

State-dependent energy allocation in the pelagic Antarctic silverfish *Pleuragramma antarcticum*: trade-off between winter reserves and buoyancy

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ABSTRACT: Icefishes of the perciform suborder Notothenioidei dominate the Antarctic ichthyofauna. These species originated from a benthic ancestor and do not possess a swimbladder. However, some notothenioids have achieved neutral buoyancy through skeletal reductions as well as storage of lipids to reduce body mass relative to seawater. These adaptations enable them to exploit the highly productive pelagic realm. Mobilizing these lipid reserves in periods of critically low food intake may lead to buoyancy problems. Accumulating and conserving these reserves may slow down the development of somatic and reproductive tissues and hence future reproductive output. We constructed a dynamic state variable model to investigate how ingested energy is partitioned over 3 state variables: lipid reserves, structural protein body mass and egg development. Two forms of the model differed in that lipid reserves were either included in or excluded from the total metabolic energy budget of an individual. The model was parameterised for the Antarctic silverfish *Pleuragramma antarcticum*, a key species in the pelagic food web of the high Antarctic zone of the Southern Ocean. In *Pleuragramma*, lipids are stored in unique extracellular lipid sacs, which are thought to serve as buoyancy aids and energy reserves. The model predicts optimal habitat selection and an optimal energy allocation strategy by maximizing future reproductive output. The environment is simulated using vertical gradients in water temperature, optical properties, food availability and predation risk. The form of the model that considers lipids as metabolically inactive reserves best replicates field measurements of fat content and yields high values for fitness in *Pleuragramma*. Uncoupling fat reserves from metabolism, through the development of extracellular lipid sacs, probably represents a key adaptation in the evolution towards a pelagic lifestyle in a fish species with a low scope for activity.

KEY WORDS: Antarctica · Dynamic state variable model · Lipid metabolism · Pelagic fish · Notothenioidei · Southern Ocean

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INTRODUCTION

Many common life history traits run through the biology of pelagic teleost fishes, suggesting convergent adaptation to pronounced and predictable selection pressures (Helfman et al. 1997). Pelagic species often possess hydrodynamically streamlined, compressed bodies with a silvery colour and forked tails. They exhibit several physiological adaptations enabling them to swim continuously, mostly in

schools. Pelagic fish feed on plankton and are rich in lipids. Reproductive traits include high fecundity and broadcast gametes. These adaptations facilitate life in an environment that offers relatively little physical structure and, particularly in temperate and high latitude ecosystems, periodic food availability due to seasonal changes in solar irradiation. In the seas and ocean surrounding the Antarctic continent, the pelagic realm is without doubt the most productive region; this is due to upwelling of nutrient rich cold

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water. The fish fauna in these ice-cold waters is dominated mainly by notothenioids, a perciform suborder of the acanthopterygian teleosts. Notothenioids originate from a bottom-dwelling ancestor (Eastman & Clarke 1998). Although they have pelagic larvae, juvenile or adult stages are typically benthic. The hypothesis is that the lack of a swimbladder in the common ancestor prevented early colonisation of the pelagic habitat after the establishment of the present climate some 20 million years ago (DeVries & Eastman 1978, Eastman 1997).

Only a few notothenioid Antarctic fish species have radiated into meso-, epi- or cryopelagic niches, including the abundant Antarctic silverfish *Pleuragramma antarcticum* Boulenger, 1902. *P. antarcticum* is the most abundant fish species in the high-Antarctic shelf areas of the Southern Ocean (Hubold 1984). It has a circumpolar distribution and occurs at depths between 0 and 1000 m (Fuiman et al. 2002). The species shows many of the anatomic and behavioural characteristics common to pelagic fishes. *Pleuragramma* are silvery coloured planktivores that aggregate in loose schools (Fuiman et al. 2002). They have achieved neutral buoyancy through a combination of skeletal reduction and lipid deposition in large subcutaneous and intermuscular lipid sacs (Eastman 1993). Fat reduces the density of the fish so that buoyancy increases. Negatively buoyant fish must use energy to maintain a vertical position; otherwise they sink.

Lipid content in *Pleuragramma* ranges between 15 and 40% of the dry body mass and represents one of the largest observed lipid values among teleosts (Friedrich & Hagen 1994, Eastman 1997, Wöhrmann et al. 1997, Hagen et al. 2000). Many animals use their fat reserves rather than proteins or sugars as a source of energy whenever demands exceed intake (Bull et al. 1996, Noren & Mangel 2004). Theoretical work suggests that the size of reserves should vary with the costs and benefits of maintaining it (Lima 1986, Clark & Mangel 2000, Garvey & Marshall 2003). However, in *Pleuragramma*, it is unclear whether or not stored lipids are metabolically active and supply energy to maintain body functions during the austral winter when productivity is low (DeVries & Eastman 1978, Eastman 1988, Hubold & Hagen 1997, Wöhrmann et al. 1997, Hagen et al. 2000). Previous histological work showed that lipid sacs are surrounded by cells that possibly regulate lipid transport (Eastman 1988). Lipid reserves in *Pleuragramma* may thus represent an energy source to be used in periods of critically low food intake as well as a buoyancy aid that should be conserved. Accumulating and maintaining energy-dense reserves necessarily reduces the allocation of ingested energy to other tissues, including structural protein body mass and reproductive tissues, thus pos-

sibly compromising future reproductive output. This is especially evident in juvenile fish that experience higher predation rates than adults. Therefore an unbalanced energy allocation has a clear fitness consequence.

In this paper, we model an optimal resource allocation strategy and optimal habitat selection, taking into account fitness consequences. We particularly focus on the lipid metabolism and impose different constraints with respect to the accumulation or utilization of lipid reserves. We use the framework of a dynamic state variable model introduced by Mangel & Clark (1988). Dynamic modelling in ecology is based on the assumption that organisms respond to changes in their environment, given their current physiological state, to maximize fitness. We simulate a 1-dimensional, seasonally changing environment, which has been parameterised for the Ross Sea. The environment is represented by vertical profiles of light intensity, temperature, availability of copepods and predation risk. Using the model, we explore how different constraints on the energy dynamics affect lipid deposition, expected fitness, fecundity and habitat use in *Pleuragramma antarcticum*. Two adaptive models are explored; these differed in that accumulated lipid reserves are either included in or excluded from the total metabolic energy budget of an individual. Under plastic energy allocation, individuals may store fat reserves but incur increased metabolic costs. A second strategy is lipid accumulation at zero maintenance costs, but once lipids are stored, they are unavailable for oxidation when food is scarce. These 2 strategies are then compared with published field data of fat content and fecundity.

MATERIALS AND METHODS

Model structure. The model simulates optimal habitat selection and an optimal energy allocation strategy using a time-step of 1 wk. We considered 3 different vertical habitats that vary in water temperature, optical properties, food availability and predation risk. These habitats represent shallow water, mid water and deep water (Alonzo & Mangel 2001). Water temperature and food abundance influence growth through intake rate and metabolism. Fish may choose between a non-visual and a visual feeding strategy depending on ambient light conditions and plankton concentration. Short feeding periods result in lower predation risk. Assimilated energy is used to offset metabolic costs first. Energy in excess may be used to invest in structural protein mass, lipid reserves or reproductive tissue. Likewise, energy in shortage can be restored from any of these state variables. The model predicts

optimal habitat use and energy allocation strategy for *Pleuragramma* by evaluating lifetime reproductive success using a dynamic state variable model (Clark & Mangel 2000).

Environment. The environment was simulated using a 1-dimensional physical model coupled to a 1-dimensional ecosystem model that had been parameterised for different regions of the Ross Sea (Goffart et al. 2000, Hecq 2003). Shallow water was modelled at 10 m, mid water at 100 m and deep water at 1000 m. These habitats were chosen as a compromise between larval habitat under sea ice and deeper juvenile or adult habitats. Using daily values for solar irradiation and monthly-averaged data of wind speed, air temperature, relative humidity, cloud cover and snow height, the model predicts formation, melting and retreat of marginal sea ice, vertical stability of the water column and nutrient availability. These physical variables essentially control primary production. Maximum chlorophyll concentrations are predicted to coincide with ice melting when entrapped algae are liberated and with the subsequent *Phaeocystis* bloom. Based on primary production, the model predicts the biomass and abundance of 3 ecological classes of zooplankton:

micro-, meso- and macrozooplankton (Fig. 1). Temperatures averaged -0.1°C at 10 m; -1.3°C at 100 m and -1.6°C at 1000 m depth. For a description of the full model, we refer to Hecq (2003).

