Free for the Doing: Some Potential Projects Using State Dependent Life History Theory  


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Context

In Chapter 9 of the book, I described potential case studies using State Dependent Life History Theory (SDLHT). None of these are fully developed, and some just included the
germ of the idea. In the material that follows, the canonical equations for activity choice and allocation refer to two equations of Stochastic Dynamic Programming (SDP). They will make an appearance in a future publication based on a different chapter (“From $R_0$ to Stochastic Dynamics Programming”) but you can read about them in Mangel, M. 2015. Stochastic Dynamic Programming illuminates the link between environment, physiology, and evolution. Bulletin of Mathematical Biology. 77:857-877; available at https://users.soe.ucsc.edu/ msmangel/Mangel%202015%20BMB.pdf in the publications section of my web site.

Although I have tried to state the problems as clearly as possible and am confident that they can be approached using SDLHT, since I have not done any of these case studies I cannot promise that things will work out for you.

**Brief Introduction**

I describe a variety biological situations for which the methods of State Dependent Life History Theory apply but have not been used or can be further developed. You will find some unevenness in the description of the case studies, because some of them involve systems that I have thought about for a long time, while others are just a germ of an idea waiting fuller development. All but one of the case studies involve a particular biological situation, but some involve a broader theoretical construct that allows modifying the canonical equations in interesting and important ways.

The topics included are these:

- After Life Contributions of Salmon and Trees
- Barnacle Flies in the Intertidal
- The Cell Quota (Droop) Model, Storage, and Population Dynamics
After Life Contributions of Salmon and Trees

During spawning season, the edges of a salmon stream can be littered with carcasses. We now understand that these carcasses provide nutrients that re-enter the system and may contribute to reproductive success by providing nourishment for offspring after they emerge. Similarly, in almost many forests one will see fallen trees in varying levels of decay and, among other things, new trees growing either out of the fallen tree or near it. Indeed in some cases (e.g. coastal redwoods, *Sequoia sempervirens*, which grow clonally) the young trees growing out of or near to the fallen tree may be genetically identical or at least offspring of the fallen tree. The literature on this topic is scattered with very few models. If this problem excites you, the lack of literature means that there is great opportunity for making a contribution.

Marine derived nutrients from salmon carcasses interact with terrestrial litter inputs and thus enhance stream biodiversity and ecosystem functioning (Bretherton et al 2011);
thus returning salmon are said to subsidize the riverine system through the delivery of marine derived nutrients that increase freshwater productivity (Samways et al. 2017). Quinn (2005, pg 129-143) provides a superb review of the ecology of dead salmon. One of the potential consequences of such increased productivity is additional resources for offspring when they emerge. Decay processes are temperature dependent (Follstad Shah et al. 2017), so that we may expect changes in the after life contribution with changing temperature.

Even parts of trees can have an after life contribution (Jahren 2016, pgs 89-90; Thomas 2014). As a willow (*Salix* spp) tree grows, the lower branches become shaded by the upper ones and can no longer photosynthesize. The trees have evolved a use for such branches. Instead of having them become dead wood, a willow tree first puts resources into the branches and then dries their attachment to the tree so that they fall off. When a willow is on the bank of a river, a fallen branch may be carried downstream, and on occasion one of those branches may land on a bank, replant itself, and grow successfully. Thus, the question that the plant faces is how much to invest in these branches that are no longer useful for itself, but might contribute to future reproduction in a different location.

An after life contribution to reproductive success requires that we rethink the canonical equations. In the canonical equation for activity choice, reproductive success depends solely upon the final value $X(T)$ of the state variable and in the canonical equation for allocation the organism accumulates reproductive success in each period but any resources left at the time of death are “wasted” in the sense that they do not contribute to reproductive success. An after life contribution means that resources remaining at the time of death can contribute to reproductive success, which begs the question of why not just invest directly in the offspring propagule? Our previous canonical equation for allocation
in its simplest form is

\[ F(x, s) = e^{-m(1 - \eta)}F(x, s + 1) + \eta \max_{r \leq x} [f(c) + e^{-m}F(x - r, s + 1)] \] (1)

An after-life contribution implies that the increment in fitness from reproductive effort \( c \) at time \( s \) depends upon resources at the time of death of the parent, and possibly the length of time between \( s \) and when the parent dies. This suggests that we multiply \( f(c) \) in Eqn 1 by a factor capturing the parental resources at the time of death and the difference between the time of death and \( s \). This resulting canonical equation will be a bit trickier to solve, but can be done via an iteration method as in Mangel et al. (1994), but begs the question: why not simply put those resources in at the time of reproduction?

**Barnacle Flies in the Intertidal**

*Oedoparena* are flies (Figure 1) commonly found in littoral habitats in the North Pacific (Knudsen 1963, Burger et al 1980, Harley and O’Reilly 2001, Harley and Lopez 2003). They exhibit a parasitoid-like life history: adults are free ranging, laying eggs on closed barnacles at low tide. The eggs hatch at a subsequent low tide and the larvae crawl into the barnacles when they open as the tide comes in. During the high tide, the larvae feed on the tissues of submerged barnacles – as if they were a parasitoid.

When flies are abundant there may be as many as 10 larvae in a barnacle, although it is not clear how many different females were involved in laying eggs. However, in general larvae cannot complete pupation in a single barnacle so that in subsequent low tides, the larvae need to leave the host barnacle and find another potential host; when they do, the larvae use their mouth parts to hold onto the prey shell and wait until the next high tide comes in so that they can enter the barnacle and feed again. Skevington and Dang (2002) call this a weird larval lifestyle, but who is to say what is weird? In some places, these
flies may be the major predator of barnacles (Harley and Lopez 2003). There is also clear host choice – hunting larvae are generally found in larger barnacles (Figure 1). When the larvae move from one host to another, they face a suite of predators that includes nemertean worms (*Amphiporus* sp.), lycosid spiders, and staphylinid beetles (Harley and Lopez 2003). Furthermore, the larvae have a nearly knife-edged survival versus temperature curve (Figure 9.1), which affects microhabitat choice. Harley and Lopez (2003) collected about 30 barnacles, half of which were north facing and half of which

Figure 1: a) The barnacle fly *Oedoparena* spp. has a parasitoid life history with barnacles as hosts. a) Putative adults (from Bodega, Bay CA laying eggs in barnacles at low tide. b) However, larvae (from Pacific Grove, CA) cannot complete development in a single barnacle, so must move between barnacles at low tides. c) There is clear size selectivity in hunting larvae in that barnacles with larvae are substantially larger than those without (Harley and Lopez 2003) d) The thermal tolerance of larvae is nearly knife-edged, so that a hunting for a large barnacle at low tide has large risk of dessication. Here, larvae were exposed to the indicated temperature for 3 hours and then allowed to recover for another 3 hours before an assessment of survival (Harley and Lopez 2003).
were south facing. They found that north-facing barnacles had more than twice larvae than south facing barnacles, statistically significant at the 1% level.

Here are three opportunities for using SDLHT to learn about the barnacle fly. First, adults face the challenge of selecting barnacles for oviposition that will not lead to dessication of their larvae. Presumably this will depend upon the egg complement and the distribution of barnacles in size and space, with interesting trade-offs such as the one between the size of the barnacle and how high it is in the intertidal. For example, a large barnacle high in the intertidal will likely support faster and better growth of the larva, so that it will emerge larger, which should allow it to move more quickly at low tide. However, that barnacle may be far from other potential hosts and are thus more likely to experience dessication.

Second, as larvae move during the low tide, they will encounter barnacles of different sizes and thus face the choice of accepting the currently encountered barnacle or moving on, continuing to search for a potentially better barnacle (and possibly returning to one that was previously rejected), all the time facing the constraint of the returning tide. Even without the presence of conspecifics (which makes this a dynamic state variable game in its fullest version), this is a complicated problem.

Third, barnacles are often found in sympatry with mussels. Thinking of barnacles and mussels together, I am reminded of *Rhagoletis pomonella*, the apple maggot fly, which made its shift from hawthorn *Crataegus* spp. to domestic apples (e.g Bush 1969). Mussels are currently a candidate for aquaculture along both coasts of North America; we may wonder if and how barnacle flies could make the shift from barnacles to mussels in an aquaculture setting and how a SDLHT model could help answer that question.
The Cell Quota (Droop) Model, Storage, and Population Dynamics

This is a theoretical potential case study, with much to be mined. Imagine a population whose size at time $s$ is $N(s)$ individuals and let us assume that the dynamics are

$$\frac{dN}{ds} = \frac{\alpha N}{1+\beta N} - MN$$

(2)

where $\alpha, \beta$ and $M$ are parameters. $M$ is the rate of mortality: Since the units of $\frac{dN}{ds}$ are individuals per unit time, the product $MN$ must have those units as well, which means that the units of $M$ are 1/time, making it a rate.

