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Physiologically based limits to food consumption, and individual-based modeling of foraging and growth of larval fishes

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ABSTRACT: Larval fish individual-based models (IBMs) that include foraging subroutines to depict prey encounter, capture and ingestion often include static parameters (e.g. a maximum feeding rate, C_{MAX}) to prevent 'overfeeding' and unrealistically high growth rates. We formulated 2 physiologically based approaches to limit food consumption rate (C) based on gut capacity and evacuation rate (GER) and feeding rate-dependent changes in assimilation efficiency (AE). Parameterizations were based on data reported for a variety of marine and freshwater teleost larvae. The effects of the 3 approaches (C_{MAX}, GER and AE) on feeding and growth were compared in IBM simulations of 12 mm larval sprat *Sprattus sprattus* L. foraging within homogenous and patchy prey fields. Prey concentrations for maximum growth were between 5 and 10 copepodites l^{-1}, similar to thresholds determined for successful foraging by larvae of other marine fish species in laboratory studies. The AE limit allowed larvae to exploit prey patches (to consume prey at higher rates but at lower AEs). In simulations using prey concentrations observed in productive areas of the southern North Sea (e.g. 21.0 copepodites l^{-1}), larvae benefited little (benefited much) from adopting this patch feeding strategy when patch prey concentrations were ≤2-fold (≥5-fold) those outside of the patches. At ≤10 copepodites l^{-1}, foraging model predictions of C were close to limits imposed by C_{MAX}, GER and AE methods. In patches (20 to 40 copepodites l^{-1}), foraging model estimates of C were 2- to 4-fold greater than the highest (AE-based) limit. Physiological-based limits to C are recommended for larval fish IBMs and will be necessary to adequately assess the impacts of prey patchiness on survival and growth of marine fish larvae.

KEY WORDS: Larval fish · Foraging · Prey patches · Individual-based models · Gut evacuation · Assimilation efficiency · *Sprattus sprattus*

INTRODUCTION

Individual-based models (IBMs) utilizing functions to depict foraging, metabolism and growth have been used to explore the impacts of extrinsic factors such as turbulence, light and prey concentration on the vital rates of larval marine fish (e.g. Letcher et al. 1996, Werner et al. 1996, Fiksen & Folkvord 1999, Hinrichsen et al. 2002, Lough et al. 2005). However, simulating 'realistic' rates of food consumption (C) by a modeled larva is somewhat of a Herculean task, since it is not a trivial matter to define what is 'realistic' for field larvae. Field estimates of C for larval fish must often be based upon a number of assumptions regarding *in situ* prey fields (i.e. that the mean prey concentration calculated from net hauls adequately represents the prey field that individual larvae encounter) and/or aspects of larval physiology (i.e. that rates of digestion and gut evacuation are adequately known; Pepin & Penney 2000). Rates of food consumption have been quantified in laboratory studies for the larvae of a variety of marine teleosts (e.g. see Houde 1989, Houde & Zastrow 1993), but these rates do not always compare well with field estimates (MacKenzie et al. 1990).

Attempting to simulate the situation in the wild, larval fish C within IBMs is influenced by an amalgam of variables including prey concentration, one of the main factors modulating contact rates of predators and

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prey. When prey concentrations are high, IBM estimates of C can be unrealistically high and 'overfeeding' can lead to unrealistically high growth rates. This problem has been solved by ignoring overestimates of C and defining growth limits (G_{MAX}) from age–length models (Hinrichsen et al. 2002, Bartsch & Coombs 2004) or laboratory growth rates during *ad libitum* feeding (Fiksen & Folkvord 1999). An upper limit to C (C_{MAX}) has also been employed (Werner et al. 1996, U. Daewel et al. unpubl. data). These approaches (G_{MAX} or C_{MAX}) supersede foraging model predictions and are not mechanistic. Moreover, growth models of larval, juvenile and adult fish are often most sensitive to such parameters (e.g. Bartell et al. 1986, Hinrichsen et al. 2002, Maes et al. 2005, U. Daewel et al. unpubl. data).

The requirement of simulating 'realistic' C in larval fish IBMs also makes it necessary to employ 'quasi-realistic' prey fields. Typically, this has been accomplished by utilizing average values of species- and/or stage-specific zooplankton concentration (no. m^{-3}) from *in situ* net sampling (e.g. Werner et al. 1996, Hinrichsen et al. 2002). These prey fields are likely adequate for projecting larval growth at relatively long time (several weeks) and large spatial scales (banks, shelves), but, at shorter time (days) and smaller spatial (frontal zones) scales, variability in prey fields may become an increasingly relevant factor affecting the vital rates of larval fish. Stochasticity in prey fields experienced, for example, by a larva foraging inside and outside of thin layers (e.g. Dekshenieks et al. 2001) or among prey patches at sub-meter scales (e.g. Owen 1989) was included in the seminal modeling work of Beyer & Laurence (1980) and Laurence (1985). However, in the following decades, modeling efforts have rarely included stochasticity in prey fields (see Letcher et al. 1996). This is interesting in light of the advances made in video sampling systems (e.g. video plankton recorder and other optical packages) that now provide estimates of fine-scale prey distributions over large areas, such as across frontal zones (e.g. Broughton & Lough 2006). Including prey field variability in models will undoubtedly become more relevant as researchers explore sources of variability in short-term larval growth rates (e.g. Lough et al. 2005, 2006). Furthermore, it has been argued that implementing stochasticity in foraging processes on both short and long time scales may be required to understand growth and recruitment variability (e.g. see Pitchford et al. 2005).

In the present modeling study, we (1) reviewed the available literature on larval feeding, gut evacuation and assimilation efficiency, (2) formulated interspecific, mechanistic limits to larval fish C and (3) conducted a series of 8 d IBM simulations within homogeneous and patchy prey fields. Model runs employed a variety of prey (copepod) concentrations that had an abundance-at-size spectrum that was characteristic of the southern North Sea. Model simulations investigated how mechanistic feeding limits, as opposed to the prevalent approach of using non-mechanistic limits (e.g. a C_{MAX} parameter), influenced short-term projections of larval feeding and growth.

MATERIALS AND METHODS

IBM foraging and growth. The IBM used in this study is thoroughly described elsewhere (U. Daewel et al. unpubl. data). Model formulations and parameterizations were based on laboratory studies on larval Atlantic herring *Clupea harengus* L. and field data collected for larval sprat *Sprattus sprattus* L., and only the main features of the subroutines are presented here. Larval growth (G, in µg dry mass per model time step) was calculated as the difference between net energy input and metabolic losses:

$$G = C \times AE \times (1 - R_{SDA}) - R \quad (1)$$

where consumed prey mass (C, µg dry mass per model time step) was reduced by an assimilation efficiency (AE) and metabolic losses (R) that were divided into several subcomponents to account for standard (R_S), feeding (specific dynamic action, R_{SDA}) and active (R_A) rates of energy loss. In Eq. (1), R represented R_S when light was below a threshold for feeding, otherwise it represented R_A. Effects of body mass (Kiørboe et al. 1987) and temperature (Almatar 1984) on R were taken from work on larval herring.

