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**APPENDIX A. A size-structured predator-prey model with two ontogenetic niche shifts in the predator: Details of model variables, parameters and functions**

In this appendix we only give the formal definition of the discrete-continuous-time model since a detailed description and justification for the model structure and parameterization is given in Appendix A in van Leeuwen et al. (2013). The model variables are listed in Table A1, individual level model functions are given in Table A2, the model parameterization is given in Table A3, and dynamic equations are listed in Table A4.

**TABLE A1.** System variables, *i*-state variables and derived variables.

Symbol	Unit	Expression	Description/Note
<b>System variables</b>			
$S_i$	$nr \cdot m^{-3}$		Number of prey individuals in cohort <i>i</i>
$C_j$	$nr \cdot m^{-3}$		Number of predator individuals in cohort <i>j</i>
$Z_S$	$g \cdot m^{-3}$		Resource for prey
$Z_C$	$g \cdot m^{-3}$		Resource for juvenile predator
$B$	$g \cdot m^{-2}$		Intermediate resource for predator
<b><i>i</i>-state variables</b>			
$a$	$d$		Age
$x$	$g$		Irreversible mass
$y_f$	$g$		Fat reserves
$y_g$	$g$		Gonadal mass
<b>Derived variables</b>			
$y$	$g$	$y_f + y_g$	Total reversible mass
$w$	$g$	$x + y$	Total body weight
$l$	$cm$	$\lambda_1 (x (1 + q_J))^{\lambda_2}$	Total body length

**Note:** In the definition of *i*-state variables and derived variables the species indices are left out for notational clarity.

**TABLE A2.** Functions related to individual level processes. Index  $i$  refers to cohort  $i$  in the prey population; index  $j$  refers to cohort  $j$  in the predator population.

Nr	Description	Function	Note
<b>Predator</b>			
1	Foraging time on prey	$t_P(l_j) = \begin{cases} 0 \\ \pi Q(l_j, \underline{l_P}, l_P) \end{cases}$	if $l_j < l_P$ otherwise
2	Foraging time on intermediate resource	$t_B(l_j) = \begin{cases} 0 \\ (1 - t_P(l_j))Q(l_j, \underline{l_B}, l_B) \end{cases}$	if $l_j < l_B$ otherwise
3	Attack rate juvenile resource	$A_{CZ}(l_j) = \chi_1 l_j^{\chi_2}$	
4	Attack rate intermediate resource	$A_{CB}(l_j) = \psi_1 l_j^{\psi_2}$	
5	Optimal prey attack rate on	$A_{CF}(l_j) = t_P(l_j)\gamma_1 l_i^{\gamma_2}$	
6	Digestion time	$H_C(l_j) = \xi_1 l_j^{\xi_2}$	
7	Maintenance requirements	$M_C(w_j) = \rho_1 w_j^{\rho_2}$	
8	Realized prey attack rate	$T_{CF}(l_j, l_i) = \begin{cases} A_{CF}(l_j) \frac{l_i - \delta l_j}{(\phi - \delta) l_j} \\ A_{CF}(l_j) \frac{\varepsilon l_j - l_i}{(\varepsilon - \phi) l_j} \\ 0 \end{cases}$	if $\delta l_j < l_i \leq \phi l_j$ if $\phi l_j < l_i < \varepsilon l_j$ otherwise
9	Encounter with juvenile resource	$E_{CZ}(l_j) = \begin{cases} A_{CZ}(l_j) Z_C \\ 0 \end{cases}$	if $l_j < l_P$ otherwise
10	Encounter intermediate resource	$E_{CB}(l_j) = \begin{cases} A_{CB}(l_j) B \\ (1 - t_P(l_j)) A_{CB}(l_j) B \end{cases}$	if $l_j < l_P$ otherwise
11	Prey encounter	$E_{CF}(l_j) = \sum_i T_{CF}(l_j, l_i) w_i \frac{S_i}{V}$	
12	Total encounter	$E_C(l_j) = E_{CB}(l_j) + E_{CF}(l_j)$	
13	Intake juvenile resource	$I_{CZ}(l_j) = (1 - t_B(l_j)) \frac{E_{CZ}(l_j)}{1 + H_C(l_j) E_{CZ}(l_j)}$	