If we ignore the density dependence entirely (e.g. set $\beta = 0$) Eqn 2 becomes

$$\frac{dN}{ds} = \alpha N - MN = rN$$

(3)

where $r = \alpha - M$; we recognize this equation as exponential growth.

If instead of ignoring density dependence entirely, we assume that $\beta N$ is sufficiently small that we can Taylor expand $\frac{1}{1+\beta N} \approx 1 - \beta N$, Equation 2 becomes

$$\frac{dN}{ds} = \alpha N(1 - \beta N) - MN = (\alpha - M)N - \alpha\beta N^2$$

(4)

so that if write that $\alpha\beta = \frac{r}{K}$ we can write this equation as

$$\frac{dN}{ds} = rN\left(1 - \frac{N}{K}\right)$$

(5)

which we recognize as logistic growth.

The objective of this potential case study is to provide more interpretation of $\alpha$, the maximum per capita reproductive success. The fundamental idea is usually attributed to
Droop (1973) and is called a quota or storage model.

In particular, we assume now that $\alpha$ is a function $\alpha(Q)$ of internal resources $Q$ that are essential for reproduction. The commonly used form for this function is

$$\alpha(Q) = \alpha_{\text{max}} \left(1 - \frac{q_{\text{min}}}{Q}\right)$$

(6)

where $q_{\text{min}}$ is the minimal level of resources required for reproduction. Note that when $Q$ falls below the minimum value, $\alpha$ becomes negative. There is no such thing as negative reproduction, but we can interpret $\alpha N < 0$ as individuals dying.

Droop (1973) and others (e.g. Flynn 2003, Hellweger and Kianirad 2007, Cherif and Loreau 2010, Reuman et al 2013) argued that $Q$ is a dynamic variable; the tradition is to give dynamics

$$\frac{dQ}{ds} = V(N, Q) - \alpha Q$$

(7)

where $V(N, Q)$ is the uptake of resources when the population size is $N$ and the individual storage is $Q$. The population dynamics (with all individuals sharing the dynamics for $Q$) are then

$$\frac{dN}{ds} = \frac{\alpha_{\text{max}} \left(1 - \frac{q_{\text{min}}}{Q}\right) N}{1 + \beta N} - MN$$

(8)

$$\frac{dQ}{ds} = V(N, Q) - \alpha_{\text{max}} \left(1 - \frac{q_{\text{min}}}{Q}\right) Q$$

(9)

Hellweger and Kianirad (2007) develop a stochastic version of these equations.

This is a wonderful opportunity to combine the canonical equations for activity choice and resource allocation into a single model. Since Eqns 8 and 9 are differential equations in continuous time, we need continuous time versions of the canonical equations (see, for
example, Mangel (1985, 1992)).

To do this, we assume that when time is incremented, it is incremented by $ds$ units instead of 1 unit and that $ds$ is small. Our interpretation of the parameters in the canonical equations must change since now $m_i, \lambda_i$ and $\alpha_i$ become rates. Thus, the probability of surviving the next $ds$ units of time, of finding food, and energy spent when activity $i$ is chosen are $e^{-m_i ds}$ and approximately $\lambda_i ds$ and $\alpha_i ds$ respectively (with additional terms proportional to higher powers of $ds$). To combine the two canonical equations, we will allow reproduction to be associated with each activity choice. Thus we let $f_i(c)/(1 + \beta n)$ denote the offspring production when $c$ units of storage are used for reproduction during activity $i$ and when population size is $N(s) = n$.

We now need two state variables. We let $N(s)$ denote population size at time $s$, with particular value $n$, and $Q(s)$ the individual storage at time $s$, with particular value $q$. Fitness $F(q, n, s)$ is now the maximum individual accumulated reproduction between $s$ and $S$ given that population size at time $s$ is $n$ and resources are $q$. If we let $n'(n, q)$ denote the population size at time $s + ds$ given $n$ and $q$ (determined from Eqns 8 and 9) then the combined canonical equation is

$$F(q, n, s) = \max_{i,c} \left[ \frac{f_i(c)}{1 + \beta n} + e^{-m_i(c) ds} \left( \lambda ds F(q - c - \alpha_i ds + Y_i, n'(n, q), s + ds) \right. \right.$$  

$$\left. + (1 - \lambda ds) F(q - c - \alpha_i ds, n'(n, q), s + ds) \right] \] (10)$$

The next steps in dealing with Eqn 10 (Mangel 1985, 1992; Pike et al 2018) are to Taylor expand in powers of $ds$, collect terms according to those powers, and only use those terms proportional to $ds$.

There are also wonderful opportunities for connecting these models to data. For example, Sacristán et al (2017) provide data on how three different decapod species (a crayfish, shrimp, and lobster) use their reserves during food deprivation.
Clownfish and Their Host Anemones

This potential case study is motivated by the mutualistic interaction between the anemone fish *Amphiprion binictus* and its host anemones *Entacmaea quadricolor* (the Bulb-tenacle sea anemone) and *Heteractis crispa* (Leathery sea anemone) (Figure 2; Allen 1975, 1980; Miyagawa 1989; Fautin 1991; and Elliott and Mariscal 2001).

Darwin recognized interspecific mutualism as a potential challenge to the theory of evolution by natural selection. A few current generalizations about mutualisms are (Bshary and Bronstein 2004, 2011) i) nearly all mutualisms inherently involve benefits (goods and services that organisms cannot affordably obtain, or obtain at all, in the absence of the partner) and costs for both species, ii) benefits and costs are rarely fixed traits of the interactions, but vary with abundance or density of partners, iii) there is positive feedback between mutualistic partners; however, at the population level there must be some kind of negative feedback, to ensure that population sizes do not grow without bound, and iv) interactions occur in a geographic mosaic of environment and selective pressures; this mosaic may cause interactions to range between antagonistic and mutualistic (Thompson 2005). For this case study, we are interested in protection and nutrition mutualisms and are required to think about mutualism as a dynamic state variable game between individuals, and from there to build up to the population level.

Although the range of *Amphiprion* is the tropical belt of the Indo-Pacific Ocean and there are about 25 species in the genus (family Pomacentridae), we focus on the northern Red Sea, because it involves just one species of fish and the two anemones.

In this system, the clownfish is protandrous and close to monogamous, with a wide range of sizes for both male and female: functional males are 61-135 mm and functional females 99-144 mm (Fricke 1983). This suggests that there is no critical size for sex change but rather social control of sex change. The larger male always changes sex before
ABSTRACT:

Habitat segregation occurs between juvenile and adult fish at all post-settlement life stages pre-
ferred for juvenile fish while they wait for space to become

We conclude that competitive exclusion drives habitat

Figure 2: a) The anemonefish *Amphiprion bicinctus* hiding in the tentacles of the sea anemone *Entacmaea quadricolor* Photo from Lindsay Heubner. b) The leathery anemone *Heteractis crispa*. Photo from Lindsay Heubner. c) The digitiform morph of the bulb-tenacle anemone *Entacmaea quadricolor* Photo from Lindsay Heubner. d) The bulbous form of *E. quadricolor* with anemonefish. Photo from Brianna Dailey.
the subdominant one. Mating takes place about 6 times per year, with peak spawning in summer months. Eggs are deposited at the base of the anemone, both parents take turns guarding and ventilating; hatch is about 10 days after spawning and the planktonic stage is 10-12 days (Maroz and Fishelson 1997). Buston and Elith (2011) showed that the primary determinants of reproductive success are male growth and experience, and female growth and size.

When juveniles encounter an anemone, the probability of settlement is essentially 1 if the anemone is empty, but the probability of not settling in an anemone with individuals already present is high; it is likely the prior residents prevent the settlement (Buston 2003a). However, N. Chadwick (personal communication) has observed up to 6 fish in an anemone during settling season. In general, competition within shelter space causes density dependent mortality (Schmitt and Holbrook 2000; Holbrook and Schmitt 2002; Holbrook and Schmitt 2004), possibly related to competition for access to reproduction (Buston 2003b). The fish are plankton feeders and territorial around their anemone (Fricke 1977). Life span may be greater than 30 months (Elliott and Mariscal 2001). The rate of juvenile mortality is very high, perhaps accounting for 95% of the overall mortality (Elliott and Mariscal 2001).

In a study of the conspecific A. clarkii, Ochi (1986) found von-Bertalanffy-like growth that had a temperature dependent component. The growth rate also depends upon the time of settling (Allen 1975). In a congeneric species, Buston (2003c) observed that growth of all but the largest individual was regulated in such a manner that a well-defined size difference was maintained between an individual and its immediate superior and suggests that there is social control of growth. Larger fish are observed to spend more time out and go further from the anemone (Allen 1975).

Groupers and other small piscivores are clownfish predators (Shpigel and Fishelson 1991). A mucus coating protects the clownfish from the nematocysts of the anemone,
thus allowing the clownfish to hide from their predators in the anemones.

