Modeling the life history of sessile rotifers: larval substratum selection through reproduction

Andrea N. Young, Rick Hochberg, Elizabeth J. Walsh & Robert L. Wallace

Hydrobiologia
The International Journal of Aquatic Sciences

ISSN 0018-8158

Hydrobiologia
DOI 10.1007/s10750-018-3802-x

Springer

Hydrobiologia
https://doi.org/10.1007/s10750-018-3802-x

ROTIFERA XV

Modeling the life history of sessile rotifers: larval substratum selection through reproduction

Andrea N. Young · **Rick Hochberg** · **Elizabeth J. Walsh** · **Robert L. Wallace**

Received: 14 July 2018 / Revised: 13 October 2018 / Accepted: 15 October 2018

Abstract Although the theoretical underpinnings of habitat selection by marine invertebrate larvae have been well studied, this theory has been neglected for freshwater sessile rotifers. To study how substratum selection affects larval fitness, we developed a dynamic model to examine influences of three elements of larval life (survival, substratum acceptance, substratum encounter probability) and substratum-dependent reproductive success in adults. Monte Carlo simulation models were run using an initial cohort of larvae. Our Basic Model assessed fitness as simply settling on a substratum using only the larval elements and revealed statistically greatest fitness when swimming speed decreased with age and when substratum preference was constant or exhibited mid-age competence. The Reproductive Model assessed fitness (mean number of offspring adult^{-1}) as a function of substratum. We compared reproduction on neutral substrata to substrata where quality varied and separately as a function of adult population density: coloniality (synergism) versus competition. The model showed fitness was statistically greatest when larval swimming speed decreased with age and when coloniality increased reproduction. We also explored conditions where populations of planktonic adults could survive. The model is applicable to sessile organisms and may be modified to examine other life

Guest editors: Steven A. J. Declerck, Diego Fontaneto, Rick Hochberg & Terry W. Snell / Crossing Disciplinary Borders in Rotifer Research

Electronic supplementary material The online version of this article (https://doi.org/10.1007/s10750-018-3802-x) contains supplementary material, which is available to authorized users.

A. N. Young
Department of Mathematical Sciences, Ripon College,
Ripon, WI 54971, USA

R. Hochberg
Department of Biological Sciences, University of
Massachusetts at Lowell, Lowell, MA 01854, USA

E. J. Walsh
Department of Biological Sciences, University of Texas at
El Paso, El Paso, TX 79968, USA

R. L. Wallace (✉)
Department of Biology, Ripon College, Ripon, WI 54971,
USA
e-mail: wallacer@ripon.edu

history activities including selection of mates, prey, or territory.

Keywords Behavior · Dynamic modeling · Gnesiotrocha · Planktonic · Substratum-dependent reproduction · Rotifera

> *Larvae … are indeed not helpless, for they are endowed with the power of choice, and with a period of time during which that choice may be made. — Wilson (1952).*

Introduction

Understanding a species requires comprehending its entire life history, not just the morphological and ecological features attendant to the adult (Werner & Gilliam, 1984; Werner, 1988). Undeniably many studies have documented ontogenetic (developmental) shifts; these include shifts in diet (e.g., polychaetes: Hentschel, 1998; harpacticoid copepods: Decho & Fleeger, 1988; fishes: Daly et al., 2009; amphibians: Schriever & Williams, 2013), behavior (Despland & Hamzeh, 2004), physiology (Woods & Wilson, 2013), and habitat use (Richards, 1992) (see de Roos & Persson, 2013).

Interpreting the life history of sessile invertebrates is no different; it requires an understanding of their distinct bipartite existence: larval life is transitory, ending either in death or with a cascade of searching and settling behaviors culminating in attachment and subsequent metamorphosis into an adult (Crisp & Meadows, 1963; Wallace, 1980; Pawlik, 1992; Burgess et al., 2009). Accordingly, a successful larva must survive planktonic life, encounter at least one substratum, attach, metamorphose to adulthood, and reproduce. Clearly, if settlement is irreversible, choice of a high-quality substratum becomes critical to maximize fitness (Hodin et al., 2015). Thus, one may infer that sessile invertebrates must make evolutionary tradeoffs that are not intuitively obvious.

Undeniably there is a rich literature on the life history of most marine invertebrate larvae (Chia & Rice, 1978; Young, 1990; McEdward, 1995; Hadfield, 1998), including conceptualizing the process of substratum selection (Doyle, 1975; Roughgarden et al., 1985; Strathmann, 1985; Rumrill, 1990; Marechal et al., 2004; Kinlan et al., 2005; Toonen & Tyre, 2007; Burgess et al., 2012). However, the life history characteristics of sessile rotifers (Monogononta: Gnesiotrocha: Atrochidae, Collothecidae, and Flosculariidae) differ from those of marine invertebrates. For example, marine invertebrates often release large numbers of relatively long-lived (days, weeks, months) larvae that may disperse over short (~ 1 m) to long (> 750 km) distances and have extended development times (days to months) (Kempf, 1981; Hadfield, 1998; Shanks, 2009). They also exhibit extreme diversity in size (~ 200 to > 3000 µm) and form (Levin & Bridges, 1995), and as a group use varied energy sources: endosymbiotic autotrophy, lecithotrophy, osmotrophy, and planktotrophy, as well as poecilogony (Vance, 1973; McEdward, 1995; Chia et al., 1996; Allen & Pernet, 2007). Additionally, during their free-swimming phase, marine larvae usually experience an extensive, relatively uniform, open-water existence, where suitable substrata are generally not encountered. As a consequence many, but certainly not all, marine larvae are capable of postponing settlement in the absence of suitable habitat (Pechenik, 1980). In contrast, sessile rotifers release relatively few, short-lived (hours to days) larvae that exhibit little variation in size (ca. 400 µm) or form (Wallace et al., 2015), and which appear to be lecithotrophic or possess limited ability to feed (Wallace et al., 1998; Hochberg, 2014; Hochberg et al. (in this volume). Moreover hatchlings immediately encounter a mosaic of habitats dominated by diverse hydrophytes that provide a rich landscape for settlement with variable morphologies and chemistries that often differ over short distances (Meksuwan et al., 2014).

Free-swimming larvae may provide sessile rotifers several advantages including (1) colonization of a preferred substratum, including new hydrophyte growth that has not been weakened by herbivores, pathogens, or age; (2) establishment of a colony or alternatively avoidance of competition; and (3) wider dispersal that may reduce inbreeding. In contrast, disadvantages include (1) death in the plankton due to starvation and/or predation; (2) delayed metamorphosis with subsequent inability to complete it; and (3) poor adult reproduction due to selection of an inferior habitat (Pechenik, 1999).

To better understand the life history of sessile rotifers, we developed a dynamic model with the capacity to vary environmental and sessile rotifer life history features including (a) relative availability of potential substrata, (b) cohort size, (c) planktonic survival, (d) substratum choice, and (e) adult survival and subsequent reproduction. Here we present our model, explore some of its results, offer testable hypotheses regarding sessile rotifer life histories based on outcomes of model runs, and suggest areas where additional research is needed.

Materials and methods

Model development

Our model reflects ideas from several previously published models of sessile animals (Doyle, 1975; Pineda & Caswell, 1997; Toonen & Tyre, 2007; Burgess et al., 2009), but emphasizes characteristics of the freshwater littoral habitat and life history features of sessile rotifers (Fig. 1). This dynamic model was developed as a system of difference equations that follow a cohort of larvae to potential endpoints of either death in the plankton or survival to adulthood with the potential for reproduction. Components of the model are fully described in Supplemental Document. In the basic model (BM), we defined fitness simply as settling and metamorphosing, with the assumption that metamorphosis leads to equal reproduction on all substrata (Doyle, 1975). In the reproductive model (RM), we defined reproductive fitness as metamorphosing with subsequent reproduction, which could vary as a function of substratum or density of settled larvae. The RM followed the behavior of the original population and one generation of offspring. We also explored conditions where adults could survive in the plankton. Following, we provide a brief overview of the environmental and life history functions (LHF) that we incorporated into the model (Table 1).

LHF 1 Larval survival in the plankton. Larval survival was set such that during each time step of the model a certain percentage of larvae die in the plankton due to predation, parasitization, or starvation (d_P). This is a classic Type II survivorship curve (Kempf, 1981). Further, we added the assumption that larvae have a maximum length of life (l). Those that reach that point immediately die due to starvation.