The mass of prey consumed was calculated as a function of encounter rate ($N_{SL,i}$), prey mass (m_i), capture success ($CS_{SL,i}$), handling time ($HT_{SL,i}$) and the time interval (Δt) (Letcher et al. 1996):

$$C = \frac{\sum_i m_i N_{SL,i} CS_{SL,i}}{1 + \sum_i N_{SL,i} HT_{SL,i}} \Delta t \quad (2)$$

where SL is larval fish standard length and i refers to a specific prey class. An optimal foraging approach was used in which different prey types were ranked according to their mass, capture success and handling time. Prey items were included in the diet sequentially on the basis of rank until profitability decreased (see Letcher et al. 1996 and references therein). The capture success was calculated as a function of prey length and larval length based on the attack success function of Munk (1992) for larval Atlantic herring parameterized using field data on larval sprat gut contents (Dickmann 2006). The handling time was calculated following an empirically derived equation from Walton et al. (1992). The model also incorporated light level and turbulence to modify prey capture success (see U. Daewel

et al. unpubl. data), but these factors were not examined in the present study.

Assimilation efficiency was given by:

$$AE_{std} = 0.7(1 - 0.3e^{-0.003(M_D - M_{DMIN})}) \quad (3)$$

where M_D was larval dry mass (µg) and M_{DMIN} was larval dry mass at first feeding (µg). The functional form of Eq. (3) was based upon measurements made on larvae of different marine fish species, including summer flounder *Paralichthys dentatus*, spot *Leiostomus xanthurus* and American sole *Achirus fasciatus* (Buckley & Dillman 1982, Govoni et al. 1982, Houde & Schekter 1983).

In the present study, the output from Eq. (2) is referred to as 'foraging model estimates of C'. In the next sections, we describe 3 different approaches to place limits on foraging model estimates of the food consumed and assimilated during each model time step.

Case 1—C_{MAX}: The first approach used to prevent overfeeding was to employ a C_{MAX} function:

$$C_{MAX} = 1.315 M_D^{0.83} 2.872^{\left[\frac{(T-15)}{10}\right]} \quad (4)$$

that yielded larval dry mass (M_D, µg)- and temperature (T)-specific limits to C that balanced *in situ* estimates of temperature-specific larval sprat growth in the North and Baltic Seas (Munk 1993, Ré & Gonçalves 1993, Huwer 2004, Baumann et al. 2006). Eq. (4) was employed when foraging model estimates of C were $>C_{MAX}$. In this case, the standard formulation of AE (Eq. 3) was used, and the product of Eqs. (3) and (4) provided the non-mechanistic limit to assimilated C.

Case 2—gut evacuation rates: A physiologically based approach to limit C was based upon gut evacuation rate (GER) and knowledge of the maximum gut fullness. This method has recently been used in an IBM for Georges Bank larval cod *Gadus morhua* (Lough et al. 2005). In that study, GER was assumed to be linear and to take approximately 4 h. A linear GER model was able to explain the rate of decrease in gut contents observed during repeated field samplings in darkness for larvae and young juveniles of 8 fish species (Bochdansky & Deibel 2001, Bochdansky et al. 2006). The rate of decrease in gut contents of larval sprat in the field also appeared to be linear, with a mean (±SE) slope (GER) of 0.46 (0.08) h^{-1} (M. A. Peck unpubl. data). This rate implies complete gut emptying within ~2 h and agrees well with that calculated for larval Atlantic herring by Pedersen (1984) and rates calculated for similar-sized larvae of other species at similar temperatures (Table 1).

The effect of body size and temperature (T) on GER was based upon an analysis of data presented within 27 studies on 22 fish species (Table 1). The effect of T on GER was described by a Q_{10} of ~2.4 for Atlantic herring larvae feeding upon *Balanus* nauplii (Blaxter 1962), and the same value was found for northern pipefish *Syngnathus fuscus* feeding upon wild zooplankton (Ryer & Boehlert 1983). Boehlert & Yoklavich (1983) measured GERs of 0.0190, 0.0293 and 0.0385 h^{-1} at 7, 12 and 18°C (Q_{10} = 1.88) in juvenile (69 to 82 mm SL) black rockfish *Sebastes melanops*. Temperature-normalized (12°C, Q_{10} = 2.0), log-transformed GERs of 16 species (studies for which both fish size and water temperature were provided) decreased with log body size in a linear fashion (Fig. 1A). Based upon the literature review, an equation relating GER to body size and temperature was formulated:

$$GER = 1.79 SL^{-0.83} Q_{10}^{\left[\frac{(T-12)}{10}\right]} \quad (5)$$

where the Q_{10} parameter was set to 2.0.

A review of the literature also suggested that a 2- to 5-fold increase in GER occurred when measurements made during feeding were compared to those made after the cessation of feeding (e.g. Chiba 1961, Pedersen 1984, Talbot et al. 1984, Shepherd & Mills 1996; see Table 1). In one study, prey passed through the guts of bay anchovy *Anchoa mitchilli* within minutes during continuous feeding (Chitty 1981). Correspondingly, GER calculated using Eq. (5) was employed when a larva was not feeding (e.g. at the onset of darkness), and the rate was tripled during periods when feeding was continuous.

During any time step, the ingested mass of prey was limited by the available empty space in the gut, which was based upon previous gut fullness and the rate of removal of food from the gut per time step. The maximum capacity of the gut was based upon the length-specific maximum dry mass of prey found within the guts of larvae of 10 different marine fish species (Pepin & Penney 2000, their Fig. 2). The pooled (digitized) data indicated that the mean (±SE) maximum gut prey biomass increased isometrically with larval size and was equal to 6.4 (0.7)% of larval dry mass (Fig. 1B). In this case, if foraging model estimates for C were greater than the maximum capacity of the gut, the product of Eq. (3) (AE) and the maximum capacity of the gut were used to limit assimilated C.

Case 3—digestive capacity: Case 3 was based upon the relationships among C, GER and AE, as affected by both larval body size and temperature. Results of laboratory studies on a variety of organisms (i.e. mollusks, insects, rotifers, copepods) including fish larvae indicated that AE tends to decline when foraging takes place within increasing prey concentrations (PC) (Doohan 1973, Dagg & Walker 1978, Boehlert & Yoklavich 1984, Broekhuizen et al. 2002). This is thought to be associated with the positive relationship between GER and PC. In copepods, the shapes of the GER–PC relationship and the GER–AE relationship

Table 1. Gut evacuation rates for marine and freshwater fish larvae and early juveniles of different species at different body sizes, temperatures (*T*) and prey concentrations. In all cases, prey were zooplankton (either calanoids, cyclopoids, or daphnids), except for rockfish (ground squid) and Atlantic salmon (pellet diet). dph: days post-hatch; n.p.: not provided