The precise nature of the symbiosis is still unclear (Godwin and Fautin 1992); residence is essential for reproduction – so that the interaction is obligate for the fish. However, “[D]ependence of fish on actinians is behavioral, not physiological, as evidenced by their ability to survive alone in captivity” (Fautin 1991, pg 38). Since the fish defend the anemone aggressively, the symbiosis is mutualistic (Godwin and Fautin 1992). Of the two host anemones, *H. crispa* appears to be an unsuitable host for the entire life history, possibly because tentacles are too thin for effective protection of the adult fish and their eggs; however, this anemone can serve as a nursery. In a congener *Amphiprion ocellaris*, Kegler et al (2013) found no evidence that shelter provides a metabolic advantage. Clownfish aggressively defend host anemones from their predator, the butterfly fish *Chaetodon fasciatus*, which is territorial and makes patrols on a regular cycle, since anemones will retract in response to attack by the butterfly fish.

There is a positive relationship between growth rate of anemone and combined size of fish. The nutrient basis of the symbiosis is still unknown; one possibility is turbulence created by the fish enhances flow in the anemone. Over a 4 year period, anemones possessing small or no clownfish either shrunk or completely disappeared, while those with at least 1 large fish survived and grew (Porat and Chadwick 2004). Clownfish excretion may enhance anemone growth; ammonia, provided to both anemones and zooxanthellae, is a likely candidate for the relevant resource. This effect may have the potential to provide benefits to breeders from non-breeders (also see Buston (2004)). Very little is known about the reproductive cycle of the host anemones, except that they have separate and fixed sexes and that *E. quadricolor* may also reproduce asexually through the division of a polyp (Fautin and Allen 1997, pg 120ff).

These observations lead to a series of questions about the anemone, the butterfly fish, and the clownfish.
About the Anemone: i) When is it predicted that an anemone will retract, as a function of the number and size of its defenders and the attack rate by butterfly fish? The answer to this question must take into account the costs of lost photosynthesis and the possible loss of the fish symbiont, e.g., if the anemone retracts into a hole that is too small for the fish to follow. ii) When is a retracted anemone predicted to reexpand following an attack? This will depend upon the frequency and severity of recent attacks, the number and size of resident anemonefish, and the anemone’s physiological state through the length of time that it has been contracted (cf. Mangel (1990c)). iii) Under what conditions is an anemone predicted to move to a new hole?

About the Butterfly fish: i) What is the predicted cycle of revisits in the territory, as a function of the total number of anemones and the time since contraction of focal anemones? ii) At what point in harassment by clownfish is a butterfly fish predicted to leave the current anemone, as a function of attacks by the clownfish and richness of the territory?

About the Clownfish: When thinking about the clownfish, it is helpful to separate pre- and post-settlement questions. For pre-settlement: i) Under what circumstances is a fish in the water column predicted to settle at H. crispa, rather than continue searching? ii) What are the conditions under which a fish is predicted to leave H. crispa and begin searching for E. quadricolor? iii) Under what conditions is a fish predicted to attempt to settle in an anemone that already has other fish? That is, under what circumstances is social queuing (sensu Kokko and Johnstone (1999) or Ragsdale (1999)) advantageous?

For post-settlement: i) Under what circumstances is the dominant female predicted to allow another fish to settle? Buston (2003 abc) suggests that it is the individual of rank $n$ who determines if an individual of rank $n + 1$ is allowed to join; does SDLHT lead to a prediction similar to this? ii) What is the nature of the social control of growth and mortality? iii) Under what circumstances is a host not worth defending at all (e.g.,
because it is too small)? iv) When a host is attacked, under what circumstances is it predicted that both fish, the larger fish, or the smaller fish will leave to defend the host? v) How does geographic variation in predation pressure affect the behavior of the guest clownfish?

Complex Life Histories Ephemeral Habitats

In this section, I use “complex life histories” to denote life cycles in which different life history stages are physically very different, such as larvae and adults of insects, salamanders and frogs (Eitam et al 2002, Kiflawi et al 2003ab, Blaustein et al 2004, Eitam et al 2005, Segev et al 2009, 2011, Sadeh et al 2009, 2011, 2015, Saward-Arav et al 2016, Alcalay et al 2018a,b), and/or individuals live in quite different habitats, such as the migratory salmonids, which use the entire ecosystem. I use “ephemeral habitats” to denote habitats that periodically disappear (e.g. ponds or streams that dry up), and which may be particularly sensitive changing environments.

Segev et al (2011) developed and tested a state-dependent oviposition habitat selection model that predicted that females of the endangered fire salamander *Salamandra infraimmaculata* split their larval load temporally during the rainy season across multiple pools and adjust the number of larvae deposited according to pool quality. These strategies are predicted to reduce the negative effects of larval density-dependence and limited habitat duration. We tested the predictions of the model in an outdoor experiment and female larva-position was consistent with predictions. Most importantly, when allowed to choose deposition sites among pools of different depths, gravid females spread their larvae both spatially and temporally and deposited more larvae into deeper pools.

Ephemeral habitats can be characterized in many ways: by size (which affects the time at dessication), food resources, density of potential predators (both intraspecific
and interspecific), and density of competitors. In most cases, ephemeral habitats are components of a meta-habitat (such as a collection of temporary pools, with either dry land or small runs of water between them). This gives a meta-population structure to species living in the ephemeral habitats. It seems “obvious” that ephemeral habitats will lead to an accelerated life history of their occupants, but sometimes things that seem obvious really are not. And even if true, it is not clear from verbal arguments how this will happen and what characteristics of uncertainty are most important in determining the path of the life history. To answer those kinds of questions, models are needed. It is beyond the scope of a small section like this to review all of the organisms with complex life histories that use ephemeral habitats, since they range from insects such as caddisflies, dragonflies, and mosquitoes to amphibians such as frogs and salamanders. There are so many wonderful potential case studies for this topic that I decided to briefly summarize them (Table 1) rather than write about them in more detail.
Table 1 A Few Examples of Potential Case Studies of Organisms with Complex Life Histories in Ephemeral Environments

**Alcalay et al (2018a)** showed that in the presence of predators, larvae of the mosquito *Culex pipiens* metamorphosed earlier, had lower survival but bigger size on emergence, and dispersed further than individuals in pools without predators.

**Anderson et al (2017)** studied how density influenced predation on spotted salamanders *Ambystoma maculatum* by ringed salamanders *Ambystoma annulatum*. They manipulated breeding phenology (Figure 3) in outdoor mesocosms, raising questions about how breeding females to respond to intraspecific and interspecific densities when choosing breeding sites.

**Bar-David et al (2007)** studied the movement distances of adult salamanders *Salamandra inframaculata* on Mt. Carmel; about 10% of the animals were captured at least 400 m from the initial site and in some cases animals moved more than 1 km. This raises questions such as when will a female choose to move rather than stay at the current site or how do the lost time and reduced survival of the mother trade off against a lower quality current habitat for the offspring versus a potentially higher quality habitat elsewhere?

**Beck et al (2017)** studied how poison frogs *Dendrobatidae* spp. gain information about the area and suitable reproductive resources during tadpole transport and subsequent homing.

**Bohenek et al (2017)** studied habitat selection by the mosquito *Culex restuans* while simultaneously manipulating patch size and predator density (fish presence/absence) in naturally colonized experimental landscapes, raising the need for a behavioral model that integrates patch size and quality when predicting species distributions.
Carabio et al (2017) explored the consequences of food quality in the ephemeral patches used by the South American common tree frog *Hypsiboas pulchellus* and found that developmental stage, body size, and gut size were affected by the level of food but that survival was not, raising the question of predicting developmental thresholds.

Catenazzi and Kupferberg (2017) studied local adaptation in tadpoles of the frog *Rana boylii* (Ranidae), a threatened species endemic to rivers of California and Oregon and found local adaptation in larval growth and phenotypically plastic thermoregulatory behavior. Different evolutionary endpoints in different ephemeral habitats is a form of local adaptation. Can we able predict this?

Crump and Houlahan (2017) investigated the consequences of increased predation pressure due to a longer hydroperiod on wood frogs *Lithobates sylvaticus* using translocation experiments, raising questions about when pools previously not acceptable for oviposition might become so.

Frances et al (2017) studied how temperature affected egg development in co-occurring dragonfly species and showed that in *Leucorrhinia intacta* warming temperatures lead to smaller hatchlings with increased growth and mortality rates. They observed significant intraspecific variation in the responses to warming in both egg development time and hatchling size and this variation was correlated with date of oviposition.

Gomez-Mestre et al (2013) investigated how spadefoot toad tadpoles *Pelobates cultripes* accelerated development in response to decreased water levels and found that tadpoles reduced their larval period by an average of 30% in response to reduced water levels; developmental acceleration lead to smaller juveniles with proportionately shorter limbs.