State variables. The state of an individual fish with total wet mass W is at any time t designated as $W(t)$ and characterized by its structural body mass $B(t)$, its lipid mass $L(t)$ and its gonad mass $G(t)$. The maximum possible lipid mass in *Pleuragramma* is $0.16W(t)$ (Friedrich & Hagen 1994); the maximum gonad mass is $0.3W(t)$ (Kock & Kellerman 1991). The total wet mass of a fish at time t satisfies:

$$W(t) = B(t) + L(t) + G(t) \quad (1)$$

The state of an individual changes between time t and time $t+1$ depending on an allocation strategy $\phi_i(t)$, which allocates energy in excess to lipid reserves, structural mass or gonadal development. In case of a negative energy budget, energy costs to offset metabolic demands were taken from any of these tissues. Energy provided to a fasting individual = 4.5 kJ g^{-1} wet mass for structural tissue, which is mainly composed of proteins, 5.5 kJ g^{-1} for gonads (eggs) and 9 kJ g^{-1} for lipids.

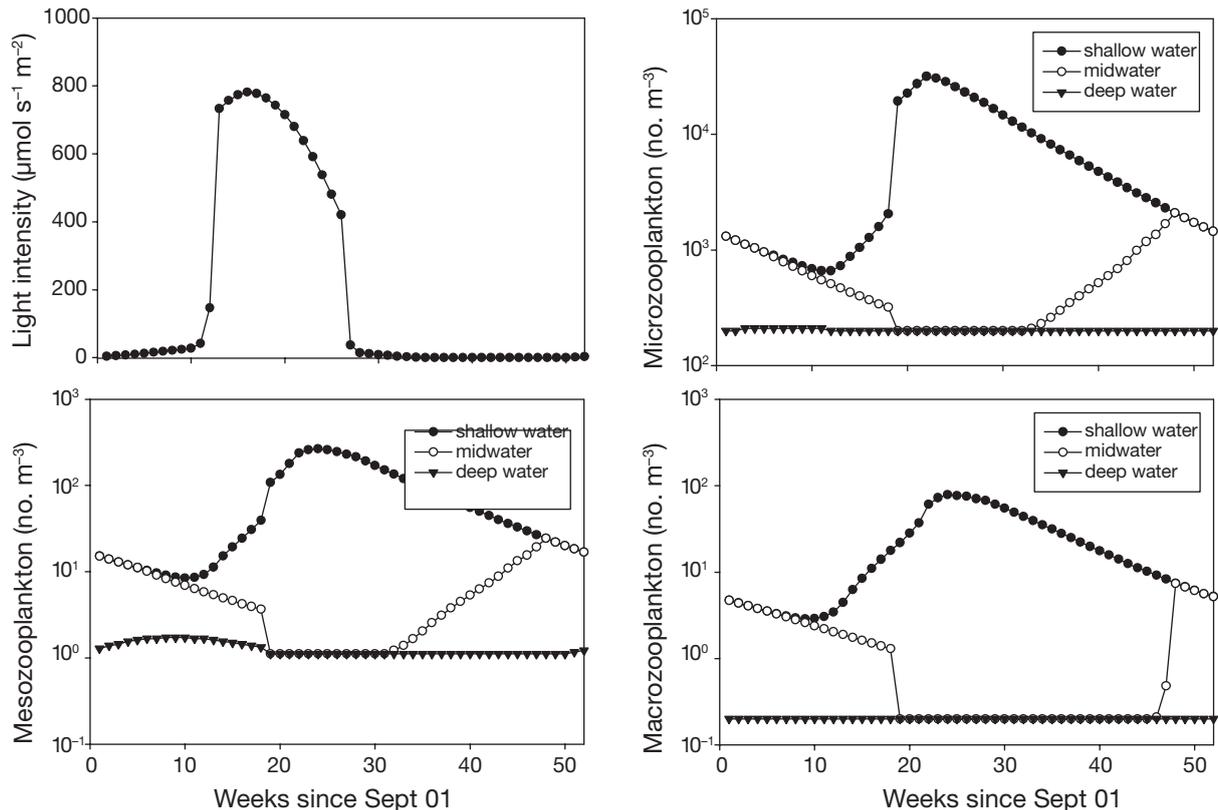


Fig. 1. Simulated light intensity at 0 m (under sea ice) and zooplankton per m^3 (\log_{10} scale) used as input variables in the dynamic state-variable model. Data was simulated for an average meteorological year, starting at the onset of the spring (1 September). Abundance of microzooplankton ($< 20 \mu\text{m}$), mesozooplankton and macrozooplankton ($> 200 \mu\text{m}$) at 3 depths is shown (shallow water: 10 m; midwater: 100 m; and deep water: 1000 m). See 'Materials and methods; Environment' for details

With $C(t)$ the assimilated energy in J wk^{-1} and $M(t)$ the metabolic needs in kJ wk^{-1} , then the dynamics of the state variables change from time t to time $t+1$ as follows:

$$\begin{aligned} B(t+1) &= B(t) + \phi_B(t) \times [C(t) - M(t)]/4.5 \\ G(t+1) &= G(t) + \phi_G(t) \times [C(t) - M(t)]/5.5 \\ L(t+1) &= L(t) + \phi_L(t) \times [C(t) - M(t)]/9 \end{aligned} \quad (2)$$

where $\phi_i(t)$ can take values between 0 and 1 and $\phi_B(t) + \phi_G(t) + \phi_L(t) = 1$. Different constraints on ϕ can be imposed. For instance, in case of a negative energy budget, energy must be provided from lipid reserves, so $\phi_B(t) = \phi_G(t) = 0$. The effect of such constraints will be discussed later. We assumed that total fish length, feeding tactics and rates as well as predation risk were related to $B(t)$ while metabolic costs were related to $W(t)$. Whenever necessary, we translated the structural mass $B(t)$ (g) to total length TL (cm) using the following allometric relationship (Kunzmann 1986 in Froese & Pauly 2005):

$$B(t) = 0.0045 TL^{3.25} \quad (3)$$

Metabolic costs and buoyancy. In the model, metabolic demands $M(t)$ are the sum of basic metabolism $M_1(t)$ and costs due to activity necessary to maintain vertical position $M_2(t)$. Basal metabolism was calculated as a function of total body mass and temperature:

$$M_1(t) = \exp[0.07 \times (T - T_{\min})] \times 0.00246 W(t)^{0.828} \quad (4)$$

where $M_1(t)$ is the metabolic rate in $\text{mg O}_2 \text{ day}^{-1}$, T is the ambient temperature in $^{\circ}\text{C}$ and is habitat-dependent, T_{\min} is the freezing temperature of seawater (-1.8°C) and $W(t)$ is in g. $M_1(t)$ was converted to J day^{-1} using a conversion factor of $13\,562 \text{ J mg}^{-1} \text{ O}_2$ ($3240 \text{ cal g}^{-1} \text{ O}_2$, Elliott & Davison 1975). We followed Forster et al. (1987) for allometric parameters in Eq. (4), which are derived for the cryopelagic *Pagothenia borchgrevinki* (Boulenger, 1902). We assumed a Q_{10} value of 2, which is in line with the conclusions of Clarke & Johnston (1999), who provided firm evidence rejecting the hypothesis of metabolic cold adaptation in polar fish.