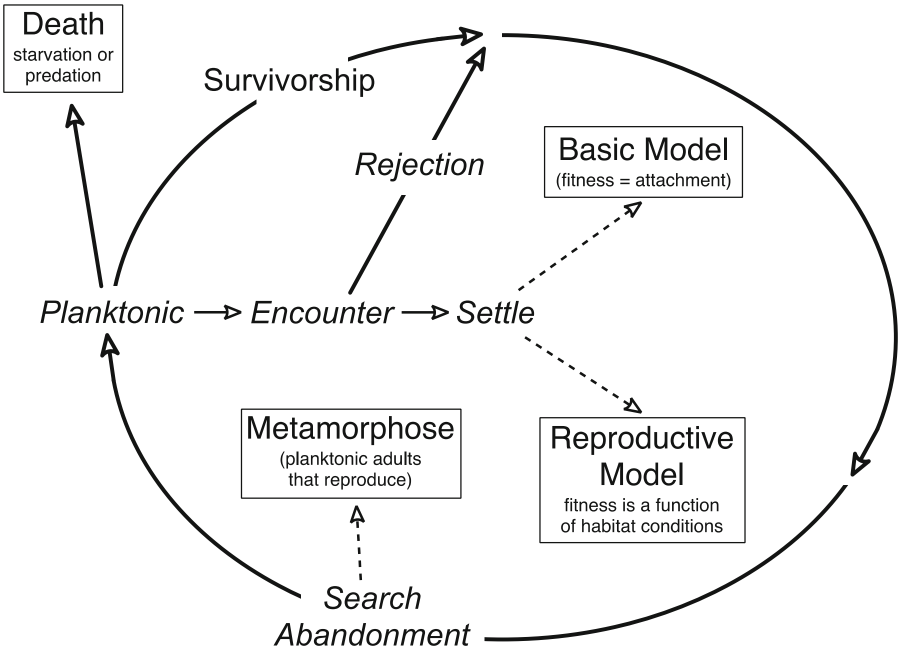

Fig. 1 Schematic overview of the life history of sessile rotifers used in this model. The model starts with a cohort of planktonic, free-swimming larvae. Boxed regions indicate endpoints for larvae and *Italic* print indicates their behaviors. This simplified, conceptual model was used to develop the fitness functions in our simulations. A more complete development of the model is explained in the text and in the Supplemental Document

Table 1 Environmental and life history functions (LHF) used in modeling substratum selection by sessile rotifer larvae

Life history functions	Description
Larval life	
LHF 1. Larval survivorship	Larval population decreases over time, either by settling or dying, such that a certain percentage of free-swimming larvae die at each iteration, but total lifespan is fixed (l), at which point all remaining larvae die
LHF 2. Substratum acceptance and metamorphosis	Values for *acceptance probabilities* varied over l in one of three ways: (A) autonomous (constant), (B) decreasing choosiness, (C) intermediate competence (follows a quadric choosiness function). Total likelihood of settling of larvae over l was kept equal among these functions
LHF 3. Substratum availability (Encounter rates)	Values for *encounter probabilities* were varied over l in one of three ways: (A) autonomous (constant), (B) increases linearly, (C) decreases linearly. But among them, total likelihood of encounter over l was kept equal
Adult fitness	
Basic model	Assumed that all settled adults reproduce equally
Adult reproduction	Adult reproduction is a function of habitat
LHF 4. Reproductive model	(A) Substratum type alone affects R_o
	(1) Positive: R_o higher for one or more *substratum*
	(2) Negative: R_o lower for one or more *substratum*
	(B) Adult density alone affects R_o
	(1) Autonomous: R_o equal for all *substrata*
	(2) Synergistic: R_o increases with increasing population sizes (e.g., coloniality), until a critical value is reached above which no additional advantage is accrued
	(3) Competition: R_o decreases with increased population size until a critical value is reached above which no additional disadvantage is accrued
LHF 5. Facultatively sessility	Larvae may settle or metamorphose in the plankton and reproduce

Additional details of these functions are described in the text; descriptions of the mathematical functions of the model are specified in the Supplemental Document

LHF 2 Larval substratum acceptance (i.e., choice, preference, or selection) and settling. Larvae accept substrata (j = 1 to n) at rates (a_j) that may vary with time over their life; this corresponds to the behavioral concept of larval 'choosiness' based on substrata possessing the appropriate settlement cue(s). We assumed that the level of cues possessed by each substratum does not vary. Rather, acceptance rate is viewed as a change in the behavior of larvae with respect to the substratum as a function of their age. Three acceptance scenarios were explored. (A) Autonomous (constant): a_j were set as constants that were randomly generated over a set range of $a_{\min} = 0$ to $a_{\max} = 0.5$. This assumes no change in acceptance rate with larval age. (B) Decreasing choosiness: probability of attachment increases with time. That is, as they age, larvae increase their propensity to attach to any substratum they encounter. This behavior was termed "desperate" by Hodin et al. (2015). (C) Intermediate competence (quadratic choosiness): mid-aged larvae are more likely to settle in response to suitable cues than either younger or older larvae (Hodin et al., 2015; Wallace, 1980). In this case, we employed a quadratic function to model competence. We kept the total likelihood of settling constant for the three acceptance scenarios.

LHF 3 Larval substratum encounter. The model can incorporate any number of potential substrata (j = 1 to n), with larvae encountering substrata at rates (e_j) that may vary with time. This constraint may be interpreted in either of two ways. It may be seen as a change in larval swimming speed with age. Thus, larval swimming speed influences its likelihood of encountering a substratum. It can also be interpreted as a change in the amount of substrata available over time. This second interpretation is unlikely for sessile rotifers; while a change in relative substratum availability will change seasonally, for a larva these changes will be insignificant during its planktonic life.

Three encountering scenarios were considered. (A) Autonomous (constant): e_j rates were set as constants that were randomly generated within the range of $e_{\min} = 0$ to $e_{\max}$, depending on the total number of substrata. This assumes no change in swimming speed with larval age. (B) Increasing: the probability of encountering substrata increases with time. (C) Decreasing: the probability of encountering substrata decreases with time. The total likelihood of encountering substrata was kept constant across the three models.

LHF 4 Adult fitness (substratum-dependent survival and reproduction). We examined two different types of substratum-dependent survival and reproduction (R_o). In the first of these variations (LHF 4A), adult R_o was defined as a function of the substratum to which a larva settled with two variations. (1) Positive: at least one substratum supports increased settling according to specific criteria. (2) Negative: at least one substratum results in decreased settling according to specific criteria. In the second variation (LHF 4B), fitness was varied as a function of adult density in three ways. (1) Autonomous (constant): reproduction was independent of substratum. In this case, reproduction rates were randomly generated and independent of substratum quality. (2) Synergism: reproduction increased as a function of population density. This variation may be seen as reflecting the improvement in lifespan and R_o seen in *Floscularia conifera* (Hudson, 1886) when two or more adults form a colony (Edmondson, 1945). We modeled synergism such that reproduction increased linearly as a function of the density of settled larvae. (3) Competition: reproduction decreased as a function of population density. For example, the aggregation of large numbers of *Collotheca campanulata* (Dobie, 1849) colonists on the abaxial (under) surface of *Elodea canadensis* Michaux, 1803 leaves has the potential to reduce adult reproduction through competition (Wallace and Edmondson, 1986; Wallace, 1987). We modeled competition such that reproduction decreased linearly as a function of settled larvae.

LHF 5 Larval abandonment of substratum selection behavior. Some sessile species have been collected in planktonic samples, a condition that we have termed facultative sessility (reviewed below). To explore this, we expanded our model to include the possibility that planktonic larvae could, after a period of time, abandon substratum searching to metamorphose in the plankton. This LHF allows larvae to become unattached, reproductive adults (Fig. 1).

