ECOS 630
Biol. Ocean. Processes
Chapter 22
Gallagher home
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VERTICAL MIGRATION

TABLE OF CONTENTS

List of Tables

Assignment

TOPIC

"Why do some macro- and mesozooplankton vertically migrate?"

REQUIRED READINGS

Ohman, M. D., B. W. Frost, and E. B. Cohen. 1983. Reverse diel vertical migration: an escape from invertebrate predators. Science *220:* 1404-1407.

SUPPLEMENTAL

Dagg, M. J., B. W. Frost and J. A. Newton. 1997. Vertical migration and feeding behavior of *Calanus pacificus* females during a phytoplankton bloom in Dabob Bay, U.S. Limnol. Oceanogr. *42*: 974-980. *[During the March phytoplankton bloom copepods had full guts only at night. The majority of copepods remained at depth apparently because there ws sufficient food sinking to them]*

Frost, B. W. 1988. Variability and possible adaptive significance of diel vertical migration in *Calanus pacificus*, a planktonic marine copepod. Bull. Mar. Sci. *43*: 675-694.

Gliwicz, M. Z. 1986. Predation and the evolution of vertical migration in zooplankton. Nature *320*: 746-748.

McLaren, I. A. 1974. Demographic strategy of vertical migration by a marine copepod. Amer. Natur. *108:* 91-102.

Miller, C. B. 2004. Biological Oceanography. Blackwell Science, Malden MA. 402 pp. *[Read pp. 178-185 on diel vertical migration]*

Ohman, M. D. 1990. The demographic benefits of vertical migration by zooplankton. Ecol. Monogr. *60*: 257-281.

Zhou, M., Y. Zhu, and K. S. Tande. 2005. Circulation and behavior of euphausiids in two Norwegian sub-Arctic fjords. Mar. Ecol. Prog. Ser. *300*: 159-178.{?}

Comments

GOALS

I have two goals in assigning **Ohman et al. (1983)**. The first is to learn about vertical migration. The second is to learn about zooplankton demography. Demography is the study of the vital rates of a population, that is, the birth and death rates. None of the ecosystem simulation models that we will be discussing after the midterm include vertical migration, but all include equations describing zooplankton demography (*i.e.*, natality and mortality rates).

COMMENTS ON THE PAPERS

Ohman *et al.* (1983) documents a reverse-diel vertical migration pattern that is the opposite of the conventional diel vertical migration pattern. **Ohman (1990)** documents that this reverse diel migration occurs at only the 185-m deep station in Dabob Bay, WA. At the shallower 55-m station, this same species undergoes a normal diel vertical migration pattern or remains at the surface all the time. The reverse diel migration pattern is the exception that proves the rule. Note that the ‘prove’ in the previous sentence means ‘tests’ the rule. The rule being the predation explanation for the adaptive significance of vertical migration.

Gliwicz (1986) describes a natural experiment in European lakes which offers strong support for the predation hypothesis of vertical migration. In a lake with visually feeding fish, *Cyclops*, a cyclopoid copepod, vertically migrates. In lakes lacking fish, it doesn’t vertically migrate. **Ohman (1990)** fleshes out the demographic analyses from his earlier paper. **Frost (1988)** documents a classic vertical migration pattern in the dominant west coast neritic calanoid, *Calanus pacificus*. He provides the field evidence for vertical migration and evaluates the theories explaining vertical migration patterns. **Dagg *et al.*(1997)** provide a closer view of the vertical migration patterns of *C. pacificus* in Dabob Bay after the spring bloom. This paper is innovative in that it uses the gut fluorescence method (see **Chapter 11**) to assess the ingestion rate of the *C. pacificus* population. Note that *C. pacificus* doesn’t feed when it has vertically migrated to depth. However, if there is abundant phytoplankton at intermediate depths, the *C. pacificus* adults will migrate only to this intermediate layer of high phytoplankton concentration to feed (25-50 m in Dabob Bay).

ADAPTIVE SIGNIFICANCE OF VERTICAL MIGRATION

There has been a long debate waged over the adaptive significance of vertical migration in zooplankton. Most would consider the debate now over, with the forces rallying under the `predator-avoidance' hypothesis flag having won the field. However, **Miller (1979)** noted that it is very difficult if not impossible to refute any of the reigning hypotheses for the adaptive value of vertical migration using field data. It is a good example of the late philosopher of science Imre Lakatos's (**1970**, p. 45) observation that *"It is not that we propose a theory and Nature shouts No!; We propose a maize of theories and Nature shouts INCONSISTENT!"*

Even though the debate is largely over, and zooplankton ecologists are well into a phase of what **Kuhn (1962)** called 'Normal Science', we will attempt to restoke the fires of the debate in class. **Ohman *et al.* (1983)** describe a reverse-diel vertical migration pattern in a small calanoid copepod. Ohman also describes the fatal flaw in **McLaren's (1974)** model of the adaptive value of vertical migration. **McLaren (1974)** is on reserve as a supplementary reading. McLaren (**1963**, **1974**) proposed that the adaptive significance of vertical migration was to increase growth rate by spending part of the day in cold water. In 1963, McLaren modeled zooplankton energetics, and in 1974, zooplankton demography. Without equations, McLaren's argument goes something like this:

> At colder temperatures, respiration costs are lower and female copepods get bigger. Bigger females produce more eggs. Thus, by residing part of the day in colder water, fecundity is increased. However, development time is slowed down in colder water, exposing females to predation for a longer period. However, the beneficial effects of cold on increased fecundity exceed the harmful effects of reduced survivorship using McLaren's fitness currency. McLaren assessed 'fitness' using the net replacement rate, $R_o = \sum l_x m_x.$ R_o is the expected number of female young born to a female over her lifetime, and l_x and m_x are the age-specific fecundity and survivorship.