Pintar and Resetarits (2017) studied how the tree frog *Hyla chrysoscelis* responds to desiccation risk and predation risk during oviposition site selection in ponds that varied in water depth and contained predatory larvae of two *Ambystoma* salamander species; they
concluded that adult oviposition site choices simultaneously minimize relative predation risk and desiccation risk.  

Pollard et al (2017) investigated the negative correlation between the distributions of tadpoles of the threatened green and golden bell frog *Litoria aurea* and the introduced mosquitofish *Gambusia holbrooki*. They drained ponds to temporarily remove mosquitofish and found that males preferentially selected fish-free ponds as breeding sites; however, pond draining did not influence female or juvenile abundances.

Rudolf and Rödel (2005) examined the oviposition behavior of the tree-hole breeding frog *Phrynobatrachus guineensis* over the course of the entire breeding season and discovered that sediment depth and maximal water depth were the best predictors of oviposition, and that these predictions carried over into the next season. They also concluded that even with the negative effects on larval growth and the availability of sites without conspecifics, ovipositing individuals were attracted to conspecific offspring because they serve as a cue for low predation risk.

Spieler and Linsenmair (1997) studied the choice of breeding sites by the anuran *Hoplobatrachus occipitalis* in rock pools and concluded that adults can assess the presence, density, and size of tadpoles in pools by chemical cues; to assess the risk of desiccation, frogs have to visit familiar pools repeatedly to monitor the decrease in volume over time and thus gain information about the water-holding capacity, thus requiring information as a state variable.

Stein et al (2017) studied intraspecific and interspecific competition between tadpoles of two anuran species, *Bufotes viridis* (Laurenti, 1768) and *Hyla savignyi* (Audouin, 1829) that co-occur in temporary pools, finding that *H. savignyi* was significantly affected by intraspecific density, but that *B. viridis* showed no intraspecific or interspecific density-dependent effects. However, *B. viridis* time to metamorphosis was negatively correlated with water temperature; survivorship was positively correlated with water temperature.
Such results await a state dependent behavioral and life history model.

Wissinger et al (2004) studied the response of larvae of *Asynarchus nigriculus* to predation and diet, oviposition strategies that include where to oviposit raising questions whether adults use some eggs as future food for other offspring and larval strategies concerning when to metamorphose.

The modification of the canonical equations requires that we link one life history stage to another. For simplicity, let us call the stages adult and offspring.

**The Adult Perspective**

It is clear that adult oviposition/larvaposition behavior is determined by the interaction of food, predator and allospecific and conspecific competitor densities, temperature, and hydroperiod/dessication risk. The challenge is to integrate these in a consistent manner capturing the idea that adult oviposition site selection simultaneously minimizes relative predation risk and desiccation risk and if not maximizing offspring growth, at least lets offspring reach the threshold needed for metamorphosis (Table 1).

This raises questions about adult reproductive strategies that include where to lay eggs or deposit larvae and whether to use some eggs as future food for other offspring. We are also forced to ask questions such as i) When is a female predicted to choose to move rather than stay at the current site? ii) How do the lost time (remember this is an ephemeral habitat) and reduced survival of the mother trade off against a lower quality current habitat for the offspring versus a potentially higher quality habitat elsewhere? iii) What role does information about the distribution of sites play in adult behavior?

**The Offspring Perspective**

When larvae can allocate resources to grow in different ways, we may ask how the density of food, competitors, and predators shapes the larval morphology. When individuals accelerate their development, thus leading to internal physiological damage we require a
state variable representing internal damage (Mangel 2003, Mangel and Munch 2005, Lee et al 2011).

Rather than assuming a fixed threshold for metamorphosis, we would like it to emerge from a firm theoretical foundation – so that we can understand how the threshold responds to the environment. Similarly, we would like a way to predict the level of local adaptation – the end points of the evolutionary trajectory – particularly when we think about translocation as a tool for conservation.

Foraminifera Behavior, the Paleotemperature Equation, and Understanding the Paleorecord

This potential case study is motivated by a talk that I heard from Jennifer Fehrenbacher, then at UC Davis and now at Oregon State in which she mentioned, somewhat incidental to the main point of the talk, that foraminifera behave in the water column, that is they are not simply passive drifters. Richerson et al (2015) make a similar point about southern ocean krill. This illustrates the importance of going to a wide variety of talks – and listening carefully – because you never know where the next good idea is going to come from. Richard Feynman was famous for being found at kinds of talks at Cal Tech.

Foraminifera are free-living, amoeboid protozoa found in the marine environment. They are single-celled eukaryotes and most of them secrete a complicated calcium carbonate skeleton called the test that contains the bulk of the cell (the foraminifera also have extra-skeletal pseudopods that emerge from the cell body). If no test is present, foraminifera will have a network of pseudopods and no definite shape (e.g. Figure 3a).

Because the test grows according to a two step procedure (accretion of chambers followed by the formation of an enveloping crust of calcium carbonate, it is possible to study the ontogeny of individual foraminifera (Schweitzer and Lohmann 1991). Foraminifera are
MARSZALEK

Iridia, however without an test or f w e l l o w i n t h a t a c o n c i e v a b l e s t h e m o t i o F O R A M I N I F E foraminifera. Th o u g h di l l 428 425 l n s o m a t h y d g o w a t e y R e x t e n d e d g r a d u a l l S o m a t o n g r a n o r e t i c u l o s i t y f r o n u n f a v o r a b l.

a n i m a l n a t u r e x p l a n a t i o n s t a t i f f i o r a m i n i f e r as ballast to keep the organism in place). From Marszalek et al (1969). b) Examples of the calcite tests of foraminifera with some benthic species shown on the left and some planktonic species shown on the right (from Pearson (2012)). These are from exceptionally well-preserved Paleogene sediments of Tanzania (33-45 Ma). Diameters are from about 0.20-0.75 mm.

generally classified as benthic and planktonic. The test is divided into a series of chambers, the number of which increases as the animals grows. Two very good introductions to the foraminifera are the book by Boudagher-Fadel (2015) and the review article by Pearson (2012). In Figure 3b, I show the tests of a wide variety of foraminifera.

**The Function of the Test** Marszalek et al (1969) considered the possible functions of the test to be i) to protect the foraminifer against predation; ii) to provide shelter against unfavorable physical or chemical conditions; iii) to serve as a receptacle for excreted matter; iv) to serve as a host for algal symbionts; v) to aid in the reproductive process; and vi) to control the bouyancy of the organism. They concluded that 1) the earliest tests were sand-like material that organisms used to counteract the bouyancy of the protoplasm, 2) later tests consist of a collection of chambers connected by narrow openings that allow the organism to respond to unfavorable changes in environmental chemistry, and 3) some tests may be adapted for symbiotic algae (e.g., *Elphidium*). They
considered the test as anti-predator structure to be not fully understood.

Marszalek (1982) returned to the idea that the test is used to control vertical movement and broadly investigated shells and skeletons of radiolaria, acantharia and foraminifera. He concluded that one of the their major functions is to provide a mechanism for regulating buoyancy. He gave an example of *Globorotali mendarii* that could move about 60 m/h through relatively small changes in the density of the protoplast. He provided additional examples of the ability of planktonic foraminifera to control their depth in the water column and of species that may undergo daily vertical migrations, rising to the surface at darkness and descending to greater depths during the day (similar to krill). Chang et al (1974) derived a von Bertalanffy-like formula relating chamber number and chamber size in *Ammonia beccarii*.

After death, foraminifera that settle in sediments are used to study evolutionary change (e.g. Pearson and Coxall 2014). Furthermore, the planktonic foraminifera found in sediments are very useful for petroleum exploration because they are easy to extract and allow biostratigraphic dating (Boudagher-Fadel 2015). The isotopic (O\(^{18}/O^{16}\)) and chemical (Mg/Ca) structure of tests can be used to inform environmental conditions during test growth, the temperature of the water column, and the nature of photosynthetic symbionts (e.g Lea et al 2000, Martin et al 2002).

**Foraminiferan Biology** Foraminifera are both prey and predators. Because they are so small, the range of potential predators in the marine environment is vast (Buzas and Carle 1979, Sliter 1971); McGurk’s (1986) allometric study of mortality suggests that in planktonic species the daily mortality of individuals with dry mass \(w_d\) is \(M(w_d) = 2.2 \cdot 10^{-4} w_d^{-0.85}\); but there is also inter-specific predation (e.g. Hallock and Talge 1994, Nielsen et al 2002) or bryozoans (Skinner 2014).

Many foraminifera have algal symbionts that are host specific and which affect where the individual is found in the water column (e.g Leutenegger 1984); other foraminifera
may tend and harvest bacteria (Langer and Gehring 1993).