Confounding factors We ignored six factors that allow us to simplify the model. (1) Substrata distribution and architecture: spatial distribution of hydrophytes was discounted by assuming that all substrata are randomly dispersed within the habitat. We also ignored potential influences of hydrophyte architecture on larval encounter, as well as their potential to influence community structure (Kuczyńska-Kippen, 2003, 2005; Kuczyńska-Kippen & Nagengast, 2006; Lucena-Moya & Duggan, 2011). (2) Water flow: the model does not account for effects of prevailing currents or their velocity on larval dispersal or their tendency to settle (Olson, 1985; Koehl & Hadfield, 2010; Hodin et al., 2015). (3) Variation in energy content of embryos: embryo size (egg volume) varies depending on species for both marine invertebrates and sessile rotifers (McEdward, 1995; Wallace et al., 1998). Similarly, in some marine invertebrates, embryo size and presumably energy content can vary as a function of the substratum occupied by its parent (Burgess et al., 2009). Disregarding these factors eliminated the need to add components varying larval lifespan or altering the probability of metamorphic competence and subsequent reproduction, i.e., a latent effect based on larval experience (Marshall et al., 2003; Marshall & Keough, 2003; Pechenik, 2006). (4) Larval memory: we discounted the possibility for larvae to sequentially evaluate substrata that they encounter; thus in our model larvae have no memory of past encounters with substrata (Thiyagarajan, 2010). (5) Geminative colony formation behavior: we ignored geminative colony formation (larvae swimming together) as is seen in *Lacinularia flosculosa* (Müller, 1773) and *Sinantherina socialis* (Linnaeus, 1758) (Wallace et al., 2015). (6) Predation: all larvae were assumed equally vulnerable to predation regardless of the presence of species-specific defensive traits of the rotifer (Wallace et al., 2015) or the architecture of the plant species (Walsh, 1995).

Model runs

There are 54 possible combinations of the various LHF that could be examined by our model, and many more are possible by making adjustments to the functions employed. For example, the BM had three substrata acceptance and three substrata encounter functions, yielding nine possible combinations. In the RM, these nine scenarios were linked to variations in reproduction by substratum type ($n = 2$) and adult density ($n = 3$) (Table 1) for a total of 54 combinations. In the remainder of the paper, we will refer to the combination of these functions as a *mechanism*. For example, one mechanism in the BM would be decreasing speed and intermediate competence; in the RM a mechanism could be decreasing speed, intermediate competence, and synergistic reproduction. Surveying all of the possible variations within this model is beyond the scope of this paper, but we do provide analyses into a variety of features of the model. To check the robustness of our results, we performed sensitivity analyses on our model with respect to different parameters (Pannell, 1997).

We have not parameterized our models with real-world data because only a few studies on sessile rotifers provide data that could be used to quantify environmental and life history functions (e.g., Edmondson, 1945; Butler, 1983; Wallace & Edmondson, 1986; Sarma et al., 2017). However, with suitable values the model may be modified to do that. To test the model's robustness and to account for the stochasticity of environmental processes, we used Monte Carlo simulations with 10,000 runs for each of the scenarios being examined (Mooney & Swift, 1999). The initial cohort of larvae in any run of the model can be varied, but for convenience we used 100 individuals.

We used the Bonferroni multiple-significance-test correction (Armstrong, 2014) when all pairs of the sample means were compared. However, because our study was exploratory, we did not hold to the normal rigor of the Bonferroni correction, which requires accepting the null hypothesis for the complete set even when only one pair within the set was not significant (Streiner & Norman, 2011).

Results

Here we examine some of the interesting outcomes of our model, recognizing that these results reflect the specific LHF we used in each scenario (also see Supplemental Document).

Basic model (BM): fitness defined as metamorphosis (LHF 1–3)

Although we did not attempt to parameterize the model using real-world data, we did use values that are likely to approximate actual conditions. As a consequence, our results should be interpreted as comparisons between mechanisms rather than being predictive scenarios. Were appropriate data to be collected, this model could be easily adapted to serve a predictive purpose.

Results of this simple model were, as expected, mixed with the outcomes (the fraction of the larval cohort that settled) ranging from ~ 7 to 18% (Table 2; also see Supplemental Document, "Model development" section). Surprisingly, of the 36 possible pairwise combinations, only one was not significantly different ($P < 0.001$). In our model, the highest fitness levels were reached when larvae had a choosiness (LHF 2) that was either constant or quadratic and decreasing larval swimming speed (LHF 3). On the other hand, the lowest fitness levels occurred when larval acceptance was constant or decreasing and when larval swimming speed was increasing.

The sensitivity analysis that examined the degree to which our results depended on the value of d_P, death rate in the plankton, showed that this parameter appeared to be related to early life behavior (see Supplemental Document, Table 3 and Figs. 6, 7). For example, the larvae with the mechanism of constant choosiness (LHF 2) and decreasing speed (LHF 3) settled on a substratum at the fastest rate of all nine mechanisms. Under moderate to high levels of predation, this mechanism yielded the highest overall fitness. However, with little to no predation, the quadratic choosiness and decreasing speed mechanism yielded the highest overall fitness. Additionally, the decreasing choosiness and increasing speed mechanism performed well under no predation, but performed the worst among all mechanisms under moderate to high predation.

The sensitivity analysis also revealed dependence on the length of life parameter, l, related to end of life behavior (see Supplemental Document, Table 4 and Figs. 8, 9). In particular, for medium to large values of l, the constant choosiness and decreasing speed mechanism gave the highest overall fitness, whereas for small values of l, the quadratic choosiness and

Table 2 Results of the nine variations of the Basic Model (BM). In the BM fitness was defined as larval settling on a substratum

		LHF 3 Larval substratum encounter (speed)		
		Constant	Decreasing	Increasing
LHF 2 Larval substratum acceptance	Constant	0.134 (0.08)	0.175 (0.10)	0.082 (0.05)
	Decreasing	0.086 (0.05)	0.100 (0.06)	0.067 (0.04)
	Increasing	0.126 (0.07)	0.157 (0.09)	0.087 (0.05)

Here we report means and standard deviations for 10,000 simulations for the nine different scenarios (3 substratum encounter × 3 substratum acceptance functions), each with three potential substrata, medium predation rate, and medium length of life. The Life History Functions, LHF 2 (Acceptance) and LHF 3 (Speed) employed in these runs are as described in the text. All but one of the pairwise *t*-Tests of the sample means were significantly different at $P < 0.05$. That comparison was between the mechanisms of acceptance = decreasing and speed = constant versus acceptance = quadratic and speed = increasing. See text for a description of the statistics

decreasing speed mechanism gave the highest overall fitness.

It is also interesting to note that for most of the mechanisms, there appears to be a global maximum for fitness values as a function of l under moderate to high loss of larvae from the plankton. Specifically, the mechanisms with quadratic and decreasing choosiness display this behavior, whereas the mechanisms with constant choosiness do not. For mechanisms with quadratic and decreasing choosiness, there is a value such that the length of life, which governs the time larvae have to search for acceptable substratum before they die due to starvation, has a diminishing return as it means more opportunity for mortality due to predation.

Reproductive models (LHF 1–4)

In the first version of the reproductive model, we modeled the nine scenarios of the BM with fitness defined as settling and subsequent reproduction (Table 3, Autonomous reproduction). This established a baseline against which we could compare the other two reproductive models (below). In the autonomous reproduction model, we found that the mechanisms with the highest juvenile fitness corresponded exactly to those having the highest fitness in the basic model. For example, under medium death in the plankton due to predation and medium length of life conditions, the constant choosiness and decreasing speed mechanism had the highest reproductive fitness. This was expected, as the autonomous reproduction model assumed a rate of reproduction proportional to the number of larvae surviving to reproduce.

The results of the autonomous reproduction model were compared to the two variations (see below): LHF 4A (reproduction as a function of substratum type) and LHF 4B (reproduction as a function of adult density).

LHF 4A—Substratum-dependent reproduction: positive versus negative habitats

When reproduction was dependent on habitat, we found that having one positive substratum (low encounter, high acceptance value) yielded overall higher reproductive fitness for a given mechanism than did having one negative substratum (high encounter, low acceptance value) (Table 3, Substratum-dependent reproduction). This result held for a range of choosiness and encounter rates (see Supplemental Document, Fig. 10).