Species	Age	Length (mean, range)		*T*	Prey concentration	Evacuation rate		Source
	(dph)	min.	max.	(°C)	(no. l^{-1})	Single meal (h^{-1})	Constant feeding (h^{-1})	
Marine species								
Clupea harengus	n.p.	10	12	7	n.p.	0.111		Blaxter (1962)
				11		0.200		
				15		0.222		
Clupea harengus	12	9	9	8	n.p.	0.125		Blaxter (1965)
				15		0.250		
Clupea harengus	8–22	10.5	12	6–9	$4–5 \times 10^3$	0.667		Fossum (1983)
Clupea harengus	26–40	12.5	18.1	9.5	0.011–0.198	0.400	0.706	Pedersen (1984)
Clupea harengus	21–63	n.p.	n.p.	9.2	3×10^1–10^2	0.143		Werner & Blaxter (1979)
					3×10^3	0.200–0.333		
					3×10^4	0.170–0.250		
Clupea harengus		35	74	n.p.	*in situ*	0.178		Arrhenius & Hansson (1994)
Cynoscion regalis	n.p.	60	70	24	n.p.	0.121–0.219		Lankford & Targett (1997)
Gadus morhua	7		(4–5)	5	n.p.	0.500–0.667		Tilseth & Ellertsen (1984)
Logadon rhomboids					*in situ*	0.380		Peters & Kjelson (1975)
Sardinops sagax		10.1	13.9	20	*in situ*	0.250–0.500		Herrera & Balbontin (1983)
Sebastes malanops	n.p.	35	93	7	*ad libitum*	0.019		Boehlert & Yoklavich (1983)
				12	*ad libitum*	0.029		
				18	*ad libitum*	0.038		
Sprattus sprattus	n.p.	13	16	8–15	*in situ*	0.460		M. A. Peck et al. (unpubl. data)
Syngnathus fuscus	n.p.	150	200	15	n.p.	0.038		Ryer & Boehlert (1983)
				23	n.p.	0.078		
				27	n.p.	0.107		
Theragra chalcogramma	<7		(5.92)	6.2	1200–1500	0.207–0.246		Canino & Bailey (1995)
Thunnus alalunga	n.p.	2.7	10	26	*in situ*	0.333–0.250		Young & Davis (1990)
Thunnus maccoyii	n.p.	2.7	10	26	*in situ*	0.250–0.333		Young & Davis (1990)
Trachurus declivis.	n.p.	2.4	14.3	15–18	*in situ*	0.167–0.250		Young & Davis (1992)
Ulvaria subbifurvata	n.p.	4	13	14	*in situ*	0.165–0.290		Bochdansky et al. (2006)
Freshwater species								
Cyprinus carpio	n.p.	8	12	18–29		0.050	0.125–1.000	Chiba (1961)
Coregonus albula	14		8.7	18	n.p.	0.280		Karjalainen et al. (1991)
Dorosoma cepedianum	n.p.	25	89	21	n.p.	0.130–0.250	0.550–1.250	Shepherd & Mills (1996)
Micropterus salmoides	n.p.	20	60[a]	18	n.p.	0.192	0.357	Laurence (1971)
				23		0.263	0.500	
Perca flavescens	n.p.		(17–19.5)	21	n.p.	n.p.	1.667	Noble (1973)
			30–40	22	n.p.	0.154	0.667	
			(60)	15	n.p.	0.083	0.167	
Perca flavescens	n.p.	20	69	14–21	n.p.	n.p.	0.417–3.333	Mills et al. (1984)
Perca fluviatilis	n.p.		(13.1)	n.p.	field	0.400		Worischka & Mehner (1998)
Salmo salar	n.p.	43	99	9–13	n.p.	0.017	0.068	Talbot et al. (1984)
Stizostedion lucioperca	n.p.		10.6	n.p.	field	0.430		Worischka & Mehner (1998)
Stizostedion vitreum	n.p.	10.4	16.2	15	n.p.	0.109		Johnston & Mathias (1996)
				20	n.p.	0.245		
				25	n.p.	0.106		
Stizostedion vitreum	21		(29.4)	22	n.p.	0.167	0.500	Corazza & Nickum (1983)

[a]Estimate based upon range in dry weights (196 to 721 mg)

were described using both power and exponential models (e.g. Dagg & Walker 1978, Xu & Wang 2001, Besiktepe & Dam 2002). In fish, a negative correlation between *GER* and *AE* was reported by Johnston & Mathias (1996) for zooplanktivorous walleye *Stizostedion vitreum* larvae and by Elliott (1976) working on juvenile brown trout *Salmo trutta*, but the functional form of the relationship was not quantified.

Working with Pacific herring *Clupea pallasi* larvae, Boehlert & Yoklavich (1984) observed that carbon retained in the guts of fish feeding on rotifers *Brachionus* sp. and brine shrimp *Artemia* sp. nauplii decreased with increasing PC, indicating reduced *AE*. This suggested that the digestive capacity decreased with increasing feeding rates. Although *GER* increases with temperature, so does the activity of digestive enzymes (e.g. Alarcón et al. 1995, Gelman et al. 2003), suggesting that digestive capacity increases with increasing temperature, although few laboratory data exist on this topic for marine fish larvae.