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14	Intake intermediate resource	$I_{CB}(l_j) = \begin{cases} t_B(l_j) \frac{E_{CB}(l_j)}{1+H_C(l_j)E_{CB}(l_j)} & \text{if } l_j < l_p \\ \frac{E_{CB}(l_j)}{1+H_C(l_j)E_C(l_j)} & \text{otherwise} \end{cases}$	if $l_j < l_p$  otherwise
15	Prey intake	$I_{CF}(l_j) = \frac{E_{CF}(l_j)}{1+H_C(l_j)E_C(l_j)}$	
16	Total food intake	$I_C(l_j) = \begin{cases} I_{CZ}(l_j) + I_{CB}(l_j) & \text{if } l_j < l_p \\ I_{CB}(l_j) + I_{CF}(l_j) & \text{otherwise} \end{cases}$	if $l_j < l_p$  otherwise
17	Acquired biomass	$N_{CA}(l_j) = \theta_A I_C(l_j)$	
18	Net biomass production	$N_{CE}(l_j, w_j) = N_{CA}(l_j) - M_C(w_j)$	
19	Allocation factor	$k_C(x_j, y_j) = \begin{cases} \frac{1}{q+1} & \text{if } \frac{y_j}{x_j} > q \\ \left(\frac{y_j}{x_j}\right)^2 (1+q)q^2 & \text{otherwise} \end{cases}$	if $\frac{y_j}{x_j} > q$  otherwise
with $q = q_J$ if $l_j < l_M$ and $q = q_A$ if $l_j \geq l_M$			
20	Fecundity	$F_C(y_g) = \begin{cases} \frac{\theta_F y_g}{(\lambda_1 L_0^{\lambda_2})} & \text{if } l_j > l_M \\ 0 & \text{and } y_j > q_J x_j \\ 0 & \text{otherwise} \end{cases}$	if $l_j > l_M$ and $y_j > q_J x_j$  otherwise
21	Starvation mortality	$d_{CY}(x_j, y_j) = \begin{cases} 0 & \text{if } \frac{y_j}{x_j} > q \\ \mu_Y \left( q_Y \frac{x_j}{y_j} - 1 \right) & \text{otherwise} \end{cases}$	if $\frac{y_j}{x_j} > q$  otherwise
22	Size-dependent mortality	$d_{CJ}(l_j) = \mu_j e^{-\left(\frac{l_j}{l_D}\right)^2}$	
23	Total mortality	$d_C(x_j, y_j, l_j) = \begin{cases} \mu_E e^{-\frac{l_0}{l_D}} & \text{if } a < a_L \\ \mu_0 + d_{CY}(x_j, y_j) + d_{CJ}(l_j) & \text{otherwise} \end{cases}$	if $a < a_L$  otherwise