LHF 4B—Adult density reproduction: synergism versus competition

Overall, the mechanisms with the highest fitness were those with constant choosiness and decreasing speed coupled with synergistic or constant reproduction (Table 4). These results were robust across a variety of critical density values (see Supplemental Document, Table 5 and Fig. 11). However, relative fitness among different reproductive functions depended greatly on the number of substrata available (see Supplemental Document, Fig. 12). In that case, the constant choosiness and decreasing speed mechanism displayed greater fitness when coupled with a competitive reproduction than with either a constant or synergistic reproduction. This was due to the fact that, with more

Table 3 Results of the first variation of the reproductive model (RM)

Choosiness/Speed	Autonomous reproduction	Substratum-dependent reproduction	
		Positive	Negative
Autonomous/autonomous	1.31	0.86	0.72
Autonomous/decreasing	1.85	1.22	0.97
Autonomous/increasing	0.71	0.45	0.40
Decreasing/autonomous	0.68	0.43	0.37
Decreasing/decreasing	0.84	0.54	0.45
Decreasing/increasing	0.48	0.29	0.26
Quadratic/autonomous	1.18	0.76	0.63
Quadratic/decreasing	1.50	1.00	0.81
Quadratic/increasing	0.72	0.47	0.39

This model defined fitness as the average number of offspring per settled larvae. These data are the means for 10,000 simulations for each scenario with three potential substrata for one of the variations of Life History Feature 4A in which reproduction was dependent on substratum only

Table 4 Results of the second variation of the reproductive model (RM)

Mechanisms examined	Adult fitness
Constant choosiness, decreasing speed, synergistic reproduction	2.23
Constant choosiness, decreasing speed, constant reproduction	1.84
Quadratic choosiness, decreasing speed, synergistic reproduction	1.76
Constant choosiness, constant speed, synergistic reproduction	1.54
Constant choosiness, decreasing speed, competitive reproduction	1.50

This model defined fitness the average number of offspring per settled larvae. These data are the mean reproductive fitness values for the highest ranked mechanisms, using 10,000 simulations for each scenario with three potential substrata for one of the variations of Life History Feature 4B

substrata options available, the likelihood of a large number of larvae settling on a given substratum decreased. That is, density never reached a critical level on any substratum, which gave the competitive mechanism an advantage.

Facultative sessility (LHF 5)

Our model has the capacity to allow larvae to metamorphose and reproduce in the plankton, as well as settling and reproducing on a substratum. By systematically varying substratum encounter and larval acceptance rates, we found that under most conditions, larvae are likely to either immediately abandon a search for substrata or to never metamorphose in the plankton (see Supplemental Document, Fig. 13). Specifically, under conditions with low encounter and low acceptance rates, the highest reproductive fitness was achieved when the larvae metamorphose and reproduce in the plankton without searching for a substratum. For conditions with high-quality and high-quantity substrata, the highest reproductive fitness was achieved when the larvae never metamorphosed in the plankton. In other words, the likelihood of reproductive success on a substratum was so great, that it was not worth the risk of metamorphosing in the plankton. However, there is a boundary zone between these two regions that yield a maximum fitness when some portion of larvae settle and some metamorphose in the plankton. It is within this range that facultatively sessile species may be found. Given that we have no information on larval choosiness and substratum encounter rates, we have not studied this aspect of the model any further (see

Supplemental Document, section 4 for additional information).

Discussion

Our study provides the first model that specifically examines the life history functions of sessile rotifers that includes both larvae and adults. Most previous research focused on larval behaviors and/or adult presence on substrata, usually with little exploration of substratum survival or reproduction (Edmondson, 1944, 1945; Wallace, 1977a, 1980; Wallace & Edmondson, 1986; Delbecque & Suykerbuyk, 1988; Meksuwan et al., 2014). As a result of these studies, we know something of larval life before settlement, e.g., swimming speed and reaction to surfaces (Wallace, 1975, 1980) and their energy sources (Hochberg et al. (in this volume); Wallace, 1993; Wallace et al., 1998). And for transition to adult life, we know something about their development and metamorphic processes, but only for a few species (e.g., Edmondson, 1944, 1945; Wright, 1959; Wallace & Edmondson, 1986; Kutikova, 1995; Fontaneto et al., 2003; Hochberg, 2014). Overall, our understanding of the evolutionary forces driving larval and adult life histories remains relatively poor. This study modeled larval behavior and subsequent adult reproduction with the aim of developing areas where additional research is needed.

Basic model (BM) (LHF 1–3)

The BM defined fitness simply as larvae settling on a substratum and metamorphosing into adults, thus offering an uncomplicated outcome to assess substratum selection. This view of fitness is similar to the one used by Doyle (1975) in his Markov chain model. However, because our model is more general than his, we did not attempt a direct comparison. Nevertheless, it is interesting to note that Doyle's model yielded a surprising prediction: "… that fitness is highest for a larva [that] either settles immediately on a substratum or never settles on it at all." While that conclusion does not seem to make biological sense, Wallace (1975) described a similar behavior in *Ptygura beauchampi* Edmondson, 1940. If not provided with their preferred substratum, *P. beauchampi* "… larvae can delay metamorphosis for up to 50 h; most die before that time." Moreover, our BM simulations indicate that the highest fitness values were achieved under two circumstances: when larval substratum choice was either constant or followed a quadratic function (i.e., so-called mid-life competence) and larval speed decreased with age (Table 2). This result supports observations by Wallace (1975) on *P. beauchampi* in which both young and older larvae were less likely to settle. We hypothesize that larvae of species exhibiting exacting preferences for particular substrata will have behavioral patterns as noted here (decreasing speed and either constant acceptance or mid-life competence), but species settling on a wide array of substrata will not.

Reproductive models (RM) (LHF 1–4)

Here we modeled reproduction in three ways: (1) unrelated to either substratum or adult density (autonomous), (2) affected by substratum (positively or negatively) (LHF 4A), or (3) dependent on adult density, either positively (coloniality) or negatively (competition) (LHF 4B).

LHF 4A—Substratum-dependent reproduction

Our model showed that larval fitness depended on the quality of substratum and that small quantities of high-quality substrata were preferable to large amounts of poor-quality substrata. Unfortunately, we know little about substratum-dependent survival and reproduction in sessile rotifers. Wallace (1980) showed that populations of *Floscularia ringens* (Linnaeus, 1758) and *Stephanoceros fimbriatus* (Goldfuss, 1820) attached to *Nymphaea* sp. were shorter than the individuals attached to other vascular hydrophytes. This could have resulted from processes unique to the substrata, e.g., biotic (unequal growth or predation rates) or abiotic (increased abrasion on the undersurface of the lily pads by submerged objects). *Collotheca campanulata* produced more offspring when attached to the under versus the upper surfaces of *E. canadensis* leaves (Wallace & Edmondson, 1986). Butler (1983) suggested that the reproductive effort of *Cupelopagis vorax* (Leidy, 1857) might be correlated to substratum quality, but to our knowledge this hypothesis has not be tested. Clearly, additional research is needed to understand the scope of substratum-dependent survival and reproduction across taxa and what makes one substratum better than another.

LHF 4B—Adult density-dependent reproduction

Here we modeled a positive effect for gregarious settlement leading to the development of colonies as Edmondson (1945) demonstrated for *F. conifera*. Presumably the juxtaposition of two or more coronae of microphagous suspension feeders will reinforce each other, perhaps making feeding more efficient (Wallace, 1987). On the other hand, we also modeled a negative effect of density on reproduction. Our assumption was that closely opposed coronae of raptorial gnesiotrochans (Atrochidae, Collothecidae) would obstruct with each other's predatory activities via interference competition. As with other aspects of our model, we are hampered by the lack of data on adult survival and reproduction as a function of substratum and/or population density.