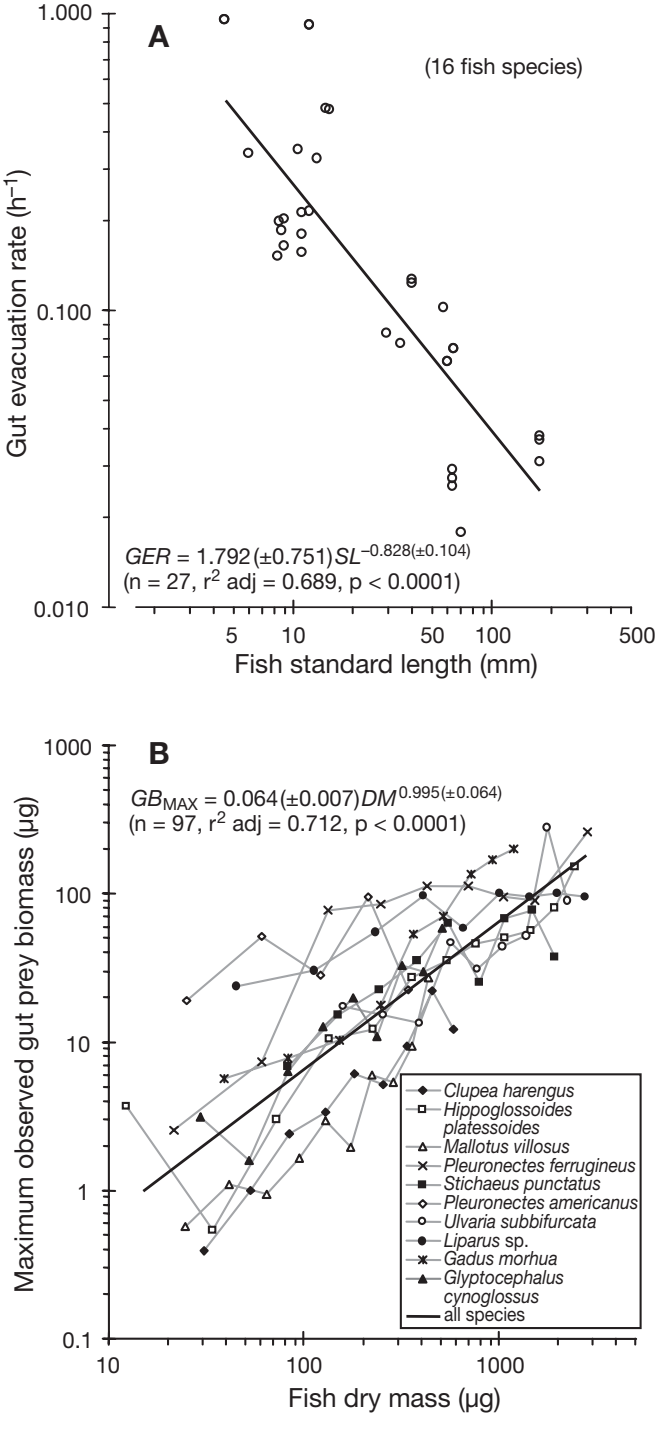

Fig. 1. Literature data on gut capacity and gut evacuation rate (*GER*) for marine and freshwater teleost larvae. (A) Temperature-adjusted *GER* (h^{-1}) versus body length (standard length, *SL*, mm) for 16 teleost species. Data are those reported in Table 1. All rates were expressed relative to 12°C using a Q_{10} of 2.0. (B) Maximum prey biomass (GB_{MAX}, µg) measured in the guts of larvae of each of 10 marine fish species versus larval dry mass (*DM*, µg). Data were digitized from Pepin & Penney (2000, their Fig. 2). The regression line is the best fit for the pooled data. In both panels, mean (±SE) regression parameter estimates are shown

In summary, the literature on fish physiology support the method explored in Case 3, in which *AE* and *GER* both change with body size and are negatively correlated with one another. In this case, a temperature-dependent *GER* and knowledge of the maximum biomass of prey in guts was used to define a body size–specific maximum gut capacity (Gut_{CAP}) (similar to the 'plug-flow reactor' model, e.g. see Canino & Bailey 1995). After Gut_{CAP} was exceeded, an exponential decrease in *AE* with increasing food consumption rate was assumed (Fig. 2), based upon the work of Boehlert & Yoklavich (1984):

$$AE = \begin{cases} AE_{std} & \forall C \le Gut_{CAP} \\ AE_{std} e^{-9.441\left(\frac{C - Gut_{CAP}}{M_D}\right)} & \forall C > Gut_{CAP} \end{cases} \quad (6)$$

Due to a lack of information, the decrease in *AE* after the Gut_{CAP} threshold was considered to be temperature independent in one case (Case 3A) and temperature dependent in another (Case 3B) (see Fig. 2 insert). Furthermore, to be ecologically and/or biologically reasonable, *C* increased with increasing prey concentration until the point where the product of *C* and *AE* declined (i.e. where the gross energy obtained by the larvae was maximal). In this study, no attempt was made to assess the potential impact of prey composition, another factor that affects both *GER* and *AE* in fishes (Karjalainen et al. 1991, Lankford & Targett 1997).

Model simulations and prey fields. Three different 8 d simulations (1-dimensional model, 1 h time step) were run using 12 mm *SL* (~275 µg dry mass) sprat larvae that foraged during a 14 h photoperiod. In each simulation, we used C_{MAX} (Case 1), *GER* (Case 2), or *AE* (Case 3) feeding limits. In Simulation 1, growth rates (mm d^{-1}) were quantified for larvae foraging at each of 8 prey concentrations and 3 temperatures (Table 2). In Simulation 2, the effect of different magnitudes of prey patchiness on modeled growth rates was investigated by allowing larvae to forage for different amounts of time within prey patches of 2-, 5-, or 10-fold increased prey concentrations. In Simulation 3, larvae experienced random fluctuations in the prey field and food consumption; assimilated food and growth rates within each hourly time step were compared among the 3 cases (1, 2 and 3).

Copepods form the vast majority of prey consumed by the larvae of marine fishes, including sprat (Dickmann 2006). The range of copepod concentrations and the relative abundance of different size classes used in this study were based upon zooplankton measurements at German GLOBEC Station 32 in the southern North Sea (54.66° N, 7.66° E). At Station 32, the total abundance of the 200 to 600 µm size classes of the 3 dominant copepods in larval sprat guts (*Acartia* spp.,