Ohman *et al.* (1983), **Frost (1988)** and **Ohman (1990)** document the fatal flaw in McLaren's (1974) demographic theory. Their criticism is based on the variable used to measure population growth rate. **McClaren (1974)** maximized current return on reproduction, using the variable R_o or net replacement rate, without considering the long-term effects of reproduction by subsequent generations. The net replacement rate, R_o, is defined as:

$$R_o = \sum l_x m_x. \tag{1}$$

Ohman *et al.* (1983) argued that fitness should be assessed using the instantaneous or per capita growth rate, also known as 'little r'. It can be estimated using the Lotka-Euler equation:

$$\begin{aligned} 1 &= \int e^{-rx}\, l_x m_x \, dx. \\ 1 &= \sum e^{-rx}\, l_x m_x. \\ \text{where, } l_x &= \text{age-specific survivorship.} \\ m_x &= \text{age-specific fecundity.} \\ r &= \text{per capitata population growth rate.} \\ x &= \text{age.} \end{aligned} \qquad \textbf{(2)}$$

Excursis: survivorship curves

Deevey (1947) described different forms of survivorship curves, and labeled the archetypical patterns Type I, Type II, Type III and Type IV. The instantaneous mortality rate, the negative of the slope of the survivorship curve on a log scale, is the hazard rate. Harrell (**2002, p 395**) derives the instantaneous mortality rate function from the survivorship curve l(x) [S(t) in the original]:

$$mortality\ \ rate = q(x) = -\frac{\partial \log l(x)}{\partial x}.$$

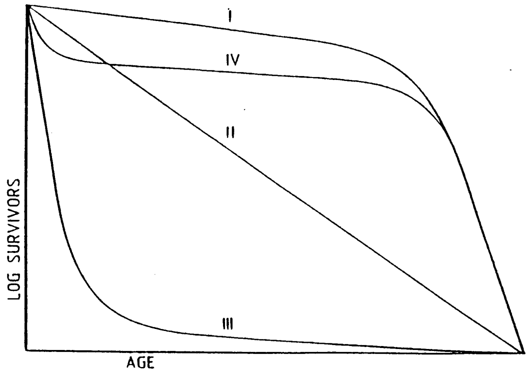


Fig. 4.3: Four types of survival distributions. For details see text.

Figure 1. Idealized survivorship curves from **Deevey (1947)**. Constant instantaneous mortality (a constant hazard function in statistical parlance) gives rise to the Type II curves. Hutchinson (1969) summarizes evidence showing that some birds seem to fit the Type II Deevey survivorship curve.

A constant mortality rate (or hazard rate in statistical parlance) would would produce a Deevey Type II survivorship and might be modeled with a Weibull distribution with Weibull γ parameter = 1 (the Weibull distribution with γ=1 is an exponential distribution with constant mortality, see **Harrell 2002 p 399**). Humans and other mammals tend to have survivorship curves with bathtub shaped instantaneous mortality rates (high at the ends and relatively constant in the middle). These mortalities or hazard functions

Birch (1948) discussed how the Lotka-Euler equation could be solved with field data and approximated using: **r=*ln*(R$_0$)/Generation time**. But as **Birch (1948)** pointed out, this shortcut doesn't save any effort in collecting field data, because the generation time requires precisely the same data needed to solve the Lotka-Euler equation:

$$\boldsymbol{T} = \frac{\sum x\ l_x m_x}{\sum l_x m_x} = Generation\ \ time. \qquad \textbf{(4)}$$

Lewontin (1965) used both theoretical life tables and real tables for fruit flies to show that the most important variable controlling r is the age to first reproduction. If two populations have identical values of the net replacement rate, R_o, the one with a lower age to first reproduction will have a much higher r. This can be seen most easily in this approximation: $r=ln(R_o)$/Generation time. **McLaren (1974)** failed to realize that females producing large numbers of eggs late in life would have a much lower population growth rate than females that turned out fewer eggs earlier in life. The difference in growth occurs because the fast reproducer's progeny are also producing young at an earlier age. It is a compound interest problem. Think of a real-life example. The Commonwealth of MA pays each of its employees weekly. What if the Commonwealth of MA paid each of its employees at the same rate with a monthly or yearly paycheck? If you consider only the interest that accrues in the bank from depositing these paychecks, a worker paid with a weekly paycheck earns more than one being paid with a monthly paycheck because each dollar deposited at the beginning of the week will be earning interest. And this interest will be earning more interest the next week. One measure that could save the Commonwealth tens of millions of dollars in the annual budget is to switch all workers to monthly paychecks since the Commonwealth would accumulate the interest that is now going to the workers. A state official telling you, "your rate of pay is the same" is analogous to McLaren saying that R_o is the same. You have to consider the long-term consequences of compound interest, the e^{-rx} in the Lotka-Euler equation.