Pleuragramma antarcticum has no swimbladder and achieves neutral buoyancy through a combination of lipid deposition in subcutaneous sacs and skeletal reduction (Eastman 1988). Physically, neutral buoyancy is achieved when gravity exerted on the fish ($F_g = W(t) \times 9.81$) is balanced by upward buoyant force in seawater, $F_b = \text{volume} \times 1028 \times 9.81$. If the resultant force $F_r = F_b - F_g$ is < 0 , fish are negatively buoyant. Here, we were particularly interested in how changes in relative lipid content result in changes in buoyancy. Triacylglycerol is the dominant lipid in *Pleuragramma*; so we used a density of 920 kg m^{-3} for fat tissue (Lewis 1970). We also used a density of 1050 kg m^{-3} as average for other fish tissue (Alexander 1967). Hence, increasing the proportion of fat relative to total wet

body mass, $L(t)/W(t)$, will result in increased buoyancy. Positively or negatively buoyant fish must use energy to maintain their vertical position in the water column, otherwise they float or they sink. Hydrodynamic forces created by hovering or swimming while using pectoral fins as hydrofoils compensate for non-zero buoyancy (Strand et al. 2005). *Pleuragramma* are sluggish due to a low amount of red fibre muscle relative to other fish (Kunzmann 1990) and swim slowly (Fuiman et al. 2002). Therefore, we assumed that costs due to hovering would reflect well the extra metabolic costs (DeVries & Eastman 1978). For a fish that uses a pair of fins with a length σ (m) through an angle π (180°) to create a force in seawater equal to F_r , the energetic cost would be (Alexander 2003):

$$M_2(t) = H_{\text{ground}} \times [F_r^3 / (2\pi \times 1028 \times \sigma)]^{1/2} \quad (5)$$

where $M_2(t)$ is measured in J s^{-1} . We measured fin length relative to total length in a number of frozen *Pleuragramma* and subsequently used $0.06 TL$ to approximate fin length. H_{ground} is a dimensionless factor with a value < 1 close to the bottom and 1 for all other situations (Strand et al. 2005). Benthic habitats were not considered, so we assumed $H_{\text{ground}} = 1$. Fig. 2 shows the effect of lipid content on the energy expenditure of hydrostatic lift production.

Intake rate. For each habitat h , we modelled the number of prey eaten per second $F(t)$ as a Type 2 functional response to food concentration $N(h,t)$ (number m^{-3}). We assumed that fish < 3 cm total length prey upon microzooplankton, fish between 3 and 7 cm on mesozooplankton and larger sized fish on macrozooplankton (Fig. 1) (Hubold & Hagen 1997). Using a handling time of $\lambda = 1$ s and a burst speed v of 5 body lengths s^{-1} when food is detected (Fuiman et al. 2002, Franklin et al. 2003), the feeding rate became:

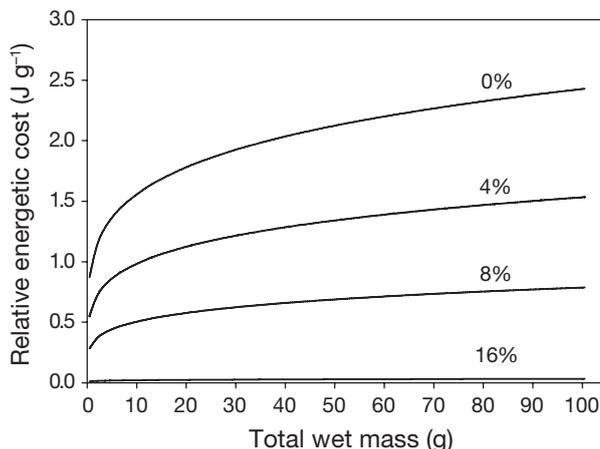


Fig. 2. *Pleuragramma antarcticum*. Energetic expenditure per gram body mass to maintain a vertical position in the water column by hovering as a function of total wet mass for 4 different states of lipid content (% total wet mass)

$$F(t) = \lambda^{-1} N / [(\lambda V v)^{-1} + N] \quad (6)$$

where V denotes the visual or non-visual search field (m^3) (Fig. 3). In the model, cruising speed is total length linked to structural mass $B(t)$. We assumed that fish feed at a rate $F(t)$ until gut capacity is approached. Maximum daily loading $C_{\max}(t)$ (g day^{-1}) was modelled as an allometric function of structural mass $B(t)$:

$$C_{\max}(t) = 0.0747 B(t)^{0.718} \quad (7)$$

We referred to Pääkkönen et al. (2003) for the allometric parameters in Eq. (7), who experimented with *Lota lota* (L.), a gadoid species, at 2.4°C .

Depending on the ambient environmental conditions at depth z , individuals select for the most profitable feeding tactic (Montgomery et al. 1997) that minimizes the time τ (in hours) needed to achieve maximum daily prey loading. Two possible feeding modes are visual feeding and non-visual tactile feeding. The difference between the 2 modes depends on the search field and, in particular, the reaction distance (Fig. 3). Assuming a prey energy content of 2.8 kJ g^{-1} wet mass and using $C_{\max}(t)$ and $F(t)$, we calculated the daily assimilated energy $C(t)$ in J d^{-1} as:

$$C(t) = p \times 2800 \times (1 - \gamma) \times \min(C_{\max}(t), F(t) \times 3600 \times T) \quad (8)$$

where p is a factor used to scale intake rate. In the nominal model, we set $p = 1$. Lost energy due to egestion, excretion and digestion is subtracted from the ingested

energy via a bulk factor $\gamma = 0.391$. T is the total time in hours available for feeding. Under the non-visual feeding tactic, fish have 24 h to achieve maximum loading. Under the visual feeding tactic, the total daylight period limits the time available for feeding.

Survival. In the model, the probability of individual *Pleuragramma* surviving $S(t)$ from time t to time $t+1$ was the product of size-dependent survival $S_B(t)$ and habitat-dependent survival $S_h(t)$. For each habitat, we assumed a baseline mortality depending on structural mass $B(t)$. To account for baseline mortality, we included a size-dependent survival term with an allometric exponent of 0.3 (Lorenzen 1996):

$$S_B(t) = \exp[-1/52 \times B(t)^{-0.3}] \quad (9)$$

where the coefficient 1/52 converts from an annual survival probability to weekly survival. The main predators of *Pleuragramma* are piscivorous fish, penguins and seals, which we assumed to be visual predators. Therefore, predation risk varies as a function of ambient light intensity, $I(t)$, and ambient light intensity varies with time t (Fig. 1) and with depth z . The habitat dependent portion of survival at time t is:

$$S_h(t) = \exp[-\rho I(t)]^{(1+\tau/T)} \quad (10)$$

where $\tau/T < 1$ is a ratio that increases the predation risk during feeding. The values for τ and T are derived from the feeding model. $I(t)$ is calculated using solar irradiance at the surface $I_0(t)$ and depth z (m) as $I(t) = I_0(t) \exp(-Kz)$. K is an attenuation coefficient. Here we