Facultative sessility (LHF 5)

Reports of sessile species collected in planktonic samples are uncommon and often difficult to interpret; it has been assumed that sessile rotifers may become dislodged from their substratum and thus are present in plankton samples after a net has been towed through a bed of hydrophytes, e.g., *F. ringens* (Green, 2003). Nevertheless, four sessile species have been reported to exhibit facultative sessility. (1) The intra-subspecific form of *Collotheca ornata* (Ehrenberg, 1830) is known to be sessile (Edmondson, 1944; Koste, 1978), but its subspecific variation *C. ornata natans* (Tschugunoff, 1921) is planktonic (Koste, 1978; Sendacz et al., 2006). (2) While sessile, *Lacinularia flosculosa* is also known to occur in the plankton as adult colonies (Koste, 1978; RLW pers. obs). (3) *Ptygura wilsonii* (Anderson & Shepard, 1892) has been described as both free-swimming and sessile (Murray, 1913; Edmondson, 1949). (4) Although *Limnias ceratophylli* Schrank, 1803 is considered to be sessile (Nilsen & Larimore, 1973; Koste, 1978; Meksuwan et al., 2014), Beach (1960) reports it to be an "adventitious plankter." Because no photographic evidence was provided, we should treat Beach's account with some skepticism (Wallace et al., 2018). Also Bērziņš (1951) reported the occurrence of sessile species on the surface of sediments (i.e., biogenous or organogenous) in a few habitats in Sweden. These were *Collotheca edentata* (Collins, 1872), *Collotheca edmondsoni* Bērziņš, 1951, and *Collotheca heptabrachiata* (Schoch, 1869). Unfortunately, it is not known whether the specimens observed were adults that had survived dislodgement from their substratum or whether they came from larvae that metamorphosed in the plankton and subsequently sank to the bottom. Regardless of the validity of these reports, the concept of facultative sessility is intriguing and represents an interesting Evolutionary Stable Strategy (ESS) that should be examined. No doubt such a switch in the life history of a population must be determined by local conditions, i.e., the combined effects of larval death rate coupled with reproductive potential of sessile as compared to planktonic populations. Although those conditions suggest outcomes whereby planktonic, sessile, or facultative taxa might exist, lack of information to parameterize our model hampers understanding of this phenomenon. Thus, additional data on larval and adult survival in the plankton and the reproductive ability of planktonic species are needed. Without those data, facultative sessility remains an intriguing, but untested supposition.

On the other hand, many motile rotifers may also attach to surfaces. Examples of this behavior include species of *Seison*, *Paraseison,* bdelloids, and numerous monogononts (May, 1989; Wallace et al., 2006; Fontaneto & Ambrosini, 2010; Dražina et al., 2018). For example, *Brachionus rubens* Ehrenberg, 1838 opportunistically settles on the carapaces of cladocerans thereby receiving a respite from interference competition and predation (Iyer & Rao, 1995; Diéguez & Gilbert, 2011; Gilbert, in this volume). *Ptygura seminatans* Edmondson, 1939 has been termed semi-sessile (Edmondson, 1944). When disturbed, adults of this species detach and swim away, but return to a substratum after the disturbance has subsided. *Sinantherina semibullata* (Thorpe, 1889) also attaches to hydrophytes for short periods of time (RLW, pers. obs.). These species exhibit the behavior of being sequentially sessile, a strategy whereby temporary attachment leads to a gain in fitness due to reduced swimming costs and perhaps increased feeding efficiency (Vadstein et al., 2012). We suggest that such temporary attachment behaviors be studied by applying concepts of Ideal Free Distribution theory (van der Hammen et al., 2012).

When sessile rotifers are not sessile

Some species within Collothecidae and Flosculariidae are obligatorily planktonic. Examination of the taxonomic literature pertaining to those families indicates that ~ 12% are obligatorily planktonic (Koste, 1978; Segers et al., 2012; Jersabek & Leitner, 2015). Therefore, obligatorily planktonic existence must be considered to be an ESS. Thus, gnesiotrochans may have four major life history strategies: obligatorily sessile, facultatively sessile, sequentially sessile, and obligatorily planktonic. In our conceptual model, we envision loss of the sessile condition in these families to be delimited by three evolutionary constraints: (1) larval survival before metamorphosis, (2) availability of substrata allowing adequate reproduction, and, in contrast (3) relative fitness of planktonic adults (Fig. 2). However, the transition barrier between the two endpoints of these life history strategies must be difficult as only a few species occupy the middle region in this behavioral space, i.e., facultative (n = 4) and sequential (n = 2) sessility. In contrast, obligate sessility has two extremes (monopatry and polypatry). These extremes are probably regulated by the quality of the substrata available and the niche requirements of each species. The unusually restricted habitat of *P. beauchampi* for certain trap doors of the carnivorous hydrophyte *Utricularia macrorhiza* Le Conte, 1824 (Wallace, 1978) illustrates an extreme example of a monopatric species. On the other hand, propensity of *C. campanulata* larvae to settle everywhere including the bottom of culture dishes represents a polypatric species (Wallace & Edmondson, 1986). Two species serve as examples of intermediate substratum selectivity. *Floscularia conifera* will settle on a variety of hydrophytes, but has a strong propensity for settling on conspecifics thus forming colonies (Edmondson, 1945; Wallace, 1977a); *Ptygura crystallina* (Ehrenberg, 1834) accepts a wide variety of substrata, as does *Limnias melicerta* Weisse, 1848 (Wallace, 1977a; Meksuwan et al., 2014). Additionally, the molecular phylogenetic analysis of family Conochilidae by Meksuwan et al. (2015) must also be considered in this discussion. That study offers support for aligning this planktonic, colonial taxon to *Ptygura*, thereby asserting that the family is really a group of specialized Flosculariidae. Using that perspective raises the percentage of sessile taxa that have an obligatorily planktonic life style to ~ 16%.

Obviously, obligatorily sessile and obligate planktonic rotifers have their own evolutionary constraints. While there are evolutionary tradeoffs between these extremes, we cannot yet appreciate their scope until much more information on the life history of sessile taxa has been obtained. Indeed, we need to understand that the behavioral and morphological characteristics of sessile rotifers, or their planktonic counterparts, cannot be optimized simultaneously. According to the Pareto Optimality Theory, evolutionary tradeoffs occur such that the performance function of each feature collectively contributes to fitness (Tendler et al., 2015). After additional data are obtained, as we have noted here, a next logical step is an integration of the behavioral space of the sessile taxa with their morphological space (Dera et al., 2008). Once those data are available, performing phylogenetic generalized least squares or logistic regression analyses may provide a better understanding of the forces driving evolution of the sessile taxa.

Comparisons with models of other sessile species

As we noted previously a large number of models have explored substratum selection by marine invertebrates; while we developed our model within that context, we focused specifically on life history functions likely to be experienced by sessile rotifers. Our model allows for flexibility in each life history function, and thus it accounts for the behaviors employed by different species.

Although it is possible, we did not use either the BM or RM to explore the intensification effect (IE) as defined in the model developed by Pineda & Caswell (1997). In the IE, larval settlement is disproportionately higher in circumstances "… where the amount of suitable [substratum] is reduced, either due to occupation by other individuals or to physical processes." However, both aspects of the IE may have been observed in sessile rotifers. For example, as noted above the preferred substrata of *P. beauchampi* includes the trap doors of *U. macrorhiza* (Wallace, 1977b). In his study, Wallace reported some of the greatest densities (> 25 individuals/mm^2) occurred on the doors of intermediate size; smaller and larger doors did not achieve that density. In addition, Wallace (1980) speculated that individuals of both *F. ringens* and *S. fimbriatus* achieved smaller stature when attached to the undersurfaces of lily pads (*Nymphaea*)