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<b>Prey</b>			
24	Resource attack rate	$A_{SZ}(l_i) = \hat{A} \left( \left( \frac{l_i}{l_{opt}} \right)^{\lambda_2} \exp \left( 1 - \left( \frac{l_i}{l_{opt}} \right)^{\lambda_2} \right) \right)^\alpha$	
25	Digestion time	$H_S(l_i) = \xi_1 l_i^{\xi_2}$	
26	Maintenance	$M_S(w_i) = \rho_1 w_i^{\rho_2}$	
27	Resource encounter	$E_{SZ}(l_i) = A_{SZ}(l_i) Z_S$	
28	Acquired biomass	$N_{SA}(l_i) = \theta_A \frac{E_{SZ}(l_i)}{1 + H_S(l_i) E_{SZ}(l_i)}$	
29	Net biomass production	$N_{SE}(l_i, w_i) = N_{SA}(l_i) - M_S(w_i)$	
30	Allocation factor	$k_S(x_i, y_i) = \begin{cases} \frac{1}{q+1} & \text{if } \frac{y_i}{x_i} > q \\ \left( \frac{y_i}{x_i} \right)^2 (1+q)q^2 & \text{otherwise} \end{cases}$	
		with $q = q_J$ if $l_i < l_M$ and $q = q_A$ if $l_i \geq l_M$	
31	Fecundity	$F_S(y_g) = \begin{cases} \frac{\theta_F y_g}{(\lambda_1 L_0^{\lambda_2})} & \text{if } l_i > l_M \\ 0 & \text{and } y_i > q_J x_i \\ 0 & \text{otherwise} \end{cases}$	
32	Starvation mortality	$d_{SY}(x_i, y_i) = \begin{cases} 0 & \text{if } \frac{y_i}{x_i} > q \\ \mu_Y \left( q_Y \frac{x_i}{y_i} - 1 \right) & \text{otherwise} \end{cases}$	
33	Size-dependent mortality	$d_{SJ}(l_i) = \mu_J e^{-\left(\frac{l_i}{l_b}\right)^{a_2}}$	
34	Predation mortality	$d_{SP}(l_i) = \sum_j \frac{T_{CF}(l_j, l_i) C_j}{1 + H_C(l_j) E_C(l_j)}$	
35	Total mortality	$d_S(x_i, y_i, l_i) = \begin{cases} \mu_E e^{-\frac{l_i}{l_b}} & \text{if } a < a_L \\ \mu_0 + d_{SY}(x_i, y_i) + d_{SJ}(l_i) + d_{SP}(l_i) & \text{otherwise} \end{cases}$	

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<b>Resources</b>		
36	Prey resource growth	$P_{SZ}(Z_S) = \beta (\kappa_P - Z_S)$
37	Juvenile resource growth	$P_{CZ}(Z_C) = \beta (\kappa_P - Z_C)$
38	Intermediate resource growth	$P_B(B) = \beta (\kappa_B - B)$
39	Grazing on prey resource	$G_{SZ}(I_i) = \sum_i \frac{E_{SZ}(I_i)}{1+H_S(I_i)E_{SZ}(I_i)} \frac{S_i}{V}$
40	Grazing on juvenile resource	$G_{CZ}(I_j) = \sum_j \frac{A_{CZ}(I_j)Z_C}{1+H_C(I_j)E_{CZ}(I_j)} \frac{C_j}{V}$
41	Grazing on intermediate resource	$G_{CB}(I_j) = \sum_j I_{CB}(I_j) \frac{C_j}{U}$

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Continuous, differentiable, piecewise function

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$$Q(n, \underline{n}, \bar{n}) = \begin{cases} 0 & \text{for } f(n, \underline{n}, \bar{n}) \leq 0 \\ \frac{1}{6} f(n, \underline{n}, \bar{n})^3 & \text{for } f(n, \underline{n}, \bar{n}) \leq 1 \\ -\frac{3}{2} f(n, \underline{n}, \bar{n}) + \frac{3}{2} f(n, \underline{n}, \bar{n})^2 - \frac{1}{3} f(n, \underline{n}, \bar{n})^3 + \frac{1}{2} & \text{for } f(n, \underline{n}, \bar{n}) \leq 2 \\ \frac{9}{2} f(n, \underline{n}, \bar{n}) - \frac{3}{2} f(n, \underline{n}, \bar{n})^2 + \frac{1}{6} f(n, \underline{n}, \bar{n})^3 - \frac{7}{2} & \text{for } f(n, \underline{n}, \bar{n}) \leq 3 \\ 1 & \text{otherwise} \end{cases}$$

$$\text{Where: } f(n, \underline{n}, \bar{n}) = \frac{3}{2} \frac{n - \underline{n}}{\bar{n} - \underline{n}}$$


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**TABLE A3.** Parameter symbols, descriptions, and values.