Frost (1988) describes the competing adaptive explanations for vertical migration and tests several of the models with his own data on *Calanus pacificus* vertical migration patterns. He provides an insightful analysis of **Enright's (1977)** vertical migration model. Enright had proposed that the 'starvation response' (copepods with empty stomachs feed at a high rate) could help account for the adaptive significance of vertical migration. Enright proposed a key test of their model: copepods should rise to the surface shortly before sunset. This prediction was tested by **Enright & Honegger (1977)**, with mixed results. This pair of papers inspired a nasty note by **Miller (1979)**, with a spirited defense of the work by **Enright (1979)23**.

There are many open questions regarding vertical migration, and many logical and evolutionary pitfalls awaiting the unwary. First one should distinguish between the proximal and ultimate causes of vertical migration in copepods. On a daily or short-term basis, the proximal or immediate cause of vertical migration may be a change in light intensity or a change in gut fullness (*e.g.*, the midnight sinking of full zooplankters) or the perception (through chemoreception perhaps) that members of the population are being eaten. This proximate cause should be distinguished from the ultimate or long-term cause, which may be a response to visually feeding or invertebrate predators or perhaps due to a demographic advantage from spending part of the day in colder food-poor water (*e.g.*, **McLaren's (1974)** energetic-demographic adaptive explanation). A seasonal change from a non-migrating to a migrating phenotype in the population could be due to either a phenotypic adaptation (*e.g.*, the species migrates when there is a strong thermocline) or due to natural selection (*e.g.*, the non-migrators are eaten). The phenotypic selection (*e.g.*, due to predators) may not produce a directional change in the population's gene frequencies (*i.e.*, evolution, see **Appendix 1**) if the population is not reproducing.

Mangel & Clark (1988) briefly review some of the theories of the adaptive value of vertical migration, which include:

1. A method of population self-regulation (**Wynne-Edwards 1962**)
2. Prudent grazing (**Hardy 1958**)
3. Maximizing rate of genetic exchange (**David 1961**)
4. Maintaining constant food input (**Kerfoot 1970**)
5. Minimize the effect of competition (**Dumont 1972**, **Lane 1975**)
6. Avoiding damaging solar radiation (**Hairston 1976**, **Aarseth & Schram 2003**)
7. Horizontal movement (**Mackintosh 1937**)
8. Response to prey movement and patchiness (**Hardy 1958**)
9. Predator avoidance (**Hutchinson 1967**, **Zaret & Suffern 1976**)
10. A method to achieve optimal alternation of temperature (**Moore & Corwin 1956**)
11. Adaptation to bioenergetic requirements (McLaren **1963**, **1974**, **Enright 1977**)

Several explanations of vertical migration (1-4 above) require group selection. For example, **Wynne-Edwards (1962)** argued that zooplankton vertically migrate to concentrate the population in one depth stratum (in a social epideictic display) so that the population could self-regulate reproductive intensity. **Hardy (1958)**, **Kerfoot (1970)**, **McAllister (1969)** and **Enright (1977)** all argue that the zooplankton would be more prudent grazers of phytoplankton if the prey population were allowed to grow uneaten during the daylight hours. Both **Wynne-Edwards' (1962)** epideictic display hypothesis and the McAllister-Kerfoot prudent grazer hypothesis imply group selection and neither is an Evolutionary Stable Strategy (ESS) in **Maynard Smith's (1982)** terminology because cheater genotypes that do not restrain their appetites during the daytime or reduce reproductive output would always increase in frequency in the population at the expense of the prudent grazers or prudent reproducers.

Hutchinson (1967) clearly stated the predator-avoidance hypothesis, but **Zaret & Suffern (1976)** are credited as the first to describe with comparative field data the effects of visually feeding predators on the migration phenotype of prey populations. Their field data from Connecticut lakes and Gatun Lake were consistent with the visual predation hypothesis. **Gliwicz (1986)** has an interesting paper on the evolutionary effects of fish on cyclopoid copepod vertical migration in lakes. In lakes with fish, the copepods have a diel vertical migration pattern. In lakes lacking fish, they stay near the surface.