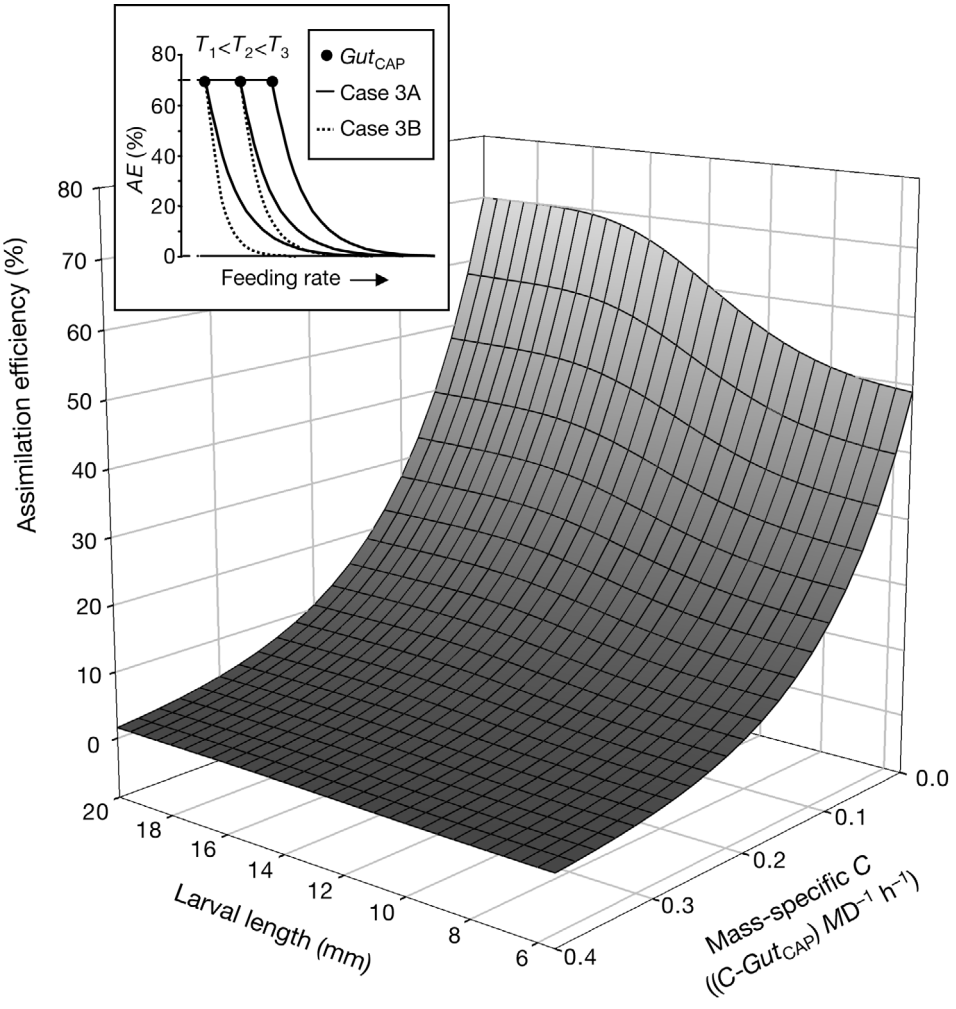

Fig. 2. Case 3 assimilation efficiency (*AE*,%) versus fish size (mm length) and food consumption rate in relative units of gut capacity (Gut_{CAP}). A relative consumption rate value of 0.0 indicates that the rate of food consumption within a model time step was equal to Gut_{CAP}. Insert: Diagram depicting the decrease in *AE* at each of 3 different temperatures (*T*). In Case 3A, the same decrease was used at each temperature. In Case 3B, the decrease was more rapid with decreasing temperature, a response that was based upon considerations of larval growth rates and threshold prey concentrations at different temperatures

Table 2. Summary information for 8 d individual-based model simulations comparing C_{MAX}, *GER*- and *AE*-based limits to larval fish food consumption rate. Copepod concentration is given as the relative abundance in 50 µm size classes 200:250: ... 550 µm = 1.00: 0.80: 0.64: 0.51: 0.41: 0.32: 0.26: 0.21. n.a.: not applicable

Simulation	Temp. (°C)	Prey patches	Copepod concentration (no. l^{-1}) Mean	Outside patch	Inside patch
1	5, 12, 18	No	1.5, 1.7, 2.0, 2.6, 3.4, 5.1, 10.2, 51.0	n.a.	n.a.
2a	12	Yes (2×)	21.0	14.8	29.7
2b	12	Yes (5×)	21.0	9.4	47.0
2c	12	Yes (10×)	21.0	6.6	66.4
3	12	Yes (random)	4.9	(0.3 to 30.0)[a]	

[a]Mean values for lower and upper 10% of cumulative frequency of prey concentrations encountered

Temora longicornis and *Pseudocalanus elongatus*) was ~21.0 l^{-1}. Starting at 200 µm, copepod abundance (*AB*, no. l^{-1}) decreased exponentially with increasing 50 µm size class (*SC*) as: $AB = 12.5 \times e^{-0.0045 \times SC}$ ($r^2 = 0.96$, $p < 0.001$). The range in prey sizes eaten by sprat increases with increasing larval length; 12 mm *SL* larvae eat prey of 200 to ~500 µm, while 18 mm *SL* sprat can eat 800 µm prey (Dickmann 2006). Although information on copepod patchiness in the southern North Sea is lacking, Owen (1989) reported that small-scale (dm to m) plankton patches in the Pacific most commonly contained 2-fold

higher concentrations of organisms, but that patch concentrations exceeded mean concentrations by >10-fold in some cases. We used (at most) a 10-fold range in prey concentrations within and outside patches in Simulation 2 and a 10-fold increase above the mean concentration in Simulation 3 (Table 2).

RESULTS

Temperature, prey and growth

Simulation 1 results indicated that (1) growth rate (G) was positively correlated to temperature (T) at higher prey concentrations, (2) G was negatively correlated to T at low prey concentrations and (3) the threshold prey concentration at which G was food-limited increased with increasing T (Fig. 3). The relationship between G and prey concentration had the same functional form in all 3 cases, but threshold prey concentrations were slightly higher in the *GER* and *AE* cases. The effect of T on G and on prey threshold concentration was similar in the first 2 cases, but was relatively small in Case 3A (*AE*). However, the influence of T on G was similar in all 3 cases when the decrease in *AE* with increasing C (above gut capacity) was temperature dependent (this is Case 3B, see Figs. 2 & 3). Relative to C_{MAX}, maximal growth rates resulting from *GER* and *AE* limits were higher at the same temperatures and prey concentrations, but were in closer agreement with G at C_{MAX} when Case 3B was employed.

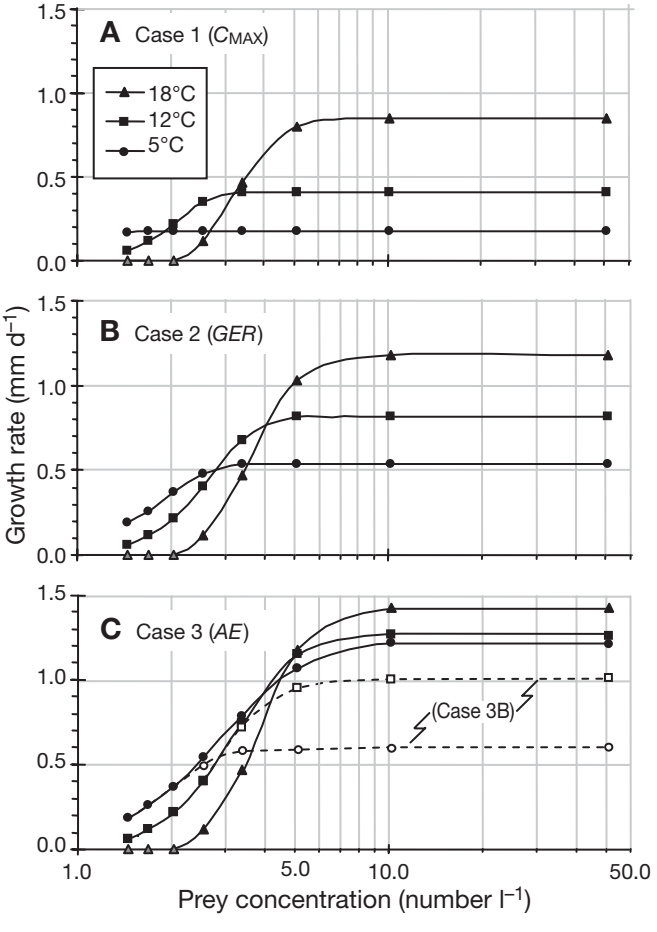

Fig. 3. Simulated growth rates (mm d^{-1}) of larvae after foraging for 8 d at 8 different prey concentrations at each of 3 temperatures (5, 12, or 18°C). Each panel depicts a different method of limiting modeled food consumption. Unfilled symbols in Panel C denote growth rates for larvae limited using the Case 3B approach (see Fig. 2). Gray-filled triangles denote mortality. All larvae were 12 mm *SL* at the start of simulations

Prey patches

When *GER* or *AE* feeding limits were used in Simulation 2, relative larval growth rates were increased by ≥10% when larvae spent only 12% of the 8 d foraging period within patches having 10-fold higher prey concentrations than outside patches (Fig. 4). Using the *GER*- and *AE*-based limits, when prey patches had