Subject	Symbol	Unit	Description/ Interpretation	Value	Prey value	ref	Predator value	ref
Global/ species independent	$V$	$m^3$	System volume	1				
	$V : U$	$m$	Ratio of volume to surface, i.e. average depth	50				
Season	$year$	$d$	Duration of growing season	250				
	$\sigma$	-	Spawning decision date (spawnset)		200		200	
Resources	$\beta$	$d^{-1}$	Resource growth rate	0.1				
	$K_P$	$g \cdot m^{-3}$	Carrying capacity prey resource and juvenile resource	varied				
	$K_B$	$g \cdot m^{-2}$	Carrying capacity intermediate resource	varied				
Length-weight	$\lambda_1$	$g \cdot cm^{-\lambda_2}$	Length-weight conversion constant		5.4	1	4.64	2
	$\lambda_2$	-	Length-weight conversion exponent		0.33	1	0.33	2
Form of 2 <sup>nd</sup> niche shift	$\pi$	-	Partial (1/2) vs complete (1) shift scenario				1 or 1/2	
Ontogeny (and reproduction)	$\theta_F$	-	Gonad – offspring conversion		0.5	3	0.5	3
	$l_0$	$cm$	Size at birth		0.44	4	0.39	5
	$l_D$	$cm$	Characteristic size in size-dependent mortality rate		4.30	6	3.68	6
	$l_M$	$cm$	Length at maturation		9	7	30	8
	$l_B$	$cm$	Length at start foraging on the intermediate resource				5	9
	$l_B$	$cm$	Length at 50% switch to intermediate resource				10	9
	$l_P$	$cm$	Length at start predation				15	9
	$l_P$	$cm$	Length at 50% switch to predation				20	10
	$a_E$	$d$	Duration of egg stage		6	11	15	5
	$a_L$	$d$	Duration of yolk-sac stage		8	11	7	5
	$a_J$	$d$	Age at first feeding		14	4	22	5
	$q_J$	-	Juvenile condition target		0.9	12-15	0.7	16

	$q_A$	-	Adult condition target	1.4	17	1.4	18
	$q_G$	-	Minimum spawning condition	0.9		0.7	
Handling	$\xi_1$	$d \cdot g^{-1} \cdot cm^{-\xi_2}$	Allometric scalar for digestion time	167.6	19	364.1	20
	$\xi_2$	-	Allometric exponent for digestion time	-1.91	19	-2.34	20
Metabolism	$\rho_1$	$g^{(1-\rho_2)} \cdot d^{-1}$	Allometric scalar for maintenance rate	0.03	21	0.03	5,22
	$\rho_2$	-	Allometric exponent for maintenance rate	0.8	21	0.8	5,22
	$\theta_A$	-	Food assimilation efficiency	0.5	11	0.6	23
Juvenile resource	$\hat{A}$	$m^3 \cdot d^{-1}$	Maximum attack rate juvenile resource	150	24		
	$l_{opt}$	$cm$	Length at which resource attack rate is maximum	20	24		
	$\alpha$	-	Allometric exponent in juvenile resource attack rate	0.5	24		
	$\chi_1$	$m^3 \cdot d^{-1} \cdot cm^{-\chi_2}$	Attack rate scaling constant			0.3	25
	$\chi_2$	-	Attack rate scaling exponent			1.8	25
Intermediate resource	$\psi_1$	$m^2 \cdot d^{-1} \cdot cm^{-\psi_2}$	Attack rate scaling constant			0.4	25
	$\psi_2$	-	Attack rate scaling exponent			0.6	25
Predation	$\gamma_1$	$m^3 \cdot d^{-1} \cdot cm^{-\gamma_2}$	Prey attack rate scaling constant			1.6	26
	$\gamma_2$	-	Prey attack rate scaling exponent			0.6	26
	$\delta$	$cm/cm$	Minimum prey-predator length ratio			0.08	27-30
	$\varphi$	$cm/cm$	Optimum prey-predator length ratio			0.26	27-30
	$\varepsilon$	$cm/cm$	Maximum prey-predator length ratio			0.5	27-30
Mortality	$\mu_E$	$d^{-1}$	Egg and yolk-sac mortality	0.03		0.03	
	$\mu_J$	$d^{-1}$	Size-dependent mortality	0.03		0.03	
	$\mu_0$	$d^{-1}$	Background mortality	0.005		0.003	
	$\mu_Y$	$d^{-1}$	Starvation mortality	0.2	6	0.2	
	$q_Y$	-	Minimum/ starvation condition	0.2	6	0.2	26