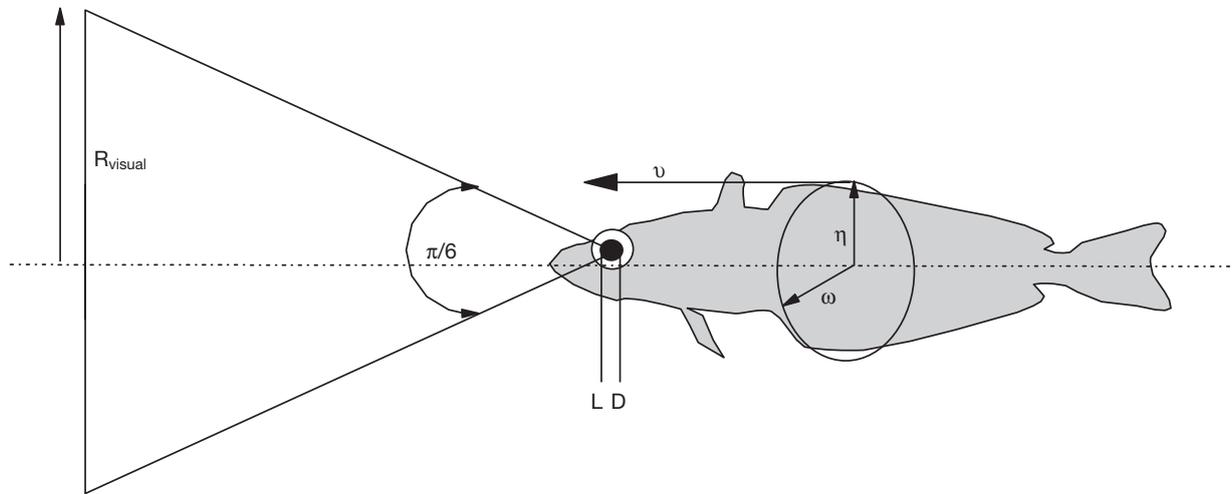


Fig. 3. *Pleuragramma antarcticum*. Visual and non-visual search volume. Non-visual search volume has a cylindrical shape determined by swimming speed (v), fish height (η) and width (ω). Fish height and width are $0.161 TL$ and $0.06 TL$, respectively (TL : total length). Visual search volume modelled as a cone defined by R_{visual} , v , and a visual angle of 30° . R_{visual} was calculated following Lovvorn et al. (2001) after Aksnes & Utne (1997): $R_{\text{visual}}^2 = [T_1 / (k_s + I(t))] \times I(t)$ where T_1 is a bulk factor, k_s is a half-saturation coefficient and $I(t)$ is the light intensity at depth (see Eq. 10). Aksnes & Utne (1997) derived T_1 and k_s for a goby feeding on the copepod species *Calanus finmarchicus* and *Acartia longiremis*. For simplicity, we used their value for k_s ($5 \mu\text{mol m}^{-2} \text{s}^{-1}$) and scaled their value of T_1 (7.5×10^{-2} for a fish with a lens diameter $[LD]$ of 1.88 mm) to the retinal area of *Pleuragramma antarcticum*, assuming that the lens diameter can be approximated by $0.0255 TL$. Under optimal optic conditions (maximum irradiance and shallow water), the model resulted in a maximum visual range of 80 cm for adult fish

used $K = 0.1 \text{ m}^{-1}$. The constant p can be used to modify the strength of the dependence of survival on optical properties. After some trial and error, we used a value of 5×10^{-4} . Modelled annual survival rates varied then between 25% in Age 1+ fish and 75% in adult fish.

Evaluating expected lifetime reproductive success.

We assumed that *Pleuragramma* reproduce annually at the end of the winter (1 September). Annually, a fish with a total weight $> 30 \text{ g}$ (Froese & Pauly 2005) can produce R_0 eggs. If an individual oocyte weighs 6 mg (Vacchi et al. 2004, M. LaMesa pers. comm.), then:

$$R_0 = G(t)/0.006 \quad (11)$$

where $G(t)$ is in g. In the model, we used net reproductive rate R_0 as a fitness currency. Given that $B(t) = b$, $G(t) = g$ and $L(t) = l$, terminal lifetime fitness $\Phi(B, G, L, t_{\max})$ at the final time of the model $t_{\max} = R_0$ for fish $> 30 \text{ g}$ total weight and zero otherwise. The value for lifetime fitness $\Phi(b, g, l, t)$ at time periods $t < t_{\max}$ depends on the current state of $B(t)$, $G(t)$ and $L(t)$ and is maximized using optimal allocation strategy $\phi_i(t)$ when present at optimal habitat $h(t)$. The value for Φ can be found through a backward iteration algorithm such that the optimal solution for fitness at time t is a function of the optimal solution at time $t + 1$ (Clark & Mangel 2000):

$$\Phi(b, g, l, t) = \max_{(b, \phi)} \{ R_0 \times \Lambda_{(t=52,104,\dots)} + S(b, t) \times \Phi(b', g', l', t+1) \} \quad (12)$$

where $\Lambda_{(t=52,104,\dots)} = 1$ if $t = 52, 104, \dots$ and 0 otherwise and b' , g' and l' are the new values for the state variables according to Eq. (2). $S(b, t)$ is the survival probability which depends on habitat use and structural mass b . Φ is zero if $L(t)$ or $G(t)$ is $< 0 \text{ g}$, or if $B(t)$ is $< [1-0.46]W(t)$; the latter equation represents the lean body mass of individuals with maximum lipid and gonad mass. Factors controlling for lifetime fitness are variables expressing the state of the organism and survival probability. Additional fitness is gained by spawning every 52 wk a batch of R_0 eggs.

Plastic and fixed allocation models. The solution of the dynamic fitness model predicts for all combinations of state the time-dependent optimal habitat use and energy allocation strategy. We used the model to conduct 2 theoretical experiments. In plastic allocation models (PAM), energy in excess can be allocated to each type of tissue, while energy in shortage can be derived from each type of tissue (Noren & Mangel 2004). In fixed allocation models (FAM), we have put constraints on the allocation rule (Noren & Mangel 2004). Although *Pleuragramma* may have small amounts of intramuscular adipose tissue (Eastman 1993), we assumed for simplicity that all fat is stored in lipid sacs. In the first model (FAM1), we assumed that lipids are metabolically inactive i.e. they can only

accumulate in the body such that $L(t) \leq L(t+1)$. Further, lipids cannot be depleted if metabolic demands exceed intake rates. Finally, lipid mass can be maintained in the body at no cost, so $W(t)$ in Eq. (4) represents only the sum of $B(t)$ and $G(t)$. In the second fixed allocation model (FAM2), only proteins can be oxidized to fuel the fish's metabolism in case of energy shortage. Lipids are considered metabolically inactive and only accumulate in the lipid sacs. Eggs serve only for spawning and cannot be used for catabolism or predation.

Parameter sensitivity. We adopted the methodology presented by Hunter et al. (2000) to perform a parameter sensitivity analysis. We evaluated the effect of variation in a set of 27 model parameters (Table 1) on the model results. Only 2 parameters of the bioenergetic equations were included, since coincident perturbations of all bioenergetic parameters lead to unrealistic model results due to strong deviations from nominal growth rates. Therefore, we assessed only the influence of specific consumption and metabolism rates on the outcome of the dynamic model. Both parameters are factors in the bioenergetic equations, so perturbations of these parameters can be interpreted as concomitant changes in total consumption or metabolism. Parameter uncertainty analyses were performed by running the 2 models (FAM1, PAM) 150 times each using a random number generator to select independently parameters from a uniform probability distribution between 90 and 110% of the nominal value (Hunter et al. 2000). We used multiple regression to relate the selection of input parameters to 4 dependent variables, each expressing the deviation from the nominal model results. The dynamic program calculates for each state an optimal energy allocation ϕ_i to 3 different tissues as a proportion of ingested energy; optimal habitat use as a proportion of time spent at 3 different habitats; and survival (as a weekly rate). In our study, we included 4 of these variables in the sensitivity analysis to represent the model end products: the proportion of consumed energy allocated to structural mass (ϕ_B); the proportion of consumed energy allocated to lipid mass (ϕ_L); the proportion of time spent at 1000 m (h_{1000}); and survival (S). For each of these variables, we calculated the squared difference between the nominal result and the result of a single sensitivity run summed over all the states. Multiple regression was essentially used to partition the total variance (total SS) over the variance explained by the regression model and the error. Finally, partial SS indicated the amount of variance in model uncertainty explained by variation of individual parameters with the effect of other parameters removed. To speed up computations, we performed this analysis on a Linux high performance computer cluster available at LUDIT (Service centre of the Katholieke Universiteit Leuven for Informatics and Telematics) ICT support.

Table 1. Results of a sensitivity analysis for the plastic allocation model (PAM) and the fixed allocation model 1 (FAM1). Multiple linear regressions were used to relate model parameters to 4 model results: proportion of energy allocated to structural mass (ϕ_B) or to lipid mass (ϕ_L); proportion of time spent at 1000 m (h_{1000}); and survival (S). Model uncertainty calculated by partitioning the variance (Total SS) over the parameters (SS_{effect}), the regression intercept ($SS_{\text{intercept}}$) and the remaining error (SS_{error}). Contributions of each parameter to total model uncertainty presented as relative partial sum of squares (RPSS), (%)