Mangel & Clark (1988) produce a dynamic stochastic model to explain the vertical migration patterns of cladocera, Ohman's *Pseudocalanus*, and visually feeding fish. Their most intriguing model, also described by **Clark & Levy (1988)** is for the vertical migration of juvenile salmon, a medium-sized fish. These fish migrate to the surface to feed during a 'anti-predation window' of only an hour or so at dawn and dusk. At this point there is enough light for them to feed, but unfortunately there is also sufficient light for their larger fish predators to feed on them. If the light intensity is lower, there is insufficient light to feed and at higher light intensity the risk of being eaten by large fish is too great. **Mangel & Clark's (1988)** model of *Pseudocalanus* migration predicts that *Pseudocalanus* should alter its migration pattern as a function of 1) the time remaining in the growing season, and 2) the size of the copepods. Near the end of the phytoplankton growing season, Mangel & Clark's model predicts that Pseudocalanus should spend the entire day at the surface feeding. A copepod that is not large enough to overwinter should incur more risk of being eaten, because the alternative is the failure to acquire sufficient lipid reserves to overwinter.

The genetic basis for vertical migration is not yet clear. One simple-minded model would predict that macrozooplankton begin the year with a diverse set of phenotypic behaviors including vertical and non-vertically migrating populations. After several generations of selective predation on the non-vertically migrating phenotypes, the population will be composed predominately of vertical migrators. This would be a beautiful example of natural selection in action. **Weider (1984)** has documented genetic differences between migrant and non-migrant phenotypes. The problem is, what accounts for the maintenance of phenotypic diversity from one year to the next?

WHAT IS GAME THEORY?

Rarely has a field been so thoroughly defined from the outset as has game theory. Von Neumann & Morgenstern published their 'Economic behaviour and the theory of games' in 1944. In this book von Neumann, who many regard as being the most influential mathematician of the 20th century, extended his seminal work on two-person games to multi-person and N-person games.

Games can be described using a number of formal conventions. In an extensive form description of a game, the moves are described in the form of a decision tree. In a normal-form game, the payoffs from the moves in a game are described in a payoff matrix. The "payoffs" in a game are important. In games of economic behavior, the payoff matrix is often defined as money. **Von Neumann & Morgenstern (1944)** generalized on this concept and used a general utility to describe the payoff of the game. In ecology, the payoff is usually defined in terms of units of fitness.

Lewontin and **Maynard Smith & Price (1973)** were the first to apply game theory to evolutionary and ecological problems. To date, most of the ecological examples of game theory are drawn from the field of two-person games, not from the conceptually more challenging and less quantitative n-person cooperative game theory.

The program GAMBIT is available on the web (**http://econweb.tamu.edu/gambit/**) to solve two-person and multiperson games in extensive and normal form. More information on the GAMBIT program is provided **below**.

TWO-PERSON GAMES

Zero-sum games

John von Neumann was the first to establish the solution to two-person zero sum games. This solution is embodied in the minimax theorem. There are two general types of solution to a zero-sum game: a pure strategy and a mixed strategy. I will demonstrate this concept using a simple game described in **Thomas (1986)**.

The Hun-in-the-Sun game

In this game, there are two players: the commander of a bomber squadron and the commander of a squadron of fighter pilots. The payoff matrix in a zero-sum game only needs to show the payoffs for one player, usually the player whose strategies are described by the rows in the normal form payoff matrix.

Here is the section from **Thomas (1986, p. 32)** describing the game:

> *In World War II, the normal tactic of fighter planes when attacking opposing bomber planes was to swoop down on their target from the direction of the sun—known in boys' comics as the 'Hun in the Sun' strategy. However, if every plane employs this strategy, the bomber pilots put on their sunglasses and just keep staring into the sun looking for the fighters. Thus, a second method of attack was suggested, which was to attack straight up from below. This is very successful if the fighter is not spotted, but since planes go much more slowly when climbing than diving, is likely to have fatal consequences for the fighter pilot if he is spotted. With hindsight, we can describe this as the Ezak-Imak strategy (reverse Kami-kaze).*

Thomas (1986) proposes the payoff matrix for this two-person zero-sum game as the chance of survival of the fighter plane when it attacks:

Table 1. The fighter payoff matrix for the 'Hun-in-the-sun' game (Thomas 1986). This is a symmetric, 2-person, zero-sum game, so the payoff for the bomber crew is one minus the payoff for the fighters

		Bomber Crew		**Solution**	**Expected Payoff**
		Look up	**Look Down**		
Fighter Pilot	**Hun in the Sun**	0.95	1	$\frac{20}{21}$	$\frac{20}{21}$
	Ezak-imak	1	0	$\frac{1}{21}$	$\frac{20}{21}$
	Solution	$\frac{20}{21}$	$\frac{1}{21}$		
	Expected Payoff	$\frac{20}{21}$	$\frac{20}{21}$		

This game can be solved using von Neumann's minimax theorem as implemented in **GAMBIT**. Von Neumann's minimax theorem states (**Thomas, 1986, p. 33**):

> *Minimax theorem. In a two-person zero-sum game, where Player I has n strategies and Player II has m strategies (where n and m are finite), then*

$$v_L^M = \max_{x\in X}\min_{y\in Y} = \min_{y\in Y}\max_{x\in X} e(\mathbf{x},\mathbf{y}) = v_U^M.$$

In words, player 1, the Fighter Pilot above, adopts a strategy that maximizes the minimum payoff that he can expect. This is a conservative strategy: you pick the strategy where you can be assured the maximum amount, no matter what strategy your opponent uses. That strategy, would be the "Hun in the Sun" strategy above, which has a 0.95 payoff, which is far preferable to the Ezak-imak strategy which might result in a payoff of 0. Player 2 in this zero-sum game (any benefit to one player results in a deficit to the other) should adopt the strategy that minimizes the maximum payoff to the opponent.