**Sources:**

- 1) (ICES 2010)
- 2) (Coull et al. 1989)
- 3) (Persson et al. 1998)
- 4) (Arrhenius and Hansson 1993)
- 5) (Finn et al. 2002)
- 6) (Huss et al. 2012)
- 7) (Grygiel and Wyszynski 2003)
- 8) (Vainikka et al. 2009)
- 9) (Hussy et al. 1997)
- 10) (Sparholt 1994)
- 11) (Daewel et al. 2008)
- 12) (Mathers et al. 1994, Folkvord et al. 2000)
- 13) (Mathers et al. 1994)
- 14) (Folkvord et al. 2000)
- 15) (Hjelm et al. 2006)
- 16) (Siikavuopio et al. 2008)
- 17) (Rajasilta et al. 2001)
- 18) (Kjesbu et al. 1996)
- 19) (De Silva and Balbontin 1974)
- 20) (Bjornsson et al. 2007)
- 21) (Peters 1983, Opalinski et al. 2004)
- 22) (Luna 2008)
- 23) (Peters 1983)
- 24) (Hjelm and Persson 2001)
- 25) Persson, L. 2011 - personal communication
- 26) (Claessen et al. 2000)
- 27) (Johansen 2003, Juanes 2003, Pinnegar et al. 2003, Scharf et al. 2000)
- 28) (Juanes 2003)
- 29) (Pinnegar et al. 2003)
- 30) (Scharf et al. 2000)



**TABLE A4.** Dynamics for the discrete-continuous-time predator-prey model

<b>Predator cohorts</b>	<b>Within-season processes, taking place in continuous time</b>	
		<b>Note</b>
Mortality	$\frac{dC_j}{dt} = -d_C(x_j, y_j, l_j)C_j$	
Growth in $x$	$\frac{dx_j}{dt} = \begin{cases} k_C(x_j, y_j)N_{CE}(l_j, w_j) \\ 0 \end{cases}$	if $N_{CE}(l_j, w_j) > 0$ otherwise
Growth in $y$	$\frac{dy_j}{dt} = \begin{cases} (1 - k_C(x_j, y_j))N_{CE}(l_j, w_j) \\ N_{CE}(l_j, w_j) \end{cases}$	if $N_{CE}(l_j, w_j) > 0$ otherwise
	<b>Between-season reproduction, taking place in discrete time</b>	
Number of newborns added to new cohort	$F_C(y_g) \cdot C_j$	
<b>Prey cohorts</b>	<b>Within-season processes, taking place in continuous time</b>	
		<b>Note</b>
Mortality	$\frac{dS_i}{dt} = -d_S(x_i, y_i, l_i)S_i$	
Growth in $x$	$\frac{dx_i}{dt} = \begin{cases} k_S(x_i, y_i)N_{SE}(l_i, w_i) \\ 0 \end{cases}$	if $N_{SE}(l_i, w_i) > 0$ otherwise
Growth in $y$	$\frac{dy_i}{dt} = \begin{cases} (1 - k_S(x_i, y_i))N_{SE}(l_i, w_i) \\ N_{SE}(l_i, w_i) \end{cases}$	if $N_{SE}(l_i, w_i) > 0$ otherwise
	<b>Between-season reproduction, taking place in discrete time</b>	
Number of newborns added to new cohort	$F_S(y_g) \cdot S_i$	
<b>Resources</b>	<b>Within-season processes, taking place in continuous time</b>	
Changes in prey resource, $Z_S$	$\frac{dZ_S}{dt} = P_{SZ}(Z_S) - G_{SZ}(l_i)$	
Changes in juvenile resource, $Z_C$	$\frac{dZ_C}{dt} = P_{SZ}(Z_S) - G_{CZ}(l_j)$	
Changes in intermediate resource, $B$	$\frac{dB}{dt} = P_B - G_{CB}(l_j)$	

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