Model parameter description	Value	PAM				FAM1			
		ϕ_B	ϕ_L	h_{1000}	S	ϕ_B	ϕ_L	h_{1000}	S
Allometric mortality exponent	-0.3	0.9	0.7	0.6	14.2	0.9	0.9	0.8	10.2
Light dependence of mortality (ρ)	0.005	7.1	3.3	0.5	0.0	8.0	4.3	0.3	1.8
Attenuation coefficient (K)	0.1 m ⁻¹	1.1	1.8	0.3	2.8	0.9	1.8	0.2	0.4
Specific consumption rate	0.0747 g g ⁻¹ d ⁻¹	15.6	0.1	0.0	0.0	14.5	0.9	0.0	0.1
Specific metabolic rate	0.00246 g g ⁻¹ d ⁻¹	0.4	0.3	0.0	0.5	0.2	0.0	0.0	0.0
Structural energy content	4500 J g ⁻¹	0.5	0.0	0.7	2.4	1.4	0.6	0.9	1.9
Individual egg weight	0.006 g	0.0	0.1	2.6	4.5	0.1	0.1	2.2	0.2
Egg energy content	5500 J g ⁻¹	4.6	0.1	0.2	0.5	4.6	0.2	0.2	4.6
Maximum proportion of gonads	30 %	0.0	1.2	0.0	1.0	0.0	0.7	0.0	3.4
Maximum proportion of lipids	16 %	4.3	0.0	0.1	1.6	4.2	0.5	0.0	2.5
Lipid energy content	9000 J g ⁻¹	0.1	0.2	0.7	5.7	0.2	0.3	0.4	0.5
Length-weight exponent	3.25	5.1	0.0	80.1	46.0	3.0	0.1	81.9	34.5
Length-weight coefficient	0.0045	7.1	1.3	2.9	0.4	7.5	1.9	2.6	3.2
Cut-off value for length in diet	3 cm	0.0	1.2	0.1	0.4	0.1	1.3	0.1	0.3
Cut-off value for length in diet	7 cm	0.5	0.1	1.2	0.3	0.0	0.5	0.9	0.1
Ratio lens diameter:TL	2.55 %	0.2	0.0	0.0	0.0	0.3	0.0	0.0	0.6
Bulk factor (VSM) (T_i)	0.075	1.2	0.4	1.6	0.9	0.9	0.0	1.0	0.3
Sinus of visual angle (VSM)	Sin(30°)	0.3	0.0	0.0	1.3	0.4	0.0	0.0	0.6
Half saturation (VSM) (k_s)	5 $\mu\text{E m}^{-2} \text{s}^{-1}$	0.0	0.2	0.1	0.3	0.1	0.0	0.1	4.3
Burst speed (v)	5 TL s ⁻¹	0.2	0.1	1.5	0.0	0.0	0.5	1.4	0.1
Handling time (λ)	1 s	0.1	0.1	0.6	0.3	0.1	0.1	0.8	0.0
Ratio fish width:TL	6 %	0.0	0.5	0.8	0.1	0.0	0.1	0.6	1.0
Ratio fish height:TL	0.161	0.9	0.5	1.0	0.1	1.1	0.7	0.7	1.6
Fish density	1050 kg m ⁻³	44.0	73.7	0.0	14.5	47.9	77.7	0.2	5.6
Lipid density	920 kg m ⁻³	4.0	10.1	0.7	1.6	2.2	3.5	0.3	18.8
Ratio fin length:TL	6 %	0.9	0.2	0.0	0.0	0.4	0.0	0.0	0.3
Angle of fin movement	180°	0.7	1.1	0.4	0.6	0.8	0.6	0.4	3.0
SS_{effect}		214.8	99.0	154.1	0.01	99.5	50.2	160.4	0.30
$SS_{\text{intercept}}$		0.1	2.7	5.2	0.00	0.0	1.4	6.3	0.00
SS_{error}		344.8	68.6	68.2	0.02	145.9	31.8	66.0	1.13
Total SS		559.6	167.5	222.3	0.03	245.3	82.0	226.4	1.42

VSM: visual search model; TL: total fish length

RESULTS

We ran models for 2 yr, but we based our results solely on the first 52 wk to avoid terminal fitness effects. The model started at the end of winter (1 September) and ended 52 wk later with a spawning event for mature fish. We summarized model data for 850 different states of individual *Pleuragramma* ranging between 0.5 and 100 g total wet body mass. In immature fish, we considered only states for which $G(t) = 0$.

Energy allocation

All models predict ontogenetic changes in the allocation of assimilated energy to different tissues (Fig. 4). The importance of energy allocation to structural body mass

decreases with increasing size. Larger fish invest proportionally more energy in eggs. In the PAM, individuals allocate only small quantities of ingested energy to lipid reserves. During periods in which metabolic demands exceed food intake, premature *Pleuragramma* are predicted to mobilize proteins and lipids, while adults are predicted to feed cannibalistically on eggs or oxidized lipid reserves (Fig. 4). Decreasing the nominal intake rate of food 10 or 20 % though parameter p in Eq. (8) results in increased energy allocation to lipid reserves to survive periods of poor feeding conditions.

In the FAMs, lipids are considered metabolically inactive. Under this constraint, energy allocation to lipids is predicted to start early in the life history. Throughout the further life history, energy allocation to fat remains high and varies between 10 and 30 % of the assimilated food energy (Fig. 4).

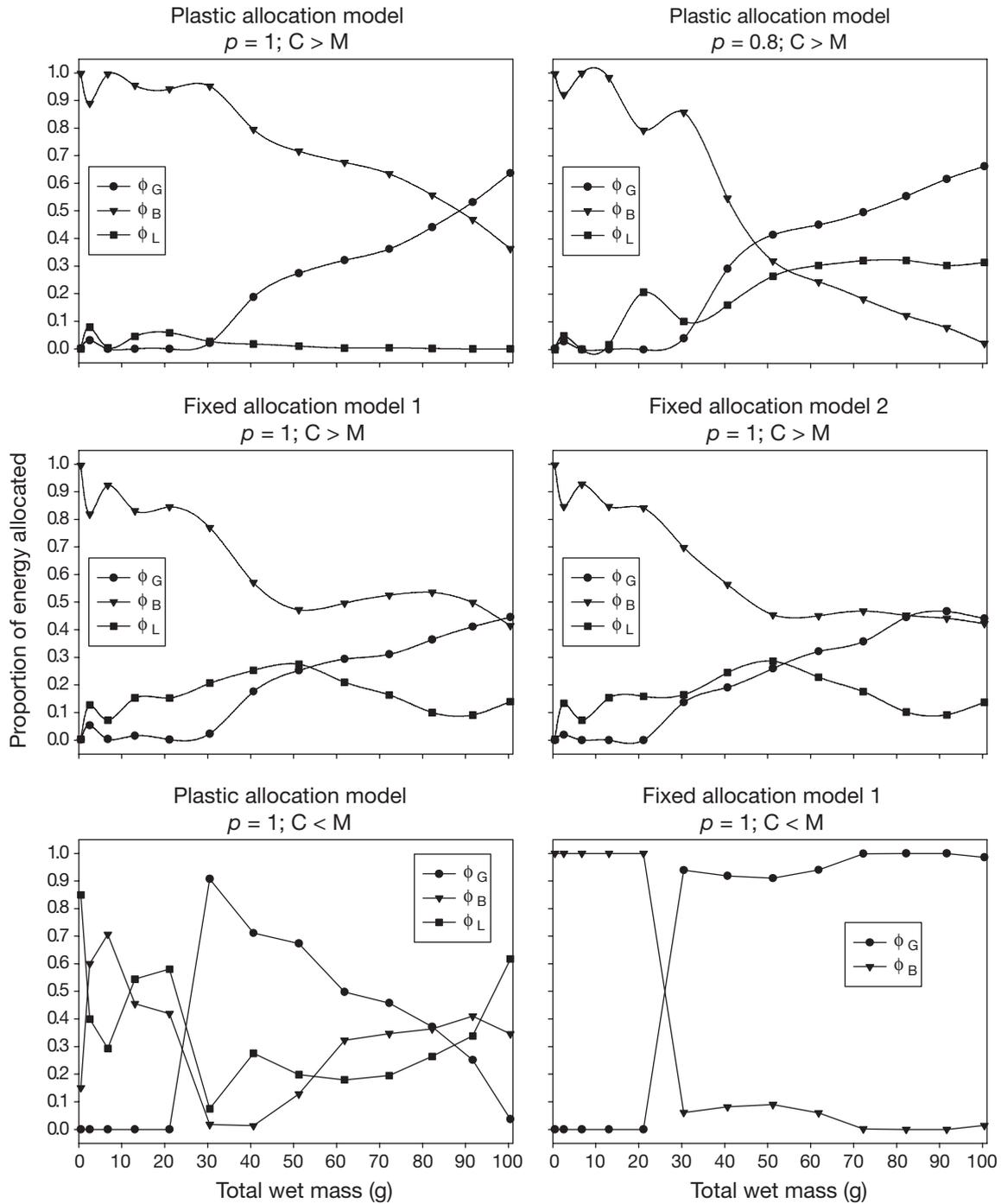


Fig. 4. *Pleuragramma antarcticum*. Allocation of energy to (or utilization from) lipid reserves (ϕ_L), eggs (ϕ_G), structural proteins (ϕ_B) for different feeding modes. Parameter p was used to scale maximum prey loading. $C > M$: energy intake exceeds metabolic needs; $C < M$: metabolic demands exceed energy intake