If there is a cell that is simultaneously the maximum of the minimum values for rows, and the minimum of the maximum values for columns, that cell is the 'pure' solution to the game. In a pure strategy, all individuals should follow one strategy. Many simple games have pure strategy solutions. In this case, there is no clear choice for player 2, since both the Look up and Look Down strategy have maximum payoffs to the opponent of 1.0. The solution to this game is a mixed strategy. In a mixed strategy, the strategy at each play of the game should be governed by chance. In this zero-sum game, the fighter pilot squadron commander should put 20 white balls and 1 black ball in a hat. If a fighter pilot draws a black ball, he should approach the bomber from below; if he draws a white ball, he should play the Hun-in-the-Sun strategy. Since the game is symmetric, the bomber gunners should also play with the same probabilities. Twenty of twenty-one bomber gunners should wear sunglasses to every one that stares down looking for the Ezak-imak attack. The same solution applies if there is a single bomber gunner and a single fighter pilot. The fighter pilot should draw balls from a hat or generate a random number such that the odds of using the Hun-in-the-Sun strategy are 20/21.

This Hun-in-the-Sun game points out a seeming flaw in applying the Von Neumann minimax solution to the 2-person zero-sum game. Imagine if you were the pilot that draws the black ball. If the gunner is looking down, your probability of survival is 0.0 For those pilots using the "Hun-in-the-Sun" strategy, their odds of survival are no worse than 0.95, even if the bomber gunner is looking up with sunglasses. Why should that one out of twenty-one pilots risk apparent certain death by slowly flying up from beneath the bomber? The increase in fitness by using the mixed strategy over a pure 'hun-in-the-sun' strategy is only the difference between 0.95 (all Hun-in-the-Sun *vs.* Look up) and 0.9524. If the bomber gunner is using his 'optimal' strategy (20/21 of bomber gunners looking up), then the expected fitness using the Ezak-imak strategy is identical to using the Hun-in-the-sun strategy (0.9524). This isn't a coincidence, the payoff or fitness of the different options in a mixed strategy will always be identical. However, if the bomber gunners are using a sub-optimal strategy of looking down more than 20/21 of the time, then the probability of survival of the Ezak-imak strategy drops dramatically and is zero if all of the bomber gunners are looking down.

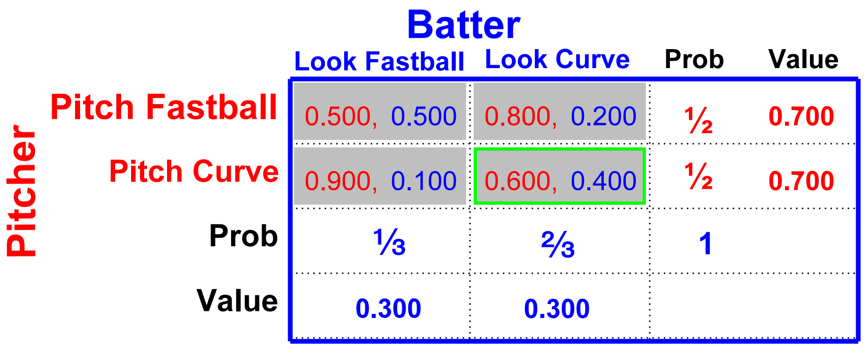
Paulos's Baseball zero-sum game

Paulos (1995, p. 30) describes a zero-sum two person game between a pitcher and batter:

> *"A pitcher and batter are facing each other. The pitcher can throw either a fast ball or a curve ball. If the batter is prepared for a fast ball, he averages .500 against such pitches but, thus prepared, he only averages .100 against a curve ball. If he's prepared for a curve ball, however, the batter averages .400 against them, but he only averages .200 against fast balls in this case."*

Based on these probabilities, the pitcher must decide which pitch to throw and the batter must anticipate this decision and prepare accordingly. There is no 'pure strategy' solution for this game.

The probabilities and strategies for this game can be entered into Gambit, producing the output shown in Figure 2. The pitcher should pitch half fastballs, half curves. The batter should look for ⅓ fastballs and ⅔ curves. This is the stable solution for both players, and would produce a 0.300 batting average for the batter. This stable solution is also known as the Nash equilibrium and, in biology, as the evolutionary stable strategy. If both batter and pitcher are using this optimum strategy, any deviation would, in Paulos's phrase, cede an advantage to the other.



		Batter			
		Look Fastball	Look Curve	Prob	Value
Pitcher	Pitch Fastball	0.500, 0.500	0.800, 0.200	½	0.700
	Pitch Curve	0.900, 0.100	0.600, 0.400	½	0.700
	Prob	⅓	⅔	1	
	Value	0.300	0.300		

Figure 2. The batter-hitter game solved by Gambit. The batter attains a 300 average by looking for fastballs ⅓ of the time, while a pitcher can hold a batter to 300 by pitching ½ fastballs. If either player deviates from these stable strategies, the opponent benefits. The game is described in Paulos (1995, p. 30).