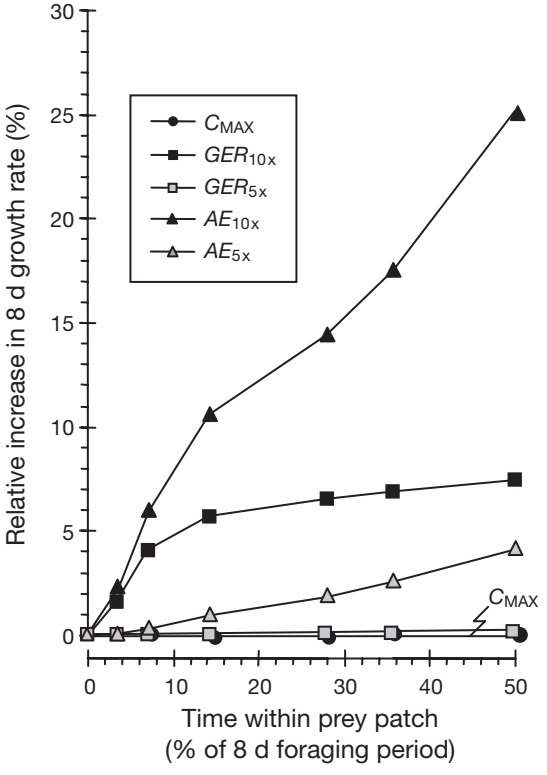

Fig. 4. Percentage increase in 8 d growth rate versus the duration of time within a patch (% foraging time). All values are case specific and relative to the no-patch condition (0). Growth responses to 5- and 10-fold patch prey concentrations are shown (see Table 2, Simulation 2a to c)

5-fold higher prey concentrations, the relative changes in growth were smaller. At 2-fold differences in prey concentration, no growth differences were detected because prey concentrations were above growth thresholds both outside and inside prey patches. Due to the lower prey threshold for maximum growth, relative growth of larvae was unchanged by the presence of prey patches when the C_{MAX} limit was employed.

Fluctuating prey fields

The differences among the 3 approaches to limit *C* were clearly evident when larvae were exposed to random fluctuations in the prey field in Simulation 3. For example, no differences in assimilated *C* were noted within and outside of prey patches using C_{MAX}, whereas 2- to 3-fold higher assimilated *C* was noted within patches using *GER* and *AE* approaches (Fig. 5). Within this random encounter simulation, larval *C* was saturated at concentrations of ≥15 copepodites l^{-1}, which were randomly encountered 11 times over the 8 d period. At these high concentrations, mean (±SD) *C* was equivalent to 41.3 (1.0), 56.3 (3.1) and 173.8 (1.1)% larval dry mass d^{-1} (hourly rates × 14 h foraging period) when feeding was limited by C_{MAX}, *GER* and *AE*, respectively. The mean (±SE) assimilated ration during the same periods was equivalent to 25.4 (0.2), 36.4 (1.0) and 49.7 (8.8)% larval dry mass d^{-1} in the same 3 cases. Estimates of assimilated *C* were more similar among the 3 cases, since *AE* within Case 3 decreased from a median value of 64% at concentrations <4 copepods l^{-1} to ~28% when larvae fed intensively within patches containing 15 to 40 copepods l^{-1}.

Foraging estimates of *C* (Eq. 2) and the limits to *C* imposed by each of the 3 approaches (C_{MAX}, *GER* and *AE*) were generally in close agreement at relatively low prey concentrations (Fig. 6A). However, at relatively high prey concentrations, foraging model estimates of *C* based on Eq. (2) were 2- to 4-fold higher than the highest *C* limit, the limit imposed by *AE* in Case 3 (Fig. 6B).

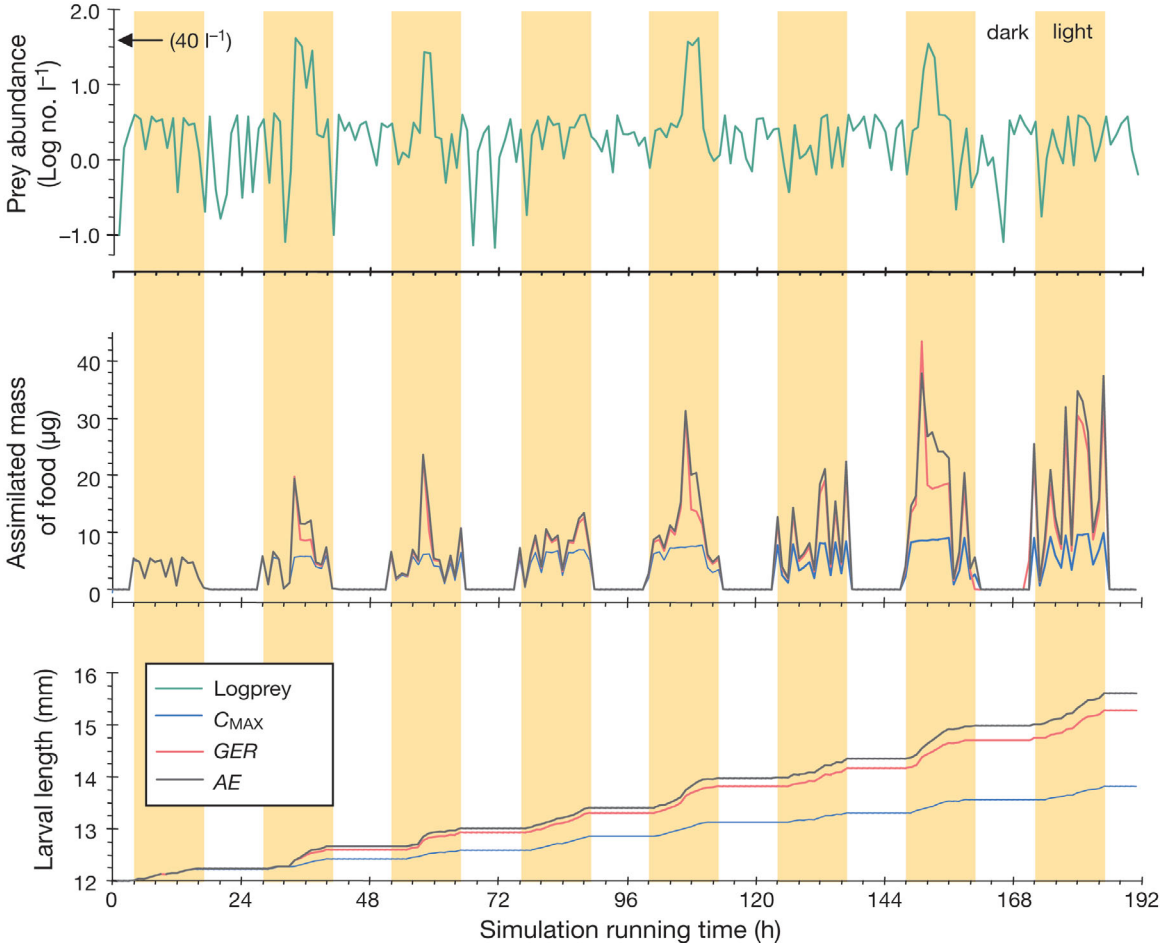

Fig. 5. Individual-based method simulation of random fluctuations in prey concentration and corresponding effect on changes in assimilated food and larval size (mm) per 1 h time step over the course of 8 d. The light regime and the value for peak prey abundance within a patch (upper panel) are indicated