Habitat use

Both plastic and fixed allocation models predict similar patterns of habitat use. Briefly, the use of shallow water habitat is predicted to decrease with increasing

size (Fig. 5). The use of deep water habitat increases with increasing size. Mid water is predicted to be the most favourable habitat throughout the life history. Models predict that all life history stages use shallow, ice-covered water during the winter. Habitat distribu-

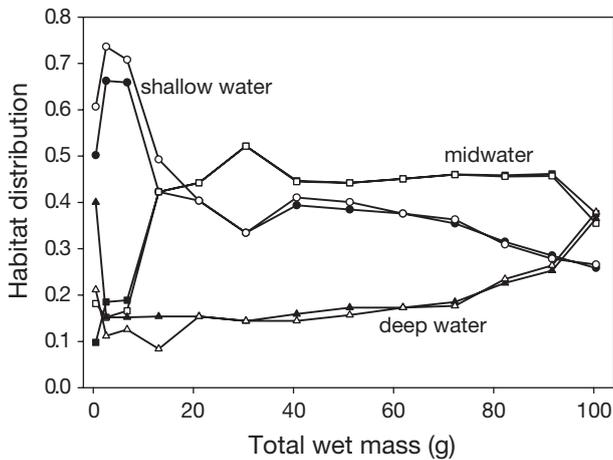
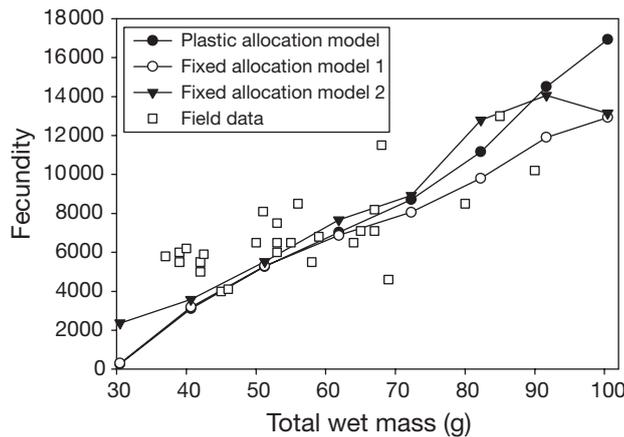


Fig. 5. *Pleuragramma antarcticum*. Size-dependent proportional habitat distribution predicted by the plastic allocation model (PAM, black symbols) and fixed allocation model 1 (FAM1, white symbols). Model results for FAM2 were almost the same as those for FAM1. Shallow water (●, ○), midwater (■, □), deep water (▲, △)

tion is mainly regulated through mortality, but patterns are similar among the models since shallow waters are annually covered by pack ice and snow, thus offering a safe refuge from visual predators during winter. Doubling light-related mortality via parameter ρ in Eq. (10) results in a slightly increased use of deeper waters.

Fecundity and lipid content

The array of decisions for energy allocation to different tissues can be used in a forward iteration procedure to estimate average, state-dependent fecundity and lipid content. All models predict that fecundity correlates positively with fish size, following field data



presented by Gerasimchuk (1987). The modelled slope of the relation between fish size and fecundity was steepest in the plastic allocation model (Fig. 6). With respect to field observations, our models underestimate fecundity in recently matured individuals (30 g) and overestimate fecundity for larger fish (100 g).

Under plastic allocation of resources, lipid content per g wet mass averages 1.9%. Assuming water content of 80% (Friedrich & Hagen 1994), fat content is close to 10% of the dry mass throughout the life history and does not accumulate. In the FAMs, lipid contents are predicted to accumulate steadily to a maximum of 14% of the fish's wet mass. Contrary to the PAM, models with a fixed allocation scheme satisfactorily replicate the observations of lipid content of *Pleuragramma* in the wild (Fig. 6).

Future expected reproductive output

Fig. 7 shows the effect of 2 state variables on fitness. Fitness is interpreted here as future expected reproductive output measured at the start of the model (Week 1). Survivorship is implicitly taken into account. A model with fixed allocation of fat and plastic allocation of proteins and reproductive tissue (FAM 1) results in the highest fitness values. In FAM 1, fitness increases with increasing size and increasing lipid content. In FAM 2 and PAM, fitness increases with increasing mass but reaches an optimum of intermediate fat content.

Sensitivity of the models to parameter perturbations

In Table 1, we present information to assess the influence of the different model parameters on the model results as well as some other model diagnostics.

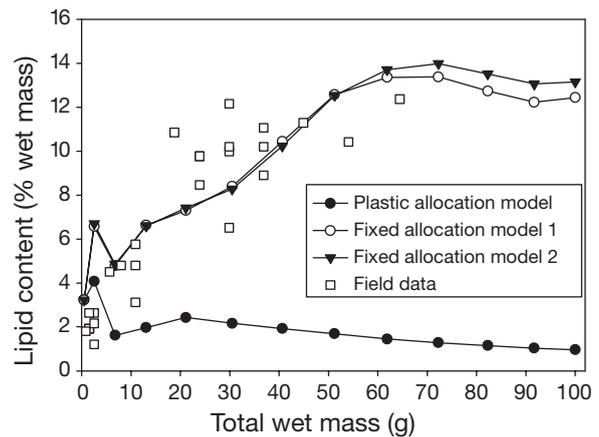


Fig. 6. *Pleuragramma antarcticum*. Size-dependent fecundity (number of eggs) and relative lipid content (% total wet mass) predicted by plastic and fixed allocation models and comparison with field data. Fecundity field data redrawn from Gerasimchuk (1987); lipid content field data redrawn from Friedrich & Hagen (1994)

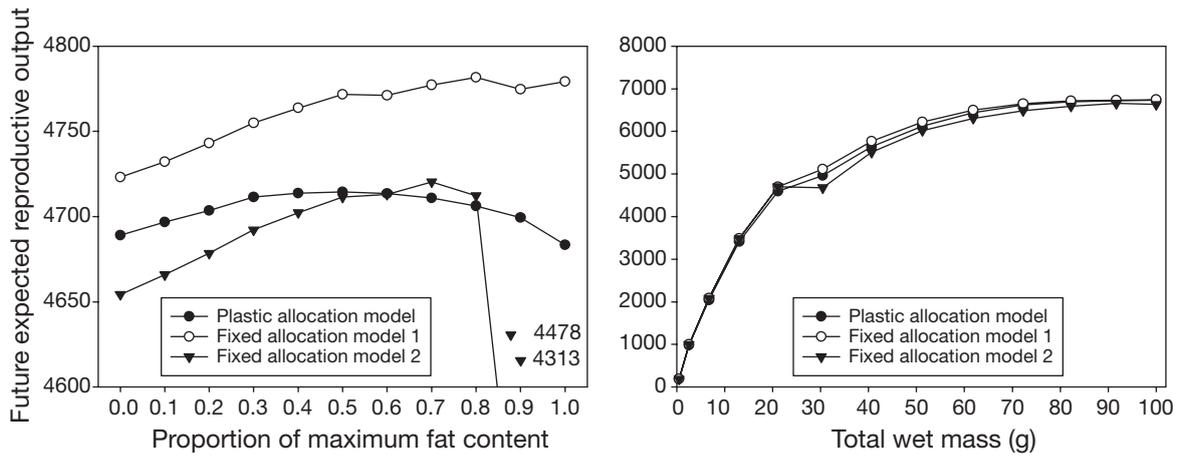


Fig. 7. *Pleuragramma antarcticum*. Effect of state on fitness. Fat content (as a proportion of the maximum fat content) and total wet mass vs. future expected reproductive output, $\Phi(B, G, L, 1)$, as a proxy for fitness

Parameters that proved to be influential in the plastic allocation model were also influential in the fixed allocation model. Regression models with survival as the dependent variable were not significant at $p = 0.05$, so parameter changes hardly affected mortality rates.