Foraminifera have life cycles that consist of an alternation of a sexually reproducing generation (gamont) and an asexually reproducing generation (agamont) (Grell 1979). Reproduction is through gametes released into the water column and may be synchronized to lunar, semi-lunar, or diurnal cycles, depending upon the species; food availability also plays a role in the reproductive activity of some species (Boudagher-Fadel 2015). Furthermore, the foraminifera show dormancy, induced either by internal physiological factors (diapause, as in insects) or by environmental factors (quiescence) (Ross and Hallock 2016); we should expect that the interaction of environmental and physiological factors determines dormancy. The foraminifera can exhibit complex population dynamics. For example, Erksian and Lipps (1987) found that rapid growth, reproduction and an alternation of generations were related to abundant food supply due to seasonal upwelling, increased wave action, and sediment transport.

**The Paleotemperature Equation**  In 1947, Harold Urey proposed that oxygen isotope distributions in the carbon dioxide-water-calcium carbonate system could be used to measure past temperatures (Urey 1947, Urey et al 1951, Epstein et al 1953).

Two ideas underlie the paleotemperature equation. The first is that calcium carbonate in the ocean will be in two forms, CaC\textsuperscript{16}O\textsubscript{3} and CaCO\textsubscript{2}\textsuperscript{18}O; the chemical equilibrium of isotopes in dissolved calcium carbonate ions depends upon temperature (see Eqns 4.9-4.11 in Emerson and Hedges (2008)). When the carbonate ion is used to make a shell, the oxygen isotope it carries is permanently recorded in the shell. In a series of crucial papers published in the 1950s, Ceasare Emiliani\(^1\) and colleagues developed this idea and demonstrated that oxygen isotopic composition (\(\delta^{18}O\)) of planktonic foraminifera is a useful tool for understanding Cenozoic environmental conditions (Emiliani 1954, 1955,

\(^1\)See Hay and Zakevich (1999) for a brief biography of Emiliani, whom they describe as the founder of paleoceanography.
1958, 1966; Berger and Gardner, 1975, Shaackleton 1967, Shackleton and Opdyke 1973, Pearson 2012). Emiliani argued that an increase in the ratio $\delta^{18}O/\delta^{16}O$ implies a lower temperature in the surface waters in which the planktonic foraminifera were growing.

For example, one can grow a shell-making organism in the laboratory at known temperature and known $^{18}O$. If $\delta_{\text{CaCO}_3}$ and $\delta_{\text{water}}$ denote the isotope ratios in parts per mil (denoted by o/oo) then one such equation is (Emerson and Hedges 2008)

$$T(\delta_{\text{CaCO}_3}, \delta_{\text{water}}) = 17.04 - 4.34(\delta_{\text{CaCO}_3} - \delta_{\text{water}}) + 0.16(\delta_{\text{CaCO}_3} - \delta_{\text{water}})^2$$  \hspace{1cm} (11)

In using this equation, one assumes that the organisms accreted calcium carbonate $\text{CaCO}_3$ in isotopic equilibrium with the ambient water (DuPlessy et al 1981) or that any non-equilibrium effect is known (Emerson and Hedges 2008), that the isotopic composition of seawater in the past is the same as today or can be estimated (Shackleton 1967, Lea et al 2002, Emerson and Hedges 2008), that isotopic composition of shells is independent of shell size (Billups and Spero 1995), that movement is limited after settling to the bottom (Kontrovitz et al 1979), and that the dissolution of shells once they settle is slow (cf Regenberg and Beil 2016). Grossman (2012) and Pearson (2012) provide very useful reviews of the history and nuances of use of oxygen isotopes in paleoceanography.

The second key idea is that when water goes from the ocean to continental ice sheets, the ice is depleted in $\delta^{18}O$ and the ocean enriched (to about 30 o/oo (Emerson and Hedges 2008, especially Chapter 7)). That is, the value of $\delta^{18}O$ in a shell is primarily determined by ambient temperature and the isotopic composition of seawater, which is affected by continental ice-volume and variations in regional evaporation and precipitation.

Bemis et al (1998) give 15 versions of Eqn 11 with differing coefficients and then offer their own versions – which are simplified in that they only include a linear term but in which the coefficients are now functions of the environment (e.g. ambient temperature,
light, and carbonate ion) and the size of the foraminifer. These linear equations are more accurate than their quadratic predecessors. But all told, Eqn 11 and its slight variants continue to be used very effectively (e.g Collins et al 2016).

In summary, foraminiferal tests are determined by environmental conditions (e.g. Cifelli 1971, Hecht and Savin 1972, Hecht 1976). Thus, assuming that species adjust their depth in order to achieve the proper temperature and water density, by measuring the levels of $\delta^{18}O$ in shells, it is possible to determine the temperatures of the environment of those foraminifera.

**Behavioral Ecology of Foraminifera in the Laboratory** The distribution of individuals in the water column is determined by environmental factors such as temperature, light intensity, food availability, and predators; this distribution can be used as a proxy for the reconstruction of paleoenvironments. Within a species, morphotype of individuals may determine where they are found in the water column. Foraminifera add calcite (thus moving lower in the water column) when they are ready to reproduce.

Especially in the last 30 years (although foraminifera had been studied in the laboratory for a long time, e.g. Jepps (1942)), it has become clear that it is possible to study foraminifera in the laboratory, with experiments concerning:

- symbionts in isolation (Lee et al 1980);
- test shape in relation to light and water motion (Hallock et al 1986);
- factors that determine the alteration of asexual and sexual generations (Harney et al 1998);
• quiesence in juveniles, sub-adults, and adults in response to environmental stress
  (Ross and Hallock 2016);
• feeding behavior (Spindler et al 1984), reproduction (Stouff et al 1999, Barras et al
  2009), and movement (Weinberg 1991, Seuront and Bouchet 2015).

A Role for SDLHT

It is time to add behavioral ecology to the paleotemperature equation, particularly to ask how we can update the paleotemperature equation to account for foraminifera behavior. A suite of questions circles around the function of the test, movement in the water column and the isotope ratio, all with the goal of improving our ability to interpret paloenvironments. These include i) How do pH, salinity, temperature, light, and food determine the movement of foraminifera in the water column? Can we expand upon Marszalek (1982) to understand and predict how and when foraminifera will move up or down in the water column and what is the role of empty chambers? Once we have a behavioral theory in hand, it can be tested in laboratory conditions. ii) How does such a behavioral theory characterize the growth of shells (cf Wang and Lutze 1986), including overall size, shape of chamber structures (lobes vs a smooth periphery) and their dependence on environmental conditions. iii) Will such a theory allow us to assess the “vital” contribution to the isotope structure of shells (e.g. Emerson and Hedges 2008)? iv) How will foraminifera respond to ocean acidification – e.g. will they change their location in the water column to avoid dissolution of their shells (Feely et al 2016)?

Life History Questions Relevant to the Management of Pacific Halibut Fisheries

The Pacific halibut *Hippoglossus stenolepis* (Figure 4a) is distributed across the North Pacific from northern California to Hokkaido, Japan; genetic studies indicate that the
stocks on the eastern and western sides of the Pacific are different but no genetic differences are found from Alaska to California. In the eastern Pacific, a commercial longline fishery for halibut began in the mid-1800s and followed the common pattern of fishing effort and catches rising rapidly, leveling off, and ultimately declining, even though fishing effort continued to increase (Thompson and Freeman 1930; Clark and Hare 2006). At the request of the industry, Canada and the United States signed a bilateral convention in 1923, creating the International Fisheries Commission (which became the International Pacific Halibut Commission [the IPHC] in 1953). The purpose of the Commission is to investigate the life history of the Pacific halibut and to recommend actions necessary for the preservation and development of the resource.

The first Director of the Commission was W. F. Thompson, one of the great fishery scientists of the 20th century. He embarked on a series of studies that remain gems of scientific thinking and writing (Thompson and Herrington 1930, Thompson and Bell 1934, Thompson and van Cleve 1936; all of which are available at the website of the IPHC: http://www.iphc.int/library/scirep.html).

Following Thompson’s recommendations, the two governments set up regulatory areas (Figure 4b; these are political creations, not biological regions) in which catch limits and other regulations apply. A new convention was signed in 1930, and quota management began in 1932. Since then, the Commission has managed the fishery using the response of catch per effort to removals and cognizant of how regulations on catch may affect the economics of the fleets. (For a simple example that will bring this issue to life, see Exercise 6.6, pg 218, in Mangel (2006)). This treaty and its modifications (McCaughran and Hoag 1992) has been very successful in maintaining both biomass and catch over 100 years (Figure 5c).

Southward (1968) described the history of the fishery as i) A period of expanding exploitation from the mid 1880s until around 1910, at which point it was clear that the
Figure 4: a) A Pacific halibut *Hippoglossus stenolepis* being sampled during an IPHC survey. b) The regulatory areas used for the management of the halibut fishery. c) A reconstruction of spawning biomass from the late 19th century until 2013, presented at the Interim Meeting of the IPHC in 2013. d) The observed rends in female size at age, also presented at the Interim Meeting in 2013.
previously large standing biomass of halibut had been reduced. ii) A period from the early 1930s to the mid 1950s in which efforts were made to manage the fishery and allow the stock to recover. iii) The period from the mid 1950s to 1968 (when Southward was writing), in which the management objective was to achieve Maximum Sustainable Yield by adjustments of fishery regulations. Models have been developed and applied by the IPHC for nearly 95 years (Clark 2003).