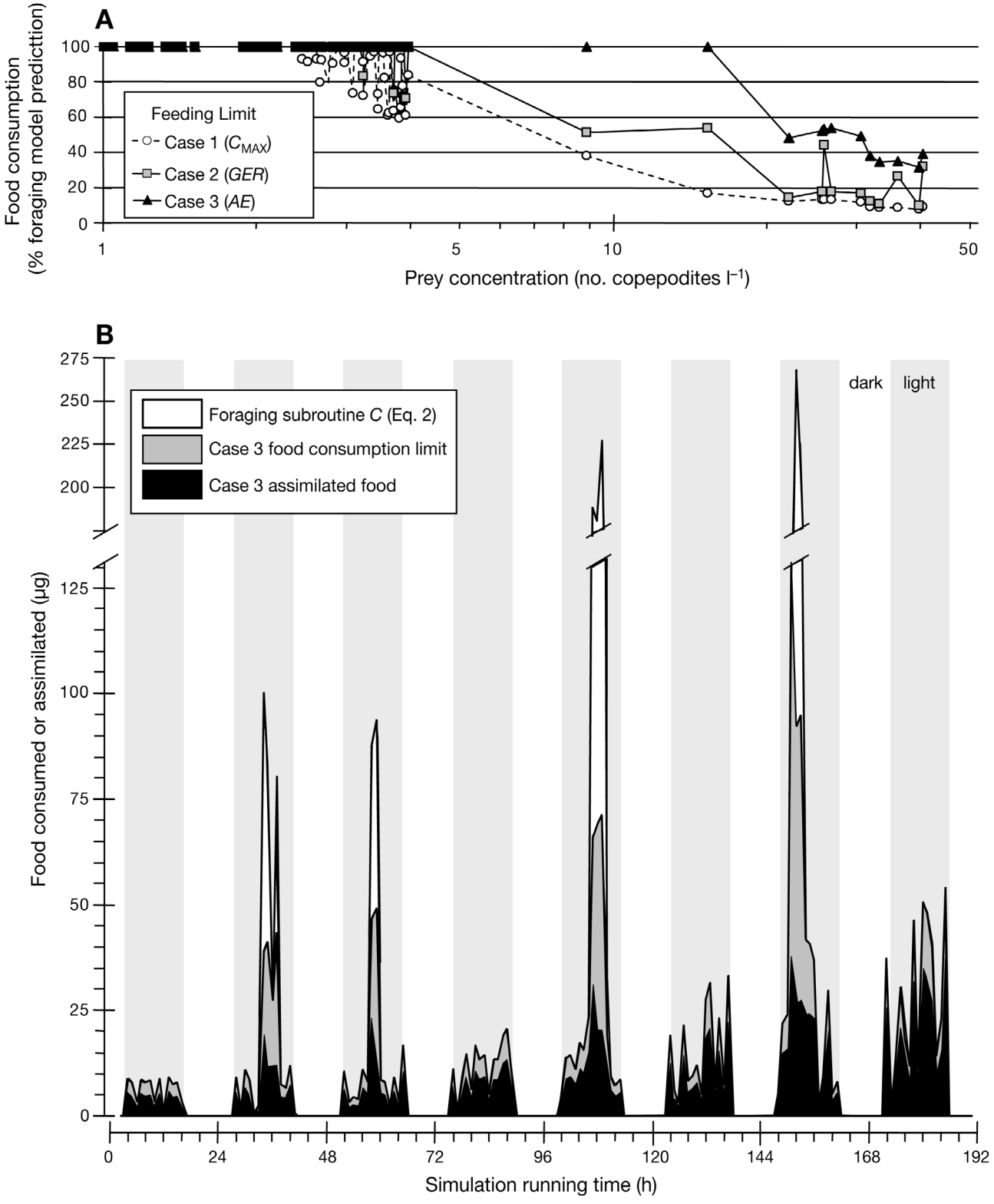

Fig. 6. (A) Food consumption rate (C) as limited by Case 1 (C_{MAX}), Case 2 (*GER*) and Case 3A (*AE*) relative to the individual-based method foraging subroutine estimate of C (based on Eq. 2 in the text) at different prey concentrations. Prey concentrations were those that were randomly encountered within model Simulation 3. (B) Comparison of foraging subroutine C, Case 3A-limited C and Case 3A-limited assimilated food ($C \times AE$) in each 1 h time step during the course of model Simulation 3. The randomly fluctuating prey field is shown in Fig. 5

DISCUSSION

Temperature, prey and growth

The results of our simulations performed at different, homogenous prey concentrations were consistent with expectations concerning larval fish physiology and interactions among temperature (T), feeding rate (C) and growth rate (G). Interestingly, for the effect of temperature on growth in Case 3 (*AE*) to be similar to that in the other 2 cases, the decrease in *AE* with increasing C (above gut capacity) had to be temperature dependent (this is Case 3B, see Figs. 2 & 3). We are unaware of any studies comparing the decline in *AE* with increasing C at different temperatures. However, the formulation appears to be biologically reasonable and laboratory studies should be conducted to test the validity of this model result. In the following discussion, we avoid further discussion of temperature and focus on comparing the 3 cases at the same temperature.

Clearly, growth rates of larval fish should be food limited in environments with low prey concentrations. However, the threshold prey concentrations reported in different studies to limit larval marine fish foraging and growth rates are equivocal. Based upon a review of laboratory functional response experiments conducted on 8 species of marine fish larvae, MacKenzie et al. (1990) calculated a threshold prey concentration of 179 µg l^{-1} below which larval fish C was food limited. Given the conversions used in their study, this corresponds to a concentration of ~660 nauplii l^{-1} or ~80 copepodites l^{-1}. In the present study, simulated growth rates declined (C was not maximal) at concentrations of 3 to 5 copepodites l^{-1} and were highest (feeding was maximal) at ~10 copepodites l^{-1} (Fig. 3). Our simulation predictions agreed well with the results of laboratory studies evaluating the effects of prey concentration on food searching and capture success of prey by larval marine fish (Munk & Kiørboe 1985, Munk 1995). In one study, 5.7 to 6.9 mm *SL* larval Atlantic cod foraged effectively at prey concentrations as low as 2 prey l^{-1} (Munk 1995).

Our estimates of C based upon the C_{MAX} limit (41.3%) and *GER* limit (56.3%) were similar to those obtained in a meta-analysis of 9 laboratory studies quantifying feeding rates by marine fish larvae (MacKenzie et al. 1990). In that study, ingestion by a 132.4 µg dry mass larva was equal to 75.8 µg d^{-1} (57% M_D) at 18.7°C, and estimates of relative ingestion varied by a factor of about 2 for the 12 species examined. Such interspecific differences underscore the problems that can arise whenever a 'generic' approach is taken to parameterize a model for a specific species. We illustrated this via the discrepancies between growth estimates using a C_{MAX} parameter (based upon data collected on sprat) and the other 2 limits (inter-specific parameterization). However, without parameter 'tuning', 2-fold differences in growth estimates were apparent among the 3 approaches, which were well within the range of inter-specific differences reported for most vital rates in teleost larvae (e.g. Houde 1989, Govoni et al. 1986, MacKenzie et al. 1990, Houde & Zastrow 1993).

