depth  $z$  where  $f_E = f_D$  is shown above only for visually orienting animals. However, as long as a pelagic fish has a vertical variable prey encounter rate increasing towards the surface, and is evacuation-limited near the surface, such a  $z$  will exist. And if this organism has visually orienting predators, eqn (14) will apply. Although not general, this situation is probably common.

An impact on diet from predation risk was demonstrated by Werner *et al.* (1983a, b). In absence of predators, small bluegills fed on pelagic zooplankton [consistent with eqn (1)] (Werner *et al.*, 1983b), but shifted to a benthic diet in presence of largemouth bass predators (Werner *et al.*, 1983a).

Vertical distribution and growth of the mesopelagic fish *Maurolicus muelleri* has been modelled by encounter-dependent feeding and mortality risk by Giske & Aksnes (1992) and Rosland & Giske (1994). Giske & Aksnes (1992) found that the daytime vertical distribution of juveniles was close to the depth where  $f_D = f_E$ , while feeding motivation was much lower for the adults. In a stochastic dynamic optimization analysis, where plantivore-plankton encounter probability was Poisson-distributed, Rosland & Giske (1994) found it most profitable for juvenile *M. muelleri* to locate somewhat shallower than this depth. In order to achieve a high growth rate, the fish overcompensated slightly for the random component in encounter rate. Thus, inclusion of the stochastic component into the encounter process may generate shallower distribution of the fish (c.f. Houston & McNamara, 1990), although the motivation then would not be diet choice but rather to reduce the probability of encounter limitation.

The potential depth range  $\Delta z$  found above is independent of the actual depth the pelagic fish resides in. One can assume that vertical gradients in prey concentrations are less pronounced in deep water than in

the epipelagic. This is partly counteracted by the profile of  $K$ , which will generally decrease with depth. However, one could imagine that a potential 17 m upward migration could give large differences in prey types in shallow water, while this depth change would be of minor importance for fish in the deep oceans. Hence, if a benefit should be achieved from diet selection in the pelagic, we assume it would be for those inhabiting the shallows.

The literature on pelagic predation contains several claims of selective feeding. The term "selective" is, however, used differently in the formulation of optimal diet theory and in many field investigations, partly due to differences in the "available" concept. In diet theory [e.g. eqn (1)] "selective" is strictly defined from predator-prey encounter rates, while field investigations compare stomach contents with biological sampling of the environment (e.g. Glova & Sagar, 1989; Angradi & Griffith, 1990), or with differences in stomach contents for different fish (e.g. Powles, 1958; Daan, 1973; Robb & Hislop, 1980). Both these comparative approaches are quite coarse. Due to the strong vertical gradient in mortality risk, zooplankton and fish will generally distribute deeper with increasing size, even more so as the fitness gain of feeding will be much lower for large adults than for smaller juveniles (Giske & Aksnes, 1992). In addition, the lower depth for digestion-limited feeding will depend on  $D$ , the relation between stomach size and fish size. So when different age groups in a fish population differ in diet, this need not indicate diet choice, but rather a vertical structure of both predators and prey and hence differences in availability. This is also the problem of most sampling gear, as they will catch prey in areas where the predator has not searched. Also, the problem of differential prey detection probability due to size and contrast (Eggers, 1977; Aksnes & Giske, 1993) and prey escape ability (Jakobsen & Johnsen, 1986) is overlooked when comparing field densities with stomach samples.

As a conclusion, we present a typical vertical profile of objective mortality risk and feeding rate limited by prey handling, digestion or encounter (Fig. 1). While handling-limited and digestion-limited feeding rates are almost constant with depth, predator-prey encounter rates will vary enormously. Handling time limitation will never occur, as the planktivores will then already be digestion-limited. There is a depth where animals will be digestion-limited above and encounter-limited below. Mortality risk will decrease more slowly than prey encounter rate with depth, as more efficient predators replace each other in the vertical. The optimal depth for fish that are evolutionarily adapted to growing to reduce their time to



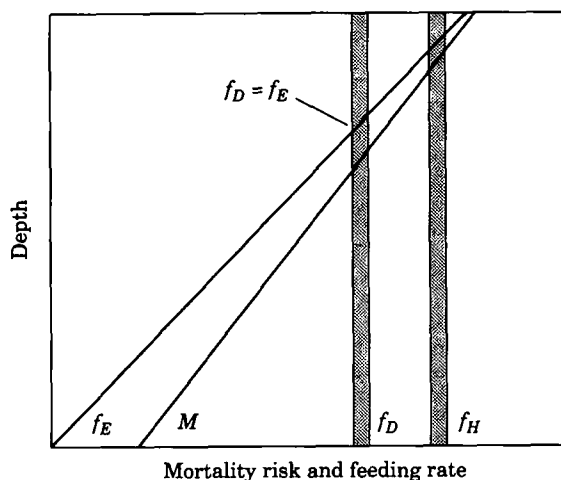


FIG. 1. Principal sketch of vertical profiles of mortality risk ( $M$ ) and feeding rate. The  $x$ -axis is exponential.  $f_H$ ,  $f_D$  and  $f_E$  are the maximum feeding rates under handling limitation, digestion limitation and encounter limitation, respectively.

maturation is where  $f_D = f_E$ , while optimal depth is even deeper for fish that are adapted to increase feeding in order to increase their fecundity. Habitat profitability decreases faster above than below this depth.

The title of this paper suggests that pelagic planktivores should not be selective upon feeding. However, by this we mean they should not be diet-selective. Rather, pelagic planktivores should be highly depth-, or better, light-selective in order to maximize their fitness. This contrasts the situations for benthic and littoral fish. For these species there will be a shelter nearby where they may hide from predators while digesting (c.f. Gilliam 1990).

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