Halibut have an annual spawning cycle associated with spawning migrations from summer feeding grounds to winter spawning grounds and spawning is evidenced by sudden ascents of 100-200 m by fish (Loher and Seitz 2008). The eggs, larvae, and post-larvae then drift for about six months before settling to the bottom and metamorphosing into the well-known flatfish form. The best current understanding is that in general the Western Gulf of Alaska and Bering Sea are nursery grounds and that juvenile fish migrate eastward. Until about age 6, females and males grow at the same rate but after that females grow faster and reach substantially larger sizes. Individual growth rates have varied greatly over the the last century. Males reach sexual maturity in their first decade of life, and females at an average age of about 11 years (Clark and Hare 2006).

By asking focussed questions about Pacific halibut, one is almost guaranteed to work in Pasteur’s Quadrant (Stokes 1997); the data – going back to Thompson’s original reports – are amazing and there is much interesting work to be done. Here are three questions whose answers I think will be particularly useful.

**What Has Caused Size at Age to Change From the 1970s Until Now?**

At their Annual Meeting, the Commissioners set separate catch limits are set for each of the regulatory areas shown in Figure 5b. Doing so requires an assessment of the state of the stock, which is often summarized in terms of the spawning biomass (i.e. reproductively active females) or exploitable biomass (biomass of fish that are above a given size threshold). What is incontrovertible from the analyses is that the measure of
halibut biomass increased through the 1970s, peaked in the late 1980s and has continued to decline since then (although in the 2010s it seems to be stabilizing).

The proximate mechanism for this change in biomass is known: halibut size at age has declined (in some cases quite dramatically – Figure 4d – the average weight of a 20-year-old female Pacific Halibut declined from 55 kg in 1988 to 20 kg in 2014 (Sullivan 2016) ) since the biomass peaked. But why this has happened is essentially unknown. Loher (2012) and Sullivan (2016) provide excellent entries into the literature. Declining size at age could be due to i) declining growth rates due to either biotic (e.g. intra- or interspecific competition for food, abundance of food) or abiotic (e.g. changing temperature) factors; ii) size dependent mortality (both natural and anthropogenic); iii) fisheries induced evolution; and/or iv) energy spent obtaining food. We should not expect that a single factor has caused the change in size at age, but rather should ask how to assess the relative contributions of each of the factors. Loher (2012) describes research approaches to each of these possible mechanisms. There is great opportunity for a model based in SDLHT that integrates bioenergetics and environmental factors in a unified manner.

**When Do We Predict Skipped Spawning?** Pop-up Archival Tags (PATs) have already provided evidence that not all mature fish spawn in each year (it is difficult to estimate exactly how many, but 10% is a good conservative estimate and 25% is a possible upper estimate (Loher and Seitz 2008, Loher 2011)). Jørgensen and Fiksen (2006) developed a SDLHT for skipped spawning in code *Gadus morhua* (also see Jørgensen et al (2008)) and I expect that many of their ideas are transferrable for predicting skipped spawning in halibut.

**What is the Behavioral Ecology of Halibut Movement?** Tags also give us an idea of the range of horizontal movements of halibut (Loher and Seitz 2006, Loher 2008). Loher and Seitz (2006) concluded that there was no single, stereotypical behavior for either seasonal or vertical migration. That said, a variety of behavioral patterns could be
inferred from the data, including long-distance migration (rather than remaining locally),
migration to the deeper waters of the shelf (rather than remaining shallow) for winter
residence, and the individual level of vertical activity.

Loher and Seitz focussed on the Gulf of Alaska, but when the other tagging studies
are included and summarized, we can state the situation as follows (Ray Webster and T.
Loher, personal communication): i) There is a strong pattern of west to east and north
to south migration, which includes apparent high movement rates of small halibut from
the Bering Sea to Gulf of Alaska. ii) Regulatory area 2B is a net importer of halibut and
area 4A is a net exporter. iii) Movement rates are generally greater for young fish. iv)
There appears to be basin-specific stock structure in the Aleutians, Bering Sea, and Gulf
of Alaska. v) Seasonal dispersal among areas is common. vi) Large (100+cm) halibut
display an apparently strong tendency toward summer site fidelity and/or active homing.
What we need now is a theory of movement that will help organize this information and
make new predictions that can be tested in the field.

Insect Parasitoids, Biological Control, and Darwin’s Finches

Because parasitoids are used in biological control and many other insects, such as the
tephritid fruit flies, have parasitoid-like life histories, almost any question that one asks
can be framed as in Pasteur’s Quadrant.

Are Parasitoid More Limited by Time or Egg Complement, What Does
that Mean for Population Dynamics, and the Analogy to Pollen Limitation

Analysis of whether parasitoids are more limited by time or egg complement has already
received attention (Heimpel et al 1996, 1998; Heimpel and Rosenheim1998, Mangel and
tion can be posed in a number of different ways. For example, we may ask if fitness
increases more if an individual had one more egg to lay or one more period to search for hosts (Mangel 2006)? Alternatively, we may ask under what conditions is egg limitation a cause for reproductive senescence in the wild (e.g. Lemaître and Gaillard 2017)?

Whether parasitoids are egg or time limited tells us something about their expectations of the environment, since one of the problems that parasitoids face is to match their egg complement with the expected reproductive opportunities as an adult (Mangel and Heimpel 1998). Egg limitation of parasitoids is very real. For example, Segoli and Rosenheim (2013abc) found that in two species of Anagrus, a parasitoid of leaf-hoppers, more than 10% of individuals ran out of eggs before they died. Similarly, whether parasitoids are egg or time limited has important evolutionary consequences (Phillips and Kean 2017), with additional consequences for the dynamics of parasitoids and hosts since egg limitation destabilizes host-parasitoid population dynamics (e.g. Okuyama 2017). Whether parasitoids are egg or time limited is basically a question of timing of encounters with hosts.

With slight modification, these become questions about limitation (Rosenheim et al 2014, 2016ab, Schreiber et al 2015). Plants face the challenge of seed production being limited by pollen delivery. Since both seeds and pollen require the use of resources by the plant, there is a trade-off between the costs of seed production and the costs of pollination. Rosenheim et al (2014) assessed the risk of pollen limitation in 80 plant species and found that in 18 of them, pre-pollination costs were about the same or greater than post-pollination costs and that in these species pollen limitation could be very real and intense. Pollination limitation can affect the evolution of the plant’s mating system (Runquist et al 2017), and with implications for productivity of plants.

**Rapid Evolution and Transgenerational Plasticity in the Transition from Natural to Agricultural Settings** It is reasonable to assume that the availability of hosts in agricultural settings is higher than the availability of hosts in natural settings,
so that individuals will need less time to find hosts and consequently can lay more eggs. Thus, we anticipate that the question of allocation to lipid or eggs is resolved with more eggs in the agricultural setting than the natural setting. However conundrums remain (Segoli et al 2018).

We can also ask if changes in parasitoid allocation to lipid for living life and eggs is a case of rapid evolution (e.g. Hendry 2017) or transgenerational plasticity? Andreazza and Rosenheim (2015) could not detect transgenerational plasticity in an Anagrus system.

The parasitoid wasp Anagrus daanei (Segoli and Rosenheim 2013ab) attacks eggs of leafhoppers of the genus Erythroneura, which feed on grapes Vitis spp. and are major pests of commercial vineyards. In the natural setting, the wasp attacks herbivores of wild grapes Vitis californica that grow in riparian habitats. Segoli and Rosenheim sampled leafhoppers and parasitoids from eight vineyards and eight riparian habitats in central California and found that leafhopper density was higher at vineyards than in riparian habitats, but leafhopper egg volume and parasitoid body size did not differ among these habitat types. Parasitoids from vineyards had higher egg loads than parasitoids from wild grapes, and fecundity was positively related to host density across field sites. Furthermore, in any single population of parasitoids collected from a vineyard, parasitoid egg load was negatively correlated with longevity.