Fish tissue density seemed to be the most influential parameter (Table 1). Increasing this parameter led to heavier fish relative to seawater. In model runs with increased density, allocation to lipid deposition increased (positive regression coefficient). Essentially,

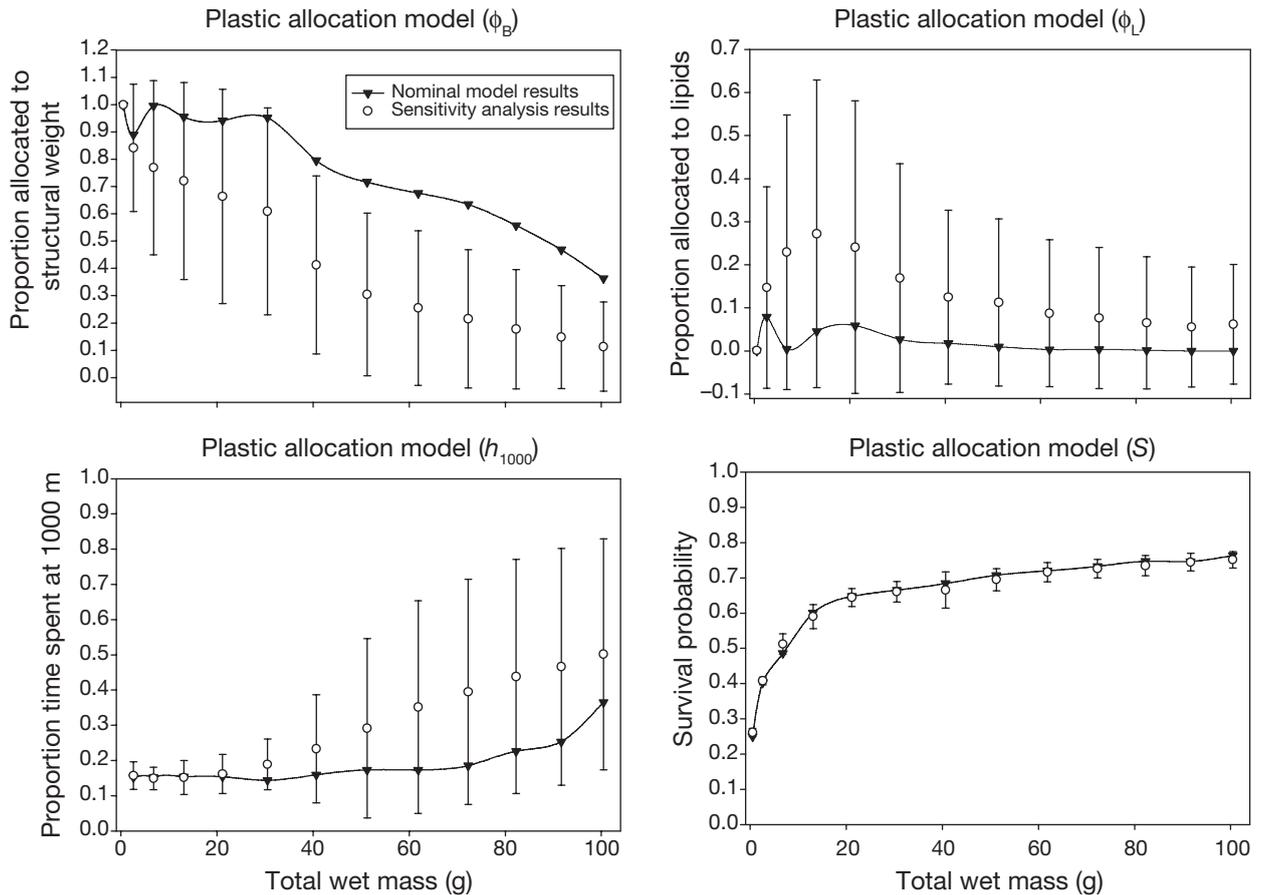


Fig. 8. Sensitivity analysis of the plastic allocation model. Nominal model results—allocation of ingested energy to structural mass (ϕ_B) and lipid mass (ϕ_L), use of deep habitat (h_{1000}) and survival (S)—are presented and compared to an average sensitivity run based on 150 models. Error bars = SD

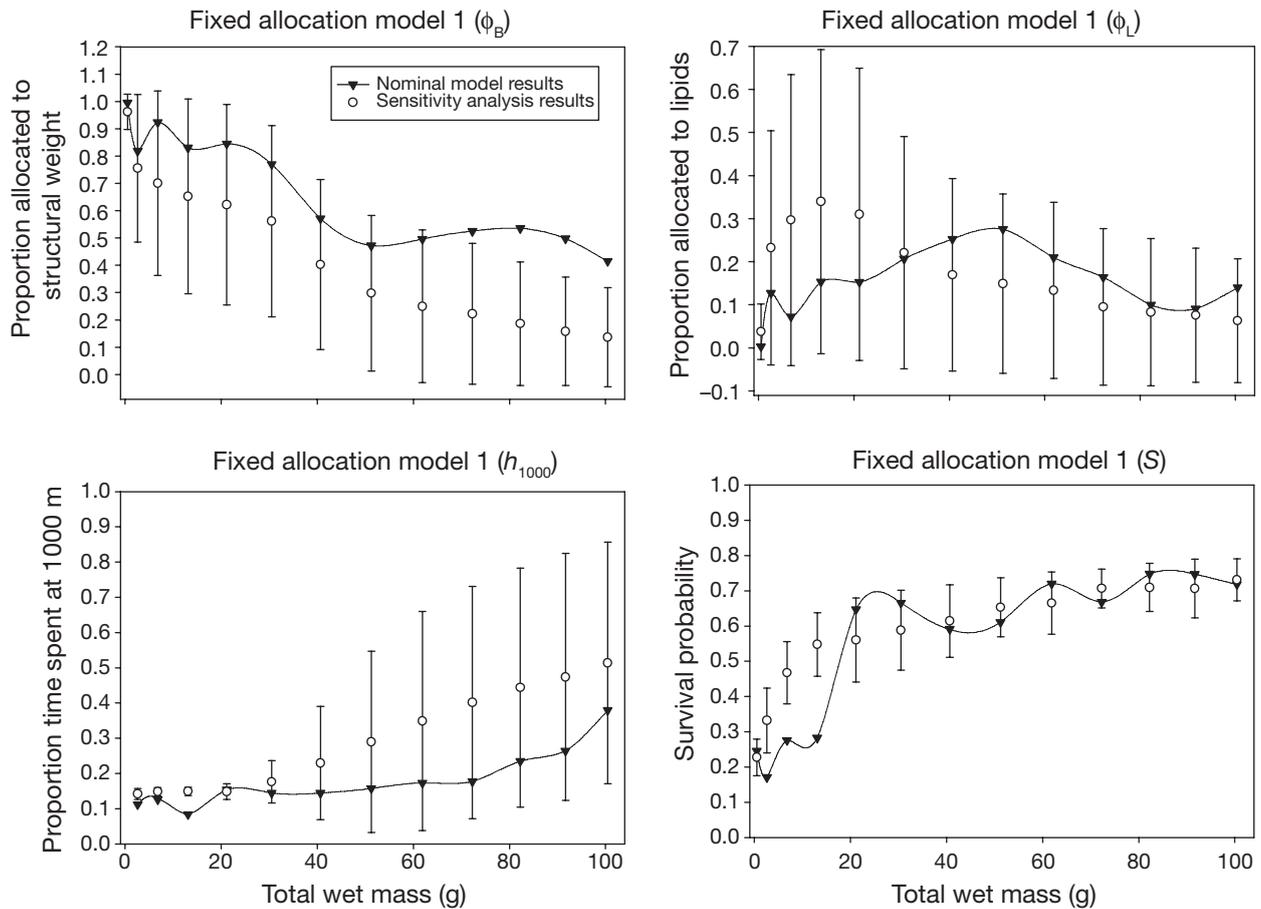


Fig. 9. Sensitivity analysis of the fixed allocation model 1 with constrained lipid dynamics. Nominal model results—allocation of ingested energy to structural mass (ϕ_B) and lipid mass (ϕ_L), use of deep habitat (h_{1000}) and survival (S)—are presented and compared to an average sensitivity run based on 150 models. Error bars = SD

this result is in line with the conclusions of this paper based on the nominal model run i.e. neutrally buoyant fish receive a fitness bonus. The mechanisms to achieve this bonus are in the short term via lipid deposition (our paper), but in the long term neutral buoyancy can be achieved through a decreased tissue density (evolutionary parameter change). Other influential parameters are the specific consumption rate and the exponent in the length-weight relationship. Altered consumption produces changes in the energy allocation patterns, while a different length-weight relationship results in changed predation risk and associated changes in habitat use.