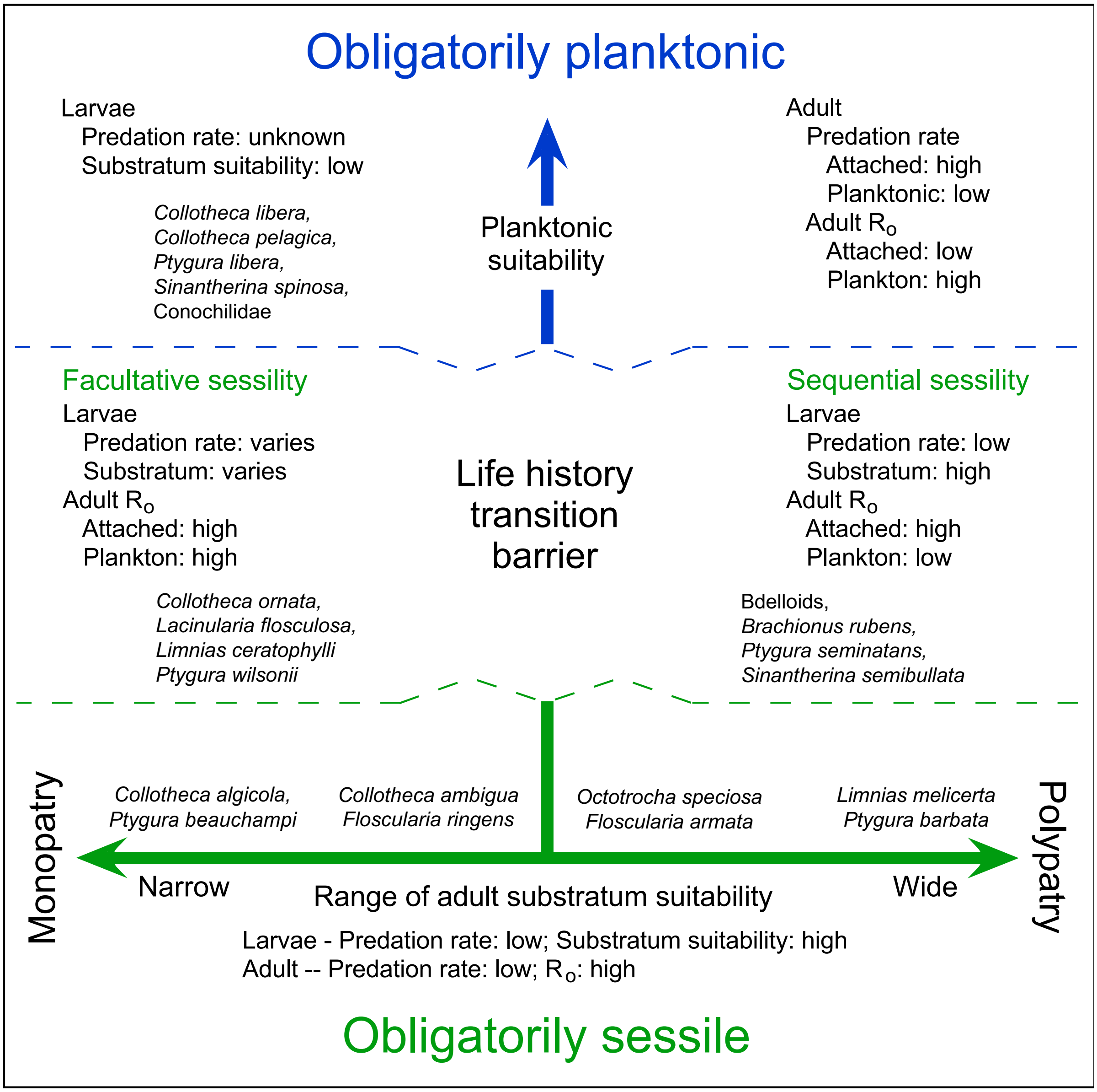

Fig. 2 A working conceptual model of the behavioral landscape for sessile versus planktonic gnesiotrochan rotifers. Obligatorily sessile taxa noted along the range of adult substratum suitability axis were inferred from Fig. 1 of Meksuwan et al. (2014). Facultatively and sequentially sessile and obligatorily planktonic taxa are discussed in the text. We note the behavior of sequential sessility in bdelloids and *Brachionus rubens* (Monogononta, Ploima) for comparative purposes

than on either *Lemna* or *Myriophyllum*. Our model could easily be adapted to explore the IE by tracking the number of settled larvae as a function of time and performing a sensitivity analysis to see how that depends on different parameter choices.

We also did not take into account larval substratum selection behaviors as a function of an instantaneous assessment of its energetics as Toonen & Tyre (2007). Our model shares features with Burgess et al. (2009) in that both take a discrete dynamical systems approach to modeling the reproductive behavior of larvae. However, our model offers much more flexibility in the five life history functions and thus it is likely to be more reflective of real-world behaviors.

Conclusions

While others have explored rotifer populations using mathematical models (e.g., Fussmann et al., 2000; Serra et al., 2011; Kovach-Orr & Fussmann, 2013), ours is the first study to model settling dynamics of sessile rotifers. However, we emphasize that our study is exploratory; our purpose was to examine aspects of sessile rotifer life history and in doing so to suggest topics for additional research and to propose testable hypotheses. As such our model provides a flexible, tractable, mechanistic approach to examine substratum selection of sessile rotifers by varying several environmental and life history features. While we recognize that models are inherently inaccurate, loss in accuracy in this model is balanced by a gain in simplicity (e.g., Shertzer et al., 2002). Still, lack of observational data on sessile rotifer life history features across all taxa is a weakness to our study. Thus, data are needed to parameterize the model with realistic values of larval survival in the plankton (Wallace, 1980). We also need information on the relative surface area available among substrata and the importance of physical and chemical variations among substrata within the Prandtl boundary (Meksuwan et al., 2014). Additional data are required on (1) the cues used by larvae in substratum selection behaviors (Wallace, 1978; Wallace & Edmondson, 1986; Segers et al., 2010), especially in light of adult population densities (Edmondson, 1945; Wallace, 1977a; Butler, 1983; Sarma et al., 2017), (2) larval swimming speed as a function of age (Wallace, 1975), (3) substratum-dependent survival and reproduction of adults (Wallace, 1980; Wallace & Edmondson, 1986; Sarma et al., 2017), and (4) the frequency of facultative sessility. This sort of information needs to be gathered across a wide variety of gnesiotrochan taxa that live in a range of habitats, but it must include a study of those taxa in Collothecaceae and Flosculariidae that are obligatorily planktonic. The model can be parameterized and refined once additional data are in hand.

Although ontogenetic shifts have been well documented, there are still more questions to be examined. Here we provide a model that can vary environmental and life history features to explore consequences to population dynamics and the evolutionary trajectories of species. Also within the context of sessile rotifers, it offers hypotheses and suggests fields for additional research. Our model can be modified to examine life histories of other sessile invertebrates; because of its flexibility, it could be applied to other selection behaviors in animals including mate, habitat, and diet. We encourage others to adapt our model to address these questions.

Acknowledgements We thank Diego Fontaneto, Holger Herlyn, Mark Kainz, Menuma Khan, McKenzie Lamb, George Wittler, and three anonymous reviewers for their comments that improved this manuscript. This research was supported in part by funds for faculty development (Ripon College), from the National Science Foundation: DEB 1257068 (EJW), 1257110 (RH), and 1257116 (RLW), and by Grant 5G12MD007592 from the National Institutes on Minority Health and Health Disparities (NIMHD), a component of the National Institutes of Health (NIH). The content is solely the responsibility of the authors and does not necessarily represent the official views of the National Institutes of Health or the National Science Foundation.

References

Allen, J. D. & B. Pernet, 2007. Intermediate modes of larval development: bridging the gap between planktotrophy and lecithotrophy. Evolution and Development 9: 643–653.

Armstrong, R. A., 2014. When to use the Bonferroni correction. Ophthalmic Physiol Opt 34: 502–508.

Beach, N. W., 1960. A study of the planktonic rotifers of the Ocqueoc River system, Presque Isle County, Michigan. Ecological Monographs 30: 339–358.

Bērziņš, B., 1951. On the Collothecacean Rotatoria with special reference to the species found in the Aneboda district, Sweden. Arkiv för Zoologi 1: 565–592.

Burgess, S. C., S. P. Hart & D. J. Marshall, 2009. Pre-settlement behavior in larval bryozoans: the roles of larval age and size. Biological Bulletin 216: 344–354.

Burgess, S. C., E. A. Treml & D. J. Marshall, 2012. How do dispersal costs and habitat selection influence realized population connectivity? Ecology 93: 1378–1387.

Butler, N. M., 1983. Substrate selection and larval settlement by *Cupelopagis vorax*. Hydrobiologia 104: 317–323.

Chia, F. S. & M. E. Rice (eds), 1978. Settlement and Metamorphosis of Marine Invertebrate Larvae. Elsevier, New York.

Chia, F.-S., G. Gibson & P.-Y. Qian, 1996. Poecilogony as a reproductive strategy of marine invertebrates. Oceanologia Acta 19: 203–208. http://archimer.ifremer.fr/doc/00094/20178.

Crisp, D. J. & P. S. Meadows, 1963. Adsorbed layers: the stimulus to settlement in barnacles. Proceedings of the Royal Society of London B 158: 364–387.

Daly, E. A., R. D. Brodeur & L. A. Weitkamp, 2009. Ontogenetic shifts in diets of juvenile and subadult Coho and Chinook salmon in coastal marine waters: important for marine survival? Transactions of the American Fisheries Society 138: 1420–1438.

Decho, A. W. & J. W. Fleeger, 1988. Ontogenetic feeding shifts in the meiobenthic harpacticoid copepod *Nitocra lacustris*. Marine Biology 97: 191–197.