In addition to lipids, carbohydrates are important for parasitoids (e.g. Segoli and Rosenheim 2013bc) and additional questions arise concerning whether a parasitoid at the current time is predicted to search for a host or a food source (see Chapter 4 in Clark and Mangel (2000)). Body size also matters: Segoli and Rosenheim (2015) suggest that larger parasitoids have higher reproductive success not because of egg complement (in Anagrus sophiae, which is a parasitoid of plant-hoppers in salt marshes, only one of about 200 individuals exhausted her eggs before dying) but because of increased longevity and/or foraging efficiency.
**Nest Parasites of Darwin’s Finches** A parasitic fly, *Philornis downsi*, was first recorded in the Galapágos islands in 1964, when it invaded from mainland Ecuador (Boulton and Heimpel 2017) and is now a major source of mortality in Darwin’s finches. Adult females lay their eggs in bird nests; first instar larvae feed in the nasal cavities of nestlings and second and third instar larvae feed on nestlings externally by puncturing the skin and ingesting blood and other fluids. The result of this parasitism is delayed growth, anemia, and death of nestlings (Koop et al 2011). In some cases complete nest failure occurs and depending upon bird species and year, between 2/3 and all nests are infested by the parasite, with about 40 pupae per nest (Fessl et al 2006). For comparison, in mainland Ecuador around 1/3 of nests are infested and the parasite load is about 12-13 per nest (Bulgarella et al. 2015).

This nest parasite makes extinction of some species of Darwin’s finches a real possibility, especially the Mangrove Finch (*Camarhynchus heliobates* (Fessl et al 2010) and Medium Tree Finch (*Camarhynchus pauper* Ridgway) (O’Connor et al. 2010). Currently, Mangrove Finches are protected from exposure to the parasite by removing eggs from nests in the field and rearing in a secure facility and then releasing fledglings into the wild (this is analogous to hatchery rearing of endangered salmonids).

A variety of control measures have been tried (Boulton and Heimpel 2017). These include treating the nests with insecticides (mainly permethrin, which the birds can deal with) and release of sterile male flies (Plant and Mangel 1987 for a review). However, there are five parasitoid species that attack pupae of *Philornis* in mainland Ecuador (and a parasitoid attacks a congener of the nest parasite in Tobago) (Bulgarella et al 2017). As of this writing, none have been released in the Galapágos, but they are being considered. A variety of questions need to be addressed, including which of these parasitoids is specific to *Philornis*, which stage of the fly is the target, what kind of density dependence acts on the flies, what (if any) non-target species would be at risk from release of a parasitoid,
composite. Default screen
Color profile: Generic CMYK printer profile

bers given in the literature, about 500 eggs·female
may vary from year to year as well as the number of successive cycles of egg production during one season. The onset and duration of the reproductive season previtellogenesis (SDS 3 and SDS 4) for adult female krill of all sizes and ages. Later on, successive cycles of vitellogenesis and mat -

tive period and a winter rest for adult female krill from age groups 2+, 3+ etc. The onset of the reproductive season is marked by


significantly different for the three populations: 650 ± 130


tained a larger average body size. Despite the differences in


sample and 1500 eggs for the Clyde krill, which also at


among the three populations studied. The largest spawn re


should reduce the bias. Counts of eggs released during the


estimate the actual size of the egg batch and cannot be taken


egg batch to a few residual eggs, the number of eggs re


spawning rhythm, the total number of eggs released per fe-


get, obtained by adding the partial spawns, was not


estimate fecundity. Adding the partial spawns ob-


as an estimate of fecundity. Adding the partial spawns ob-


egg batch


eggs·female


(a)

(b)

Figure 5: a) The seasonal pattern of ovarian development in E. superba from Cuzin-Roudy (2000). b) A similar seasonal cycle of sexual development and lipid content of male and female Thysanoessa macrura from Wallis et al (2017). In both cases, female sexual development is conceptualized by a succession of Sexual Development Stages, with the reproductive season beginning with the pre-vitellogenic stage. For both species, environmental variation will affect the duration of the reproductive season and the number of egg cycles in a single reproductive season.

and will suppression of the parasite via biological control be sufficient for recovery of finch populations? These are great opportunities in Pasteur’s Quadrant.

Krill Reproductive Cycles in Changing Environments

There are many interesting questions about how to set the harvest levels of krill (e.g. Watters et al 2013), how krill harvest will affect predators (Mangel 1994a, Mangel and Switzer 1998; Alonzo and Mangel 2001, 2002; Alonzo et al. 2003ab) and effects of changing environments including increasing water temperature, changing ice extent, and effects of changing UV due to the opening and closing of the ozone hole on the availability of krill to predators (Cresswell et al 2008, 2009, 2012; Mangel et al 2010; Wiedenmann et al 2008, 2009, 2011). Here are two others.

Cuzin-Roudy (2000, 2014) developed a conceptual framework for the seasonal pattern
of egg production in Antarctic krill *Euphausia superba* (Figure 5a). In order to reproduce in the late spring and summer, individuals must prepare themselves, through the accumulation of resources in the late summer and fall and through the winter. If resources are insufficient, individuals may skip a reproductive event. Precursors to eggs are developed in June-September (oogenesis); egg production takes place in November. However, if resources are insufficient in November-March then the potential eggs are resorbed by the female krill (oosorption) and the krill returns to a juvenile-like status. Thus *E. superba* must prepare for late spring and summer reproduction through the late fall, winter, and early spring in order to be ready for reproduction in the spring. It is the accumulation of resources during the winter that will determine reproduction the following year. Wallis et al. (2017) developed a similar conceptual framework (Figure 5b) for the euphausiid *Thysanoessa macrura* which is found over a wider range of the southern ocean than *E. superba* and may increase as a food source for predators under a changing environment (Richerson et al. 2018).

Developing quantitative versions of these conceptual frameworks, by combining proximate and ultimate considerations (Mangel 1994bc, Thorpe et al. 1998, Mangel and Satterthwaite 2008) in krill life histories, will contribute to predicting the response of krill reproduction to changing environmental conditions. Such models will be tools that allow one to predict the timing and level of krill recruitment as a function of environmental variables in the previous winter and early spring, particularly sea-ice, water temperature, and abundance of algae, all of which are subject to environmental change. Having such tools will be important as CCAMLR sets the catches in the Small Scale Management Units and will provide improved predictions of recruitment for management models such as KPFM (Watters et al. 2013).
Salmon in Hatcheries and Steelhead in the Salish Sea and in California

Salmonids provide a wealth of questions that they provide in Pasteur’s Quadrant. Here are some exciting ones.

**Domestication in Hatcheries and the Interactions of Wild and Hatchery Fish**

Salmon are raised in hatcheries to supplement wild fish populations (e.g. Naish et al 2007) and in open ocean aquaculture facilities even in places where they are invasive species (e.g. Atlantic salmon *Salmo salar* in Australia) (e.g. Lorenzen et al 2012, Tufto 2017).

The hatchery/environment differs considerably from the natural environment in that food is more abundant and more easily obtained and rate of predation is lower. These differences will change important evolutionary endpoints such as the size at which fish develop smolt characteristics (or the loss of smolt transformation entirely) and the size and time at which fish mature (and thus begin converting somatic reserves to eggs; see McLean et al (2005) for an example in steelhead trout). SDLHT is a natural tool for assessing these changes and how different the hatchery fish are from wild fish with which they might interbreed (e.g. Pacific salmon) or what the ecological effects of escaped aquacultured fish (e.g. Atlantic salmon in the Pacific or Australia) will be. SDLHT can be used to investigate the potential of moving the evolutionary endpoints through hatchery practice to lessen the likelihood of interbreeding with natural stocks (Seamons et al 2012).

In a an email conversation in September 2017, Tom Quinn (see Quinn 2005, 2018) noted that although there is considerable research on the domestication process, it may be more important to ask whether a hatchery run could survive on their own long enough to “de-domesticate” and thus function like wild fish. That is, in nature could they evolve
faster than the reduction in realized reproductive success of hatchery fish? Tom wrote
to me “I think of the first issue as ‘White Fang’ - wild becomes domesticated, and the
second as ‘Call of the Wild’ as the domestic becomes wild. I would dearly love to work
on this or help someone work on it”. Maybe that can be you.

**A Naturally Paired Experiment in the Salish Sea** Doctor et al (2014) studied
phenotypic plasticity of growth-mediated life history traits between and within two de-
pressed populations of steelhead from Hood Canal, Washington (Figure 6a). They used
a common garden experiment to explore the role of temperature and local adaptation in
steelhead smolt metamorphosis and maturity at age 1. What makes this work particularly
noteworthy is the choice of rivers: The Duckbush River originates in the Olympic Moun-
tains and flows into the western side of Hood Canal and is fed from rain and seasonal
snow melt. The Dewatto River flows at low elevation into the eastern side of Hood Canal
and is primarily fed by rainwater and springs.

One of the great concerns about changing environments is that the anadromous life
style of salmonids will be lost, particularly at the edge of the (Bond et al 2012, 2015,
Hayes et al 2016). SDLHT well-suited for investigating this question (e.g. Beakes et al

Evidence suggests that early marine survival of smolts is one of the key determinants
of the decline of steelhead trout in the Pacific Northwest (Kendall et al 2017), but there
is also contradictory evidence about survival in the Salish Sea being driven by inland
events (Moore and Berejikian 2017). In the California Current further south, it appears
that prey switching by predators (e.g. between salmon smolts and juvenile rockfish) is an
important natural determinant of smolt survival (Wells et al 2017).