This pair of optimal strategies assumes that both players are rational and will adjust their strategies in response to their opponent. In the same article **Paulos (1995)** poses a seemingly related problem dealing with a **stupid pitcher**. Suppose a **stupid pitcher** pitches ⅔ fastballs and ⅓ curves no matter how batters respond. What should the batters do? Should they ask the batting coach to run a gambit solution of the odds? No. If the stupid pitcher does not modify the type of pitch thrown in response to circumstance, the batter should identify the most frequent type of pitch and plan to hit only that pitch. In the case of a pitcher throwing ⅔ fastballs, the batter can do no better than to prepare for 100% fastballs. The batter's average would be:

$$0.5 \times \tfrac{2}{3} + 0.1 \times \tfrac{1}{3} = \tfrac{1}{3} + \frac{1}{30} \approx \mathbf{0.367}$$

If the batter made the mistake of adjusting his batting eye to match the proportion of pitches being thrown by the pitcher, i.e., looking for ⅔ fastballs and ⅓ curves, here is what the batter's average would be:

$$\tfrac{2}{3}(0.5\times\tfrac{2}{3}+0.1\times\tfrac{1}{3}) + \tfrac{1}{3}(0.2\times\tfrac{2}{3} + 0.4\times\tfrac{1}{3}) \approx \tfrac{2}{3}\times 0.367 + \tfrac{1}{3}\times 0.2667 \approx \mathbf{0.334}$$

This somewhat strange result can be summarized by saying that if your opponent isn't rational, that is changing in response to changes in the game, then don't use a mixed strategy.

Peter Frank (1981) took this argument one step further: if your opponent isn't rational and the opponent's behavior is unpredictable, and you've had at least one success, then don't change strategies. Frank asked, "Why are most intertidal organisms sessile or secondarily sessile (*i.e.*, returning to the same spot after a period of foraging)?" If the larva of the intertidal organism has metamorphosed in a favorable site, there is little advantage and considerable demographic cost to migrating away from that site. The long-term demographic costs of moving from favorable to unfavorable sites are not paid back by the advantages of moving from unfavorable to favorable sites. **Frank (1981, p. 288-289)** summarizes the argument nicely:

> *"If habitat patches differ in risk of death to organisms, and if the latter can gain no knowledge of the hazards, natural selection will favor their staying put … a sessile strategy evolves whenever variable and unknowable hazards dominate the selectional landscape…"*

In terms of the baseball game, if you got a hit when you last batted, while looking for a fastball, and you have no way of knowing the odds of the pitcher throwing a fastball again, then look for a fastball. However, if the pitcher remembers that you got a hit last time at bat when he threw a fastball, would he really throw another? No, he should throw a curve. Of course, the pitcher knows that you know that he knows that you got a hit the last time he threw a fastball, so you should be looking for a curve, and he should throw a fastball. But you know that the pitcher knows that you know that the pitcher knows that you got a hit the last time he threw a fastball, so the batter should look for a fastball. The movie, "The Princess Bride," mines this logical paradox in a battle of the wits between Wally Shawn and Cary Ewes.

Non-zero sum games

The classic two-person, non-zero sum game is prisoner's dilemma, first described by Tucker. **Thomas (1986, p. 55)** describes the game with the following payoff matrix.

Table 2. The payoff matrix for Prisoner's dilemma.

		Prisoner II	
		Confess	**Don't Confess**
Prisoner I	**Confess**	(-9, -9)	(0, -10)
	Don't confess	(-10, 0)	(-1, -1)

Two prisoners are being questioned separately after being arrested in possession of stolen goods and can either confess or keep quiet. If both keep quiet, each will only receive a one-year prison sentence. If one confesses and the other does not (*e.g.*, turning state's evidence), then that prisoner will be granted immunity while the other will receive a ten-year sentence. If both confess, each will receive a nine-year sentence. The Von Neumann-Morgenstern solution to this game is Confess-Confess, with each prisoner receiving a nine-year sentence. Using the criterion of individual rationality, each player can assure himself no more than a 9-year sentence no matter what the other prisoner does. The game poses a dilemma because using a principal of group rationality, the don't confess-don't confess strategies would yield at most a 1 year sentence.

The solution to this game is relatively simple, using von Neumann's minimax theorem and the concept of dominance. Gambit will solve the game numerically, but one initial step in Gambit and the solution to games is to eliminate dominated strategies. A dominated strategy is one that has inferior payoffs for every possible strategy used by the opponent. Dominated strategies will not be part of a solution to the game. What should Prisoner 1 do, given knowledge of this payoff matrix. Well, he can compare his payoffs for ‘Confess’ and ‘Don’t confess’ for each possible response of Prionser II. The payouts are -9 and -10 for confess & don’t confess if Prisoner II confesses and 0 and -1 if Prisoner II doesn’t confess since -9 > -10 and 0 > -1, the Confess strategy DOMINATES the don’t confess strategy. Prisoner I should always CONFESS. Similarly for Prisoner II, the Confess strategy dominates Don’t confess -9 > -10 and 0>-1, so Prisoner II should confess. The stable solution to this game is that both Prisoner I and II should confess.