Delbecque, E. J. P. & R. E. M. Suykerbuyk, 1988. A comparison of the periphyton of *Nuphar lutea* and *Nymphaea alba*. Spatial and temporal changes in the occurrence of sessile microfauna. Archiv für Hydrobiologie 112: 541–566.

Dera, G., G. J. Eble, P. Neige & B. David, 2008. The flourishing diversity of models in theoretical morphology: from current practices to future macroevolutionary and bioenvironmental challenges. Paleobiology 34: 301–317.

Despland, E. & S. Hamzeh, 2004. Ontogenetic changes in social behaviour in the forest tent caterpillar, *Malacosoma disstria*. Behavioral Ecology and Sociobiology 56: 177–184.

de Roos, A. M. & L. Persson, 2013. Population and Community Ecology of Ontogenetic Development. Princeton University Press, Princeton.

Diéguez, M. C. & J. J. Gilbert, 2011. *Daphnia*–rotifer interactions in Patagonian communities. Hydrobiologia 662: 189–195.

Doyle, R. W., 1975. Settlement of planktonic larvae: a theory of habitat selection in varying environments. The American Naturalist 109: 113–126.

Dražina, T., A. Korša, M. Špoljar, I. Maguire & G. I. V. Klobučar, 2018. Epifauna of native and alien freshwater crayfish species (Crustacea:Decapoda): a host-specific community? Freshwater Science 37: (in press). https://doi.org/10.1086/698764.

Edmondson, W. T., 1944. Ecological studies of sessile Rotatoria, Part I. Factors affecting distribution. Ecological Monographs 14: 32–66.

Edmondson, W. T., 1945. Ecological studies of sessile Rotatoria, Part II. Dynamics of populations and social structure. Ecological Monographs 15: 141–172.

Edmondson, W. T., 1949. A formula key to the Rotatorian genus *Ptygura*. Transactions of the American Microscopical Society 68: 127–135.

Fontaneto, D. & R. Ambrosini, 2010. Spatial niche partitioning in epibiont rotifers on the waterlouse *Asellus aquaticus*. Limnology and Oceanography 55: 1327–1337.

Fontaneto, D., G. Melone & R. L. Wallace, 2003. Morphology of *Floscularia ringens* (Rotifera, Monogononta) from egg to adult. Invertebrate Biology 122: 231–240.

Fussmann, G. F., S. P. Ellner, K. W. Shertzer & N. G. Hairston Jr., 2000. Crossing the Hopf bifurcation in a live predator-prey system. Science 290: 1358–1360.

Gilbert, J. J., (this volume). Attachment behavior in the rotifer *Brachionus rubens*: induction by *Asplanchna* and effect on sexual reproduction. Hydrobiologia. https://doi.org/10.1007/s10750-018-3805-7.

Green, J., 2003. Associations of planktonic and periphytic rotifers in a tropical swamp, the Okavango Delta, Southern Africa. Hydrobiologia 490: 197–209.

Hadfield, M. G., 1998. The D P Wilson Lecture. Research on settlement and metamorphosis of marine invertebrate larvae: past, present and future. Biofouling 12: 9–29.

Hentschel, B. T., 1998. Intraspecific variations in $\delta\ ^{13}C$ indicate ontogenetic diet changes in deposit-feeding polychaetes. Ecology 79: 1357–1370.

Hochberg, A., 2014. Comparative myoanatomy of collothecid rotifers (Rotifera: Gnesiotrocha: Collothecaceae) with details on larval metamorphosis and development of the infundibulum in species of *Stephanoceros*. MS thesis. University of Massachusetts at Lowell, Lowell, MA.

Hochberg, R., H. Yang, E. J. Walsh & R. L. Wallace, (this volume). Systematic distribution of birefringent bodies in Rotifera and first evidence of their ultrastructure in *Acyclus inquietus* (Gnesiotrocha: Collothecaceae). Hydrobiologia.

Hodin, J., M. C. Ferner, G. Ng, C. J. Lowe & B. Gaylord, 2015. Rethinking competence in marine life cycles: ontogenetic changes in the settlement response of sand dollar larvae exposed to turbulence. Royal Society Open Science 2: 150114.

Iyer, N. & T. R. Rao, 1995. Epizoic mode of life in *Brachionus rubens* Ehrenberg as a deterrent against predation by *Asplanchna intermedia* Hudson. Hydrobiologia 313(314): 377–380.

Jersabek, C. D. & M. F. Leitner, 2015. The Rotifer World Catalog. World Wide Web electronic publication. http://www.rotifera.hausdernatur.at/. Accessed 11 July 2018.

Kempf, S. C., 1981. Long-lived larvae of the gastropod *Aplysia juliana*: do they disperse and metamorphose or just slowly fade away? Marine Ecology Progress Series 6: 61–65.

Kinlan, B. P., S. D. Gaines & S. E. Lester, 2005. Propagule dispersal and the scales of marine community process. Diversity and Distributions 11: 139–148.

Koehl, M. A. R. & M. G. Hadfield, 2010. Hydrodynamics of larval settlement from a larva's point of view. Integrative and Comparative Biology 50: 539–551.

Koste, W., 1978. Rotatoria. Die Rädertiere Mitteleuropas. 2 volumes. Gebrüder Borntraeger, Stuttgart.

Kovach-Orr, C. & G. F. Fussmann, 2013. Evolutionary and plastic rescue in multitrophic model communities. Philosophical Transactions of the Royal Society B 368(1610): 20120084.

Kuczyńska-Kippen, N., 2003. The distribution of rotifers (Rotifera) within a single *Myriophyllum* bed. Hydrobiologia 506–509: 327–331.

Kuczyńska-Kippen, N., 2005. On body size and habitat selection in rotifers in a macrophye-dominated lake Budzyńskie, Poland. Aquatic Ecology 39: 447–454.

Kuczyńska-Kippen, N. M. & B. Nagengast, 2006. The influence of the spatial structure of hydromacrophytes and differentiating habitat on the structure of rotifer and cladoceran communities. Hydrobiologia 559: 203–212.

Kutikova, L. A., 1995. Larval metamorphosis in sessile rotifers. Hydrobiologia 313(314): 133–138.

Levin, L. A. & T. S. Bridges, 1995. Pattern and diversity and and reproduction in development. In McEdward, L. R. (ed.), Ecology of Marine Invertebrate Larvae., Marine Science Series CRC Press Inc, Boca Raton: 1–48.

Lucena-Moya, P. & I. C. Duggan, 2011. Macrophyte architecture affects the abundance and diversity of littoral microfauna. Aquatic Ecology 45: 279–287.

Marechal, J. P., C. Hellio, M. Sebire & A. S. Clare, 2004. Settlement behaviour of marine invertebrate larvae measured by EthoVision 3.0. Biofouling 20: 211–217.

Marshall, D. J., T. F. Bolton & M. J. Keough, 2003. Offspring size affects the post-metamorphic performance of a colonial marine invertebrate. Ecology 84: 3131–3137.

Marshall, D. J. & M. J. Keough, 2003. Variation in the dispersal potential of non-feeding invertebrate larvae: the desperate larva hypothesis and larval size. Marine Ecology Progess Series 255: 145–153.

May, L., 1989. Epizoic and parasitic rotifers. Hydrobiologia 186(187): 59–67.

McEdward, L. R. (ed.), 1995. Ecology of Marine Invertebrate Larvae. CRC Press Inc, Boca Raton.

Meksuwan, P., P. Pholpunthin & H. H. Segers, 2015. Molecular phylogeny confirms Conochilidae as ingroup of Flosculariidae (Rotifera, Gnesiotrocha). Zoologica Scripta 44: 562–573.

Meksuwan, P., P. Pholpunthin, E. J. Walsh, H. Segers & R. L. Wallace, 2014. Nestedness in sessile and periphytic rotifer communities: a meta-analysis. International Review of Hydrobiology 99: 48–57.

Mooney, D. D. & R. J. Swift, 1999. A course in Mathematical Modeling, Vol. 13. Mathematical Association of America, Washington, DC.

Murray, J., 1913. VI.—South American Rotifera. Journal of the Royal Microscopical Society 33(3): 229–246.