In California, salmonids live in streams are often nearly ephemeral habitats, so that
survival mechanisms in those habitats (e.g. Hwan et al 2018) and evolutionary endpoints
Figure 6:  a) The location and elevation of the Dewatto and Duckabush rivers in the Hood Canal region of Washington State, studied by Doctor et al (2014) in a common garden experiment on the expression of steelhead life history traits.  b) The mean (plus/minus 1 standard deviation) of monthly water temperatures in the two rivers, over a 15 year period.
in them are likely to be quite different than elsewhere. For example, in California summer is a period of little or no growth in many streams while it is a period of rapid growth further north, and winter is a period of good growth in California but slow or no growth further north. Here is an opportunity for a SDLHT model.

**Snook in the Gulf of Mexico**

The common snook *Centropomus undecimalis* (henceforth snook) is is a favorite for sport fishing (now catch-and-release), but also has had a history of commercial harvest (1918-1957), so that years of research have gone into understanding their life history, biology, and ecology; this research is summarized in stock assessments (e.g. Muller et al 2015). Snook are also a target for stock enhancement by releasing juvenile fish into estuarine creeks (Brennan et al 2008) and provide a test case for the responsible approach to marine stock enhancement (Lorenzen et al 2010, Lorenzen et al 2013).

Snook in Florida is a tropical fish at the northern edge of its range, but there is an aggressive poleward range expansion of snook in Florida, which has created an emerging recreational fishery in newly colonized areas. In the midst of their range, snook can thrive in temperatures of the order of 30° C (Barón-Aguilar et al 2013). To my knowledge, the TPC for snook has never been measured but the lower lethal temperature is about 12-14° C (Shafland and Foote 1983, Howells et al 1990).
Responsible Approach to Marine Stock Enhancement (Lorenzen et al 2010)

Stage I: Initial appraisal and goal setting

1. Understand the role of enhancement within the fishery system.

2. Engage stakeholders and develop a rigorous and accountable decision making process.

3. Quantitatively assess contributions of enhancement to fisheries management goals.

4. Prioritize and select target species and stocks for enhancement.

5. Assess economic and social benefits and costs of enhancement.

Stage II: Research and technology development including pilot studies

1. Define enhancement system designs suitable for the fishery and management objectives.

2. Develop appropriate aquaculture systems and rearing practices.

3. Use genetic resource management to maximize effectiveness of enhancement and avoid deleterious effects on wild populations.

4. Use disease and health management.

5. Ensure that released hatchery fish can be identified.

Figure 7: Snook in Florida. a) A juvenile snook caught on the Alafia River. b) Snook on Texas Reef (located off Martine County on the Atlantic coast). Photos from FL Fish and Wildlife Conservation Commission, Fish and Wildlife Research Institute (FL FWC/FWRI) via Alexis Trotter. c) The study system of Jennifer Rehage, Ross Boucet and colleagues (e.g. Boucet et al. 2016) in South Florida. The study sites are indicated by solid circles, while solid squares denote hydrological stations used to examine drought severity. The insert shows the three fixed transect locations sampled via electrofishing. The shaded area denotes Shark River Slough, located upstream of the study sites and the main freshwater drainage in the southern Everglades. Base map was supplied by USGS using ARC GIS.

**Responsible Approach to Marine Stock Enhancement (continued)**

*Stage III: Operational implementation and adaptive management*

1. Devise effective governance arrangements.

2. Define a fisheries management plan with clear goals, measures of success, and decision rules.

3. Assess and manage ecological impacts.

4. Use adaptive management.

Even though snook are eurythermic, they do experience thermal stress when water temperatures decline in winter months. For example, prolonged cold conditions in January
2010 produced many reports of dead fish and many of the dead fish were snook.

Snook are found in estuaries, adjacent rivers, and in nearshore waters of the tropical and subtropical western Atlantic (Muller et al 2015), so that they are euryhaline as well as eurythermic. They are most abundant on the Atlantic coast of Florida from Cape Canaveral south through the Florida Keys and on the Gulf coast from Cedar Key south to the Dry Tortugas. Snook from the Atlantic and Gulf coasts have different life histories and appear to be genetically distinct and reproductively isolated (Muller et al 2015). For example, snook from the Gulf coast inhabit a single estuary for their entire lives, while most Atlantic Snook stray or emigrate much greater distances. Fish from different coasts also have different von Bertalanffy growth parameters (Muller et al 2015), respectively for the Atlantic and Gulf coasts $L_\infty = 989.3, 947.3$ mm, $k = 0.235, 0.175$ /year, and $a_0 = -0.0976, -1.352$ years (Taylor et al 2000).

Snook eggs and larvae are found in polyhaline and euryhaline waters near estuarine passes or adjacent river mouths and size distributions lead to the conclusions that eggs hatch near the mouths of estuaries and that the larvae remain near the bottom where flood tides transport them into ocean water. Nursery habitat appears to be low-energy, shallow waters such as freshwater tributaries, salt marshes and impoundments, seagrass beds, quiet creeks, canals, and lagoons in riverine, mangrove, and saltmarsh habitats (Muller et al 2015). Snook show an ontogenetic habitat shift: the smallest fish (about 40 mm) tend to occupy coastal wetland ponds and creeks (which are a low-energy environment with sufficiently size prey to accommodate developing mouth gape, and relatively low predation risk). At around 150 mm, snook loose their ability to tolerate low dissolved oxygen and are able to consume a wider variety of prey; they then to the open estuary. Once snook are bigger than about 300 mm, they move out of the juvenile habitat and in open estuarine habitat (Muller et al 2015). Mangroves are the principal habitat for adult snook; because they are euryhaline adult snook can thus be found both in shorelines with high salinity
and freshwater rivers. Thus, snook are very active, moving within the freshwater and estuarine habitat, which affects their vulnerability to climate extremes (Stevens, et al 2016, Boucek et al 2017a). The catadromy (McDowall 1988) of snook provides a pathway for energy transfer from freshwater floodplains to estuarine and marine habitats.

Snook catadromy is best evidenced by open water spawning aggregations of snook (Boucek et al 2017b), which are protandrous hermaphrodites, beginning life and maturing as males, and then becoming mature females. We can characterize the transition from male to female as a function of either fork length \( l \) or age \( a \) and the differences between the Atlantic and Gulf coasts can be seen in the probability of being female \( p_f(l) \) or \( p_f(a) \). For example, for snook on the Atlantic coast (Muller et al 2015)

\[
p_f(l) = \frac{e^{-7.21+0.0094l}}{1 + e^{-2.283+0.307a}}
\]

\[
p_f(a) = \frac{e^{-5.71+0.0094a}}{1 + e^{-1.58+0.307a}}
\]  

and on the Gulf coast

\[
p_f(l) = \frac{e^{-5.71+0.0094l}}{1 + e^{-2.283+0.307a}}
\]

\[
p_f(a) = \frac{e^{-1.58+0.307a}}{1 + e^{-1.58+0.307a}}
\]

Setting the exponents equal to zero, we see that on the Atlantic coast a fish of length of about 770 mm or 7.5 yrs has a 50% chance of being female, while on the Gulf coast a fish of about 610 mm or 5.1 years has a 50% chance of being female. When considering these ages, keep in mind that although the maximum age of snook is unknown, it is likely to be more than 25 years (Muller et al 2015).

Snook spawn in aggregations off the coast and individuals repeatedly move in and out of the spawning aggregations. In Figure 7c, I show the study system of Jennifer Rehage
and Ross Boucet, to give you a sense of the spatial scales involved. Because of their catadromy, snook provide a linkage between coastal rivers and floodplains and estuaries and the marine environment. Disturbances that alter such cross-habitat food web linkages can lead to whole-scale changes to aquatic systems (Boucek et al 2016).

Snook move back and forth between spawning aggregations and feeding sites during the prolonged feeding season (Boucek et al 2017a) and this has implications for the design of Marine Protected Areas (MPAs). We may ask what causes the movement between the spawning aggregation and feeding area, and how that is affected by previous food abundance? In a changing environment, we may expect that climate extremes will be both more extreme and more frequent. In their habitat, snook may experience extreme cold (they are a tropical species at the boundary of their range) and drought (Boucek and Rehage 2014). For example, snook in South Florida experienced a cold front in 2010 and a drought in 2011. These events had profound effects on the invertebrate and fish communities. The cold front virtually eliminated tropical species, including snook; the drought had little direct effect on euryhaline species, but did affect food availability subsequent to the drought. Thus, a state dependent life history model would link the effects of food abundance in one season (e.g. the dry season) with survival and subsequent reproduction. A SDLHT model will also help us to understand the recovery of snook from cold shocks. There is great opportunity here to develop a state dependent version of the model in Roitberg and Mangel (2016). Finally, since snook are stocked as a means of enhancing the population, a state dependent life history model will play an important role in helping determine the consequences of stocking at different stages of the life history.
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