The Euchaeta-Pseudocalanus game

In class, I demonstrated a two-person non-zero-sum game called the *Pseudocalanus*-*Euchaeta* game. **Ohman *et al.* (1983)** describe the basic ecology underlying this game. *Pseudocalanus* is a medium-sized calanoid copepod whose primary predator is the larger calanoid copepod *Euchaeta*. Both *Pseudocalanus* and *Euchaeta*, are preyed on by fish. Most macrozooplankton are capable of vertical migration to avoid predation. *Euchaeta* generally undergoes a classic diel vertical migration: up at night and down during the day. The adaptive value for this behavior is obvious: fish must see their prey in order to feed. *Euchaeta* does not need to see *Pseudocalanus*. Like many other pelagic invertebrate predators, Jeanette Yen has shown that *Euchaeta* detects its prey through mechanoreception, sensing the vibrations made by *Pseudocalanus* while swimming or suspension feeding.

The key to describing this game is to produce a payoff matrix for the game. Following **Maynard Smith (1982)**, the payoffs to the organism in evolutionary applications of game theory are defined as relative fitness. In the non-zero-sum two-copepod game, each copepod should maximize its own fitness. If this game were zero-sum, this maximization would be synonymous with minimizing the other player’s fitness. As discussed in class, evolution by means of natural selection is a battle between predator and prey, but it is also a competition between individuals with the same species. The individual with the higher relative frequency will have its genes make up a higher proportion of the gene pool in the next generation.

In the implementation of relative fitness to the *Euchaeta-Pseudocalanus* game, a fitness of 0 is on a relative scale and doesn’t mean that the organism has no fitness. The fitness values range from 0 to 100. *Euchaeta* has 0 fitness if its vertical distribution doesn’t overlap at all with its prey *Pseudocalanus*. If *Euchaeta* can feed on *Pseudocalanus* for ½ the day but is exposed to visually feeding fish in the euphotic zone, the fitness is 20. If *Euchaeta* can feed on *Pseudocalanus* the entire day while being exposed to fish for ½ the day, the fitness is assumed to be 50. If *Euchaeta* can avoid visual fish predators while feeding on *Pseudocalanus* half the time, the *Euchaeta* fitness is 150. If *Euchaeta* avoids visually feeding fish (diel vertical migration), while feeding on *Pseudocalanus* the entire day (*Pseudocalanus* also performing a diel migration), the *Euchaeta* relative fitness is 200. Note that there are no ‘costs’ for movement.

For *Pseudocalanus*, we’ll assume that all of the food, phytoplankton, is in the surface layer. This is not true, especially since both sinking phytoplankton and animal prey could be consumed by the omnivorous *Pseudocalanus*. In this simplified game, *Pseudocalanus* staying deep is not an option. Of the possible strategies, reverse diel with *Pseudocalanus* exposed to visual predators ½ the day and invertebrate predation due to reverse-diel migrating *Euchaeta* for the entire day would have the minimum relative fitness of 0. Feeding on surface phytoplankton the entire day while being exposed to *Euchaeta* predation the entire day would produce a relative fitness of 30. Feeding on phytoplankton the entire day while being exposed to *Euchaeta* predation for half the day would produce a relative fitness of 40. Avoiding both visually feeding predators and invertebrate predators is worth 100 units of relative fitness, even while only feeding on phytoplankton for half the day.

Table 3. The payoff matrix for the *Pseudocalanus-Euchaeta* game. The first element in the payoff pair (e.g., the 30 in 30,25) is the relative fitness for *Pseudocalanus*; the second element is the relative fitness for *Euchaeta*

		Euchaeta				**Solution**	**Relative Expected Fitness**
		Surface	**Diel**	**Reverse Diel**	**Deep**		
Pseudocalanus	**Surface**	30, 20	40, 150	40, 10	90, 0	0	235/4=58.75
	Diel	80, 10	50, **200**	**100**, 0	80, 75	⅜	245/4=**61.25**
	Reverse Diel	50, 10	80, 0	0, 20	30, 75	⅝	245/4=**61.25**
	Solution	0	**5/8**	0	**3/8**		
	Expected Fitness	10	**75**	12.5	**75**		

When analyzed by **GAMBIT**, the *Pseudocalanus-Euchaeta* game has a mixed solution for both prey and predator populations. If the assumption of individual rationality is met, then both organisms should randomly select a strategy for each day's vertical migration. *Euchaeta* should undergo a diel vertical migration 5/8 of the time and stay deep 3/8 of the time. *Pseudocalanus* should undergo a reverse diel vertical migration pattern 5/8 of the time and stay at the surface 3/8 of the time.

Is this an acceptable solution to the game? Both pairs of solutions would be considered evolutionary stable strategies in **Maynard Smith's (1982)** theory. That means that if both populations were following these pairs of strategies, then no mutant phenotype with a different strategy could invade.