Nilsen, H. C. & R. W. Larimore, 1973. Establishment of invertebrate communities on log substrates in the Kaskaskia River, Illinois. Ecology 54(2): 366–374.

Olson, R. R., 1985. The consequences of short-distance larval dispersal in a sessile marine invertebrate. Ecology 66(1): 30–39.

Pannell, D. J., 1997. Sensitivity analysis of normative economic models: theoretical framework and practical strategies. Agricultural Economics 16: 139–152.

Pawlik, J. R., 1992. Chemical ecology of the settlement of benthic marine invertebrates. Oceanography and Marine Biology: An Annual Review 30: 273–335.

Pechenik, J. A., 1980. Growth and energy balance during the larval lives of three prosobranch gastropods. Journal of Experimental Marine Biology and Ecology 44: 1–28.

Pechenik, J. A., 1999. On the advantages and disadvantages of larval stages in benthic marine invertebrate life cycles. Marine Ecology Progress Series 177: 269–297.

Pechenik, J. A., 2006. Larval experience and latent effects—metamorphosis is not a new beginning. Integrative and Comparative Biology 46: 323–333.

Richards, R. A., 1992. Habitat selection and predator avoidance: ontogenetic shifts in habitat use by the Jonah crab *Cancer borealis* (Stimpson). Journal of Experimental Marine Biology and Ecology 156: 187–197.

Pineda, J. & H. Caswell, 1997. Dependence of settlement rate on suitable substrate area. Marine Biology 129: 541–548.

Roughgarden, J., Y. Iwasa & C. Baxter, 1985. Demographic theory for an open marine population with space-limited recruitment. Ecology 66: 54–67.

Rumrill, S. S., 1990. Natural mortality of marine invertebrate larvae. Ophelia 32: 163–198.

Sarma, S. S. S., M. A. Jiménez-Santos, S. Nandini & R. L. Wallace, 2017. Demography of the sessile rotifers, *Limnias ceratophylli* and *Limnias melicerta* (Rotifera: Gnesiotrocha), in relation to food (*Chlorella vulgaris* Beijerinck, 1890) density. Hydrobiologia 796: 181–189.

Schriever, T. A. & D. D. Williams, 2013. Ontogenetic and individual diet variation in amphibian larvae across an environmental gradient. Freshwater Biology 58: 223–236.

Segers, H., W. H. De Smet, C. Fischer, D. Fontaneto, E. Michaloudi, R. L. Wallace & C. D. Jersabek, 2012. Towards a list of available names in zoology, partim phylum Rotifera. Zootaxa 3179: 61–68.

Segers, H., P. Meksuwan & L.-O. Sanoamuang, 2010. New records of sessile rotifers (Phylum Rotifera: Flosculariacea, Collothecacea) from Southeast Asia. Belgian Journal of Zoology 140: 235–240.

Sendacz, S., S. Caleffi & J. Santos-Soares, 2006. Zooplankton biomass of reservoirs in different trophic conditions in the state of São Paulo, Brazil. Brazilian Journal of Biology 66: 337–350.

Serra, M., H. A. Smith, J. S. Weitz & T. W. Snell, 2011. Analysing threshold effects in the sexual dynamics of cyclically parthenogenetic rotifer populations. Hydrobiologia 662: 121–130.

Shanks, A. L., 2009. Pelagic larval duration and dispersal distance revisited. The Biological Bulletin 216: 373–385.

Shertzer, K. W., S. P. Ellner, G. F. Fussmann & N. G. Hairston Jr., 2002. Predator–prey cycles in an aquatic microcosm: testing hypotheses of mechanisms. Journal of Animal Ecology 71: 802–815.

Strathmann, R. R., 1985. Feeding and nonfeeding larval development and life-history evolution in marine invertebrates. Annual Review of Ecology and Systematics 16: 339–361.

Streiner, D. L. & G. R. Norman, 2011. Correction for multiple testing: is there a resolution? Chest 140: 16–18.

Tendler, A., A. Mayo & U. Alon, 2015. Evolutionary tradeoffs, Pareto optimality and the morphology of ammonite shells. BMC Systems Biology 9: 12.

Thiyagarajan, V., 2010. A review on the role of chemical cues in habitat selection by barnacles: new insights from larval proteomics. Journal of Experimental Marine Biology and Ecology 392: 22–36.

Toonen, R. J. & A. J. Tyre, 2007. If larvae were smart: a simple model for optimal settlement behavior of competent larvae. Marine Ecology Progress Series 349: 3–61.

Vadstein, O., L. M. Olsen & T. Andersen, 2012. Prey-predator dynamics in rotifers: density-dependent consequences of spatial heterogeneity due to surface attachment. Ecology 93: 1795–1801.

van der Hammen, T., M. Montserrat, M. W. Sabelis, A. M. de Roos & A. Janssen, 2012. Whether ideal free or not, predatory mites distribute so as to maximize reproduction. Oecologia 169: 95–104.

Vance, R. R., 1973. More on reproductive strategies in marine benthic invertebrates. The American Naturalist 107: 353–361.

Wallace, R. L., 1975. Larval behavior of the sessile rotifer *Ptygura beauchampi* (Edmondson). Verhandlungen Internationale Vereinigung Limnologie 19: 2811–2815.

Wallace, R. L., 1977a. Distribution of sessile rotifers in an acid bog pond. Archiv für Hydrobiologie 79: 478–505.

Wallace, R. L., 1977b. Substrate discrimination by larvae of the sessile rotifer *Ptygura beauchampi* Edmondson. Freshwater Biology 7: 301–309.

Wallace, R. L., 1978. Substrate selection by larvae of the sessile rotifer *Ptygura beauchampi*. Ecology 59: 221–227.

Wallace, R. L., 1980. Ecology of sessile rotifers. Hydrobiologia 73: 181–193.

Wallace, R. L., 1987. Coloniality in the phylum Rotifera. Hydrobiologia 147: 141–155.

Wallace, R. L., 1993. Presence of anisotropic (birefringent) crystalline structures in embryonic and juvenile monogonont rotifers. Hydrobiologia 255(256): 71–76.

Wallace, R. L. & W. T. Edmondson, 1986. Mechanism and adaptive significance of substrate selection by a sessile rotifer. Ecology 67: 314–323.

Wallace, R. L., J. J. Cipro & R. W. Grubbs, 1998. Relative investment in offspring by sessile Rotifera. Hydrobiologia 387(388): 311–316.

Wallace, R. L., A. Korbacheh & E. J. Walsh, 2018. Key to the currently recognized species of *Limnias* Schrank, 1803 (Rotifera, Monogononta, Gnesiotrocha, Flosculariidae). Zootaxa 4442: 307–318.

Wallace, R. L., T. W. Snell, C. Ricci & T. Nogrady, 2006. Rotifera. Volume 1: Biology, Ecology and Systematics, 2nd ed. Backhuys Publishers, Leiden.

Wallace, R. L., T. W. Snell & H. A. Smith, 2015. Phylum Rotifera. In Thorp, J. H. & D. C. Rogers (eds), Thorp and Covich's Freshwater Invertebrates, Vol. I., Ecology and General Biology Elsevier, Waltham, MA: 225–271.

Walsh, E. J., 1995. Habitat-specific predation susceptibilities of a littoral rotifer to two invertebrate predators. Hydrobiologia 313(314): 205–211.

Werner, E. E., 1988. Size, scaling, and the evolution of complex life cycles. In Perrson, L. & B. Ebenmann (eds), Size-Structured Populations: Ecology and Evolution. Springer, Berlin: 60–81.

Werner, E. E. & J. F. Gilliam, 1984. The ontogenetic niche and species interactions in size-structured populations. Annual Review of Ecology and Systematics 15: 393–425.

Wilson, D. P., 1952. The influence of the nature of the substratum on the metamorphosis of the larvae of marine animals especially the larvae of *Ophelia bicornis* Savigny. Annales de l'Institut Océanographique 27: 49–156.

Woods, H. A. & R. Wilson, 2013. Ontogenetic changes in the body temperature of an insect herbivore. Functional Ecology 27: 1322–1331.

Wright, H. G. S., 1959. Development of the peduncle in a sessile rotifer. Journal of the Quekett Microscopical Club. Series 4 5: 231–234.

Young, C. M., 1990. Larval ecology of marine invertebrates: a sesquicentennial history. Ophelia 32: 1–48.