In Figs. 8 & 9 we illustrate the effect of parameter perturbations relative to the nominal model results. In summary, parameter changes, although limited to a 10% interval, are not likely to considerably alter the main conclusions with respect to lipid storage mechanisms, since similar patterns emerged with respect to state-dependent energy allocation, habitat use and survival.

DISCUSSION

Field measurements of fat content in *Pleuragramma antarcticum* showed a pronounced ontogenetic lipid accumulation with increasing size without any notable variation among seasons (Eastman 1988, Hubold & Hagen 1997). Post larval stages have a low lipid content of about 15% of the dry weight (Hubold & Hagen 1997, Wöhrmann et al. 1997). Lipids strictly serve structural functions in these early life history stages. Juveniles continue to deposit extensive amounts of lipids reaching 20 to 30% of the dry weight (Wöhrmann et al. 1997). Lipid increment is now due to massive accumulation of triacylglycerols. In adults, lipid content levels off and contents vary between 30 and 50% of the dry mass (Friedrich & Hagen 1994, Wöhrmann et al. 1997, Hagen et al. 2000). Peak levels in adult *Pleuragramma* can be as high as 58% of the dry mass or 16% of the wet mass (Friedrich & Hagen 1994).

These data are in close agreement with model predictions of fat content relative to wet mass based on a

fixed allocation of resources to different tissues. The fixed allocation model was constrained to allow only the deposition of lipids. Such a strategy requires that, throughout the life history, a part of ingested energy is continuously and permanently fixed into lipid reserves, at the cost of somatic growth and fecundity. The reward is a higher individual fitness, relative to a plastic allocation strategy that allocates more resources into somatic and reproductive growth. It seems contradictory that plastic allocation of ingested energy results in lower fitness than an allocation strategy that is bound to follow predefined constraints. The essential difference between the 2 models is, however, the exclusion of accumulated lipid reserves from the calculation of metabolic costs. In the PAM, individuals are allowed to accumulate fat reserves, but incur increased metabolic costs to maintain reserves during periods when resources are abundant. In the FAM, lipids may only be accumulated but maintenance costs are not considered. The latter assumption is not entirely justified. *Pleuragramma* do have small amounts of adipose tissue that may be metabolically active (Eastman 1993). However, most fat reserves are stored in 100 to 200 large subcutaneous and intramuscular lipid sacs (Eastman 1988 & 1993). Sacs are present at all 53 vertebral levels and vary between 0.2 and 3 mm in diameter. Histological section of the sac wall suggests that lipid transport to and from the sacs occurs via adipose cells. However, the organisation of lipids in large aggregations rather than in individual cells clearly limits the possibilities of rapid lipid mobilization in case of food deprivation (Eastman 1993).

The model results provide quantitative support to the hypothesis that lipid sacs are a buoyancy adaptation that saves energy (DeVries & Eastman 1978). Through lipid deposition in metabolically inactive or low active structures, *Pleuragramma* may reduce its basal metabolism. Excluding the extensive fat reserves from maintenance costs would result in a proportional decrease of the metabolic rate. In addition, by decreasing the body mass relative to seawater, buoyancy increases and then energetic costs, invested in hydrodynamic lift, are reduced. In the absence of a swimbladder or any other passive aid to regulate buoyancy, fish use their pectoral fins to create a downward current (hovering), or they create lift by using their fins as hydrofoils while they swim. These costs increase with body size (Fig. 2). Consequently, avoiding energy expenditure to activity in continuously growing fish without a swimbladder necessitates the lifelong allocation of assimilated energy to lipid deposition.

Energy-saving mechanisms may represent a particular advantage in sluggish fish (Johnston et al. 1988). *Pleuragramma* presumably has a low scope for activity, due to the low amount of red muscle (Kunzman 1990).

The energy that becomes available through energy-saving adaptations may be used for the exploitation of the food-rich upper waters of the high Antarctic zone. The model predicts that shallow waters are preferentially used by juvenile life history stages. This preference for ice-covered, shallow waters decreases with increasing fish size. This pattern corresponds to field data, suggesting size segregation by depth (Hubold 1984), but the use of shallow water under heavy pack ice by adult fish may be an unexpected result. Although prey is more abundant in shallow water, this habitat presents a serious risk of predation. *Pleuragramma* are dominant prey in the diet of the emperor penguin *Aptenodytes forsteri* Gray, 1844 (Cherel & Kooyman 1998) and the Weddell seal *Leptonychotes weddellii* (Lesson, 1826) (Lake et al. 2003), both visual hunters. Exploiting these food-rich but risky waters requires therefore a rapid escape response from predators. Using an underwater video attached to a Weddell seal, Fuiman et al. (2002) estimated a maximum burst speed of *Pleuragramma* at 4.9 body lengths s^{-1} . Franklin et al. (2003) suggested a trade-off between buoyancy and swimming performance, with the most buoyant fish having the highest maximum swimming velocities. So, neutral buoyancy in combination with a low capability for sustained activity but a quick escape response would be an optimal strategy for a 'sit and wait' predator (Eastman 1993), an unusual strategy for pelagic planktivore fish species.

The fixed accumulation of fat into extracellular sacs and the presumed unavailability of lipids for metabolism may put extra pressure on the development of other tissues during periods of food paucity. In the PAM, fish start to build up considerable lipid reserves when the intake rate is set at 80% of the nominal value, and reserves are rapidly depleted in times of food paucity. In the FAM, fat reserves cannot be used, since the catabolism of lipids inevitably leads to buoyancy problems. Instead, proteins are utilized in juveniles, while adults are also predicted to feed on eggs. The interpretation of the latter is that either reproductive tissue is resorbed or spawned eggs are eaten. Egg resorption would lead to lower fecundity, while cannibalistic feeding on eggs would lead to increased egg mortality. Calculations using the parameters presented in our study show that a 50 g *Pleuragramma* would need 10% of the spawned egg mass to offset metabolic costs during 1 mo. Buoyant eggs are thus probably a viable resource at the cost of increased egg mortality. Thus the question arises as to when *Pleuragramma* optimally spawns to secure a continuous food supply in periods of scarce prey while simultaneously minimizing egg mortality due to cannibalistic feeding behaviour. Here, we used for simplicity a fixed spawning period. Kock & Kellerman (1991) reported spawning

dates in August and September, but the spawning season may span the entire period between June and December (Froese & Pauly 2005).

Two other abundant fish species in the Southern Ocean share a pelagic life history style with silverfish: the Antarctic toothfish *Dissostichus mawsoni* Norman, 1937 and the lantern fish *Electrona antarctica* (Günther, 1878). However, both species accumulate lipids in adipose cells, so their lipid reserves are theoretically available for the metabolism. *Dissostichus*, a top predator, feeds almost entirely on fish and cephalopods (Eastman 1988), which may show a more patchy distribution and a more efficient escape response than does zooplankton. When fish experience decreased prey encounter and intake, the model predicts an accumulation of lipid reserves to anticipate periods of food deprivation. This suggests that lipid deposition in sacs may only result in an evolutionary advantage if food is sufficiently available during winter. *E. antarctica* stores energy in lipid reserves during summer for winter use (Donnelly et al. 1990). However, *Electrona* possess a swimbladder and do not face a trade-off with buoyancy.

Although our paper focussed mainly on the role of lipids, we note that model predictions with regard to habitat distribution more or less match observed patterns (Hubold 1984). The role of sea ice in the life history of *Pleuragramma antarcticum* especially warrants further study. The dark, shallow waters under pack ice may offer a permanent food supply and probably provide a refuge against predators for all life history stages of *Pleuragramma*. If true, annual extension of the pack ice zone would influence the population dynamics of *Pleuragramma*, as observed in krill (Atkinson et al. 2004).

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