When considered in light of values determined for the gross growth efficiency ($GGE = 100 \times G/C$) of larval fish, our value for *GGE* (64%) in Simulation 3 Case 3 (*AE* limit) was similar to that found in some species (*Blennius pavo* = 60%, *Clupea harengus* = 62%), but higher than the average calculated for larvae of a number of species (MacKenzie et al. 1990, Houde & Zastrow 1993). That our *GGE* value resulting from the *AE* limit agreed with published accounts was somewhat unexpected, since (1) our IBM was parameterized based on data for clupeids (sprat and Atlantic herring), (2) *GER*, gut capacity (Gut_{CAP}) and feeding-induced limits to *AE* were based upon data collected on a variety of non-clupeid species, and (3) no model tuning was used to adjust parameter values. A justifiable example of the latter would be adjustments made to active metabolism (R_A). Clearly, intensive feeding within patches would be expected to increase R_A, leading to lower energy available for growth (and lower values of *GGE*).

Prey patches and foraging

Our simulation results suggested that static limits to C such as C_{MAX} may not be adequate when modeled larvae forage in habitats with marked spatial and/or temporal variability in prey resources. In Case 3 (*AE*-based limit), larvae could exploit prey patches by consuming more food (at lower *AE*) per model time step. However, it should be noted that exploitation of prey patches in this manner could only benefit larvae (lead to higher growth rates) if prey concentrations outside the patch were lower than the growth-threshold prey concentration (~10 copepodites l^{-1}, see Fig. 3). The present simulation depicted a southern North Sea habitat having a mean copepodite concentration of 21.0 l^{-1}, with 2-, 5-, or 10-fold differences in concentrations within and outside patches (see Table 2). Foraging in this habitat, larvae benefited little (benefited much) from adopting a patch feeding strategy when prey concentrations in patches were ≤2-fold (≥5-fold) those outside patches.

An important finding of the present study was that, at high prey concentrations, a large discrepancy existed between foraging model estimates of C and the limits to C imposed by C_{MAX}, *GER*, or *AE* approaches. At concentrations >40 copepodites l^{-1}, the foraging

model predicted 2- to 4-fold higher C than the limit imposed by Case 3 (where C was highest among the 3 limits; see Fig. 6A). Differences between foraging model C and the limits imposed by C_{MAX} were not unexpected. A C_{MAX} parameter is derived from mass-based parameter rates of a balanced bioenergetics budget (e.g. metabolic losses and growth), while the foraging subroutine contains functions utilizing larval length (e.g. visual distance, capture success, swimming velocity). Since sprat larvae have relatively low mass-at-length compared to larvae of other teleosts (Peck et al. 2005), the foraging model prediction of C (based on length) exceeds the estimates of C required to obtain *in situ* growth rates (based on mass). However, the discrepancy of the foraging model estimates of C and the limit imposed by both of the other approaches (Cases 2 & 3) (e.g. see Fig. 6B) suggests that the current (commonly used) formulation of larval fish foraging yields unrealistically high C when larval fish encounter high prey concentrations.

Working knowledge

The physiologically based approaches to limit food consumption explored in this study relied upon knowledge of *GER* and *AE* and how these parameters were affected by changes in larval fish size, temperature and prey concentration. How robust are the estimates of *GER*? There appear to be many studies evaluating *GER* in fish, and the rates reported were similar after temperature and fish body size differences were taken into account. *GER* was generally between 0.2 and 0.5 h^{-1} for young larvae of a variety of marine and freshwater fish species, including 0.165 to 0.290 for larval radiated shanny *Ulvaria subbifurvata* (Bochdansky et al. 2006), 0.207 to 0.246 for walleye pollock *Theragra chalcogramma* (Canino & Bailey 1995), 0.38 for pinfish *Logadon rhomboids* (Peters & Kjelson 1975), 0.40 for perch *Perca fluviatilis* and 0.43 for zander *Stizostedion lucioperca* (Worischka & Mehner 1998). *GER* for post-larval stages tended to be lower, and was between 0.13 and 0.29 for young-of-the-year Atlantic herring (Arrhenius & Hansson 1994) and from 0.032 to 0.052 for larger, juvenile Atlantic salmon *Salmo salar* (Talbot et al. 1984). A 2- to 5-fold increase in *GER* during continuous feeding is also well documented. It appears as though laboratory studies indicating no effect of prey density on *GER* of larval and young juvenile fishes (e.g. Bochdansky & Dielbel 2001, Bochdansky et al. 2006) measured *GER* in fish that were no longer feeding.

How robust are estimates of *AE*? Compared to *GER*, far fewer studies have been conducted on *AE* using fish larvae. 'Inasmuch as it has bearing on models of larval growth and survival, the question of changing digestive and assimilative abilities with larval development… warrants the most immediate attention' (Govoni et al. 1986, p. 73). This statement is still true today. The values of *AE* differ depending upon the species. For example, *AE* was about 90% (based on carbon contents of copepod prey) in 13 to 34 dph (days post-hatch) Atlantic herring larvae (Pedersen & Hjelmeland 1988), but a range of lower values (i.e. from 30 to 90%) have also been reported (for reviews see Govoni et al. 1986, Houde & Zastrow 1993). In the present study, the effect of body size (developmental state) was incorporated into *AE* by evaluating literature data on a variety of species. It is reasonable to assume an improvement of *AE* with increasing body size (developmental stage), and this has been shown in several studies (Govoni et al. 1986). However, the largest species-specific differences in *AE* will undoubtedly be manifested in the effect of body size via differences among species in developmental characteristics. For this reason, more work is needed on *AE* in larval fish. Our simulation results (Case 3B) suggested that growth rates at different temperatures were only reasonable when the reduction of *AE* with increasing feeding rate was temperature dependent, and this should be tested.

CONCLUSIONS

Feedbacks between a marine fish larva and its environment have recently been explored using an IBM approach (e.g. behavioral modifications necessary to optimally forage within prey patches; Pitchford et al. 2003). In the present study, we included an interaction between the feeding physiology of a larva (consumption, digestion and assimilation of food) and characteristics of its prey field (different concentrations having patchy or homogenous distributions). Two physiologically based alternatives to C_{MAX} were parameterized, based upon the available literature on *GER* and *AE* for the larvae of a variety of freshwater and marine fish species. We recommend that larval fish IBMs utilizing foraging and growth subroutines also employ physiologically based limits to food consumption rate and that non-mechanistic parameters (C_{MAX} and/or G_{MAX}) be avoided. Employing mechanistic limits to feeding may be critical if models attempt to explore (and hope to understand) the consequences of both short- and long-term prey field variability on the growth and survival of marine fish larvae.

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