Of course, neither of the coevolving populations could expect to maintain the same strategy for long. **Van Valen (1973)** proposed the Red Queen hypothesis to describe the coevolution of predators and prey and strong competitors. Coevolving populations must continually adapt to their competitors or predators to maintain their position on the fitness landscape. Like Lewis Carroll's Red Queen, they must evolve as fast as they can to stay where they are. If they ceased to evolve in response to the evolution of their predators or competitors, they would be like Paulos's stupid pitcher (described on p. 12) whose failure to change pitch frequencies would allow competitors a distinct advantage in the coevolutionary game.

In the reference list below, I have included many of the references from the ecological literature on the adaptive value of vertical migration. Mixed strategies appear to be common among zooplankton populations. The evolutionary mechanism driving such patterns is a ripe field for theoretical research. **Mangel & Clark (1988)** analyzed the *Pseudocalanus* vertical migration pattern with their stochastic dynamic programming approach. They asked a slightly different question: when relative to the onset of diapause should copepods begin to vertically migrate and when should they stop?

GAMBIT

GAMBIT is a C++ program that implements most of the algorithms for solving 2-person and multi-person games, but not n-person cooperative games. I used GAMBIT to solve the *Pseudocalanus-Euchaeta* and "Hun in the Sun" games. Here is the URL:

http://econweb.tamu.edu/gambit/

GAMBIT is a C++ program that has been compiled into executable versions for a variety of platforms, including Linux, and all versions of Windows.

GAMBIT has a nice GUI (Graphical User Interface) that allows you to input the payoff matrix for two person games and analyze the solutions. These algorithms could be programmed in MATLAB™, but the solution of 2-person non-zero sum games involves linear programming. The classic algorithm for linear programming problems is the minimax algorithm, but this algorithm is only available in the MATLAB™ optimization toolbox.

The only type of problem for which GAMBIT is not suited is the solution of games described symbolically. For example, **Maynard Smith (1982)** provides fitness values for some games in numerical form: this can all be solved using GAMBIT. **Maynard Smith (1982)** then provides payoffs in symbolic form, *e.g.*, (1-x +d). GAMBIT cannot solve symbolic equations.

Outlines

REQUIRED READING

Ohman, M. D., B. W. Frost, and E. B. Cohen. 1983. Reverse diel vertical migration: an escape from invertebrate predators. Science *220:* 1404-1407.[3, 4, 5, 22]

I. Introduction:
    A. Diel vertical migration extremely common.
    B. Reverse diel vertical migration observed in freshwater.
II. The site and pattern
    A. Dabob bay in WA: 185 m
    B. *Pseudocalanus* underwent a reverse diel vertical migration in Aug. '73.
    C. *Euchaeta elongata*, *Sagitta elegans* and *Euphausia pacifica*, invertebrate predators all, exhibit classic diel vertical migration **Fig 1c**.

1. All 3 are predators on *Pseudocalanus*.
2. *Euchaeta* and *Sagitta* are obligate predators.
3. *Euphausia pacifica* is an omnivorous.
4. feeding rates are higher at night then during the day

D. *Pseudocalanus* females descend rather than ascend at night

E. Explanation incompatible with standard models.

III. Analysis of McLaren's model.

A. **Table 1: because of increased development time, a non-migrating *Pseudocalanus* has a higher r than a migrating population. A 16% reduction in adult mortality rate results in a demographic advantage for the migrant.**

1. 13 to 9 degree temperature difference
2. a 16% reduction in adult mortality rate produces a demographic advantage.

B. McLaren (1974) failed to use r in his calculations: he used R_o, the wrong demographic currency

SUPPLEMENTAL

Dagg, M. J., B. W. Frost and J. A. Newton. 1997. Vertical migration and feeding behavior of *Calanus pacificus* females during a phytoplankton bloom in Dabob Bay, U.S. Limnol. Oceanogr. *42*: 974-980. *[During March phytoplankton bloom copepods had full guts only at night. The majority of copepods remained at depth apparently because there was sufficient food sinking to them]*[3]

Frost, B. W. 1988. Variability and possible adaptive significance of diel vertical migration in *Calanus pacificus*, a planktonic marine copepod. Bull. Mar. Sci. *43*: 675-694[3, 4, 6]

1. Abstract
   a. *Calanus pacificus*
   b. Seasonal and interannual variability
      i. unrelated to food availability
      ii. *in situ* female growth
      iii. thermal stratification
   c. population growth model
   d. differential mortality between migrants and non-migrants.
2. Introduction
   a. circumstantial evidence for mortality
   b. Two testable hypotheses
      i. foraging behavior optimizing individual growth rate (**McLaren 1963**, **Enright 1977**)
      ii. Habitat selection models optimizing population growth rate
         (1) **McLaren (1974)**
         (2) **Ohman *et al.* (1983)**
   c. Metabolic models can't cut it theoretically (**Ohman *et al.* 1983**) or experimentally (**Stich & Lampert [1984]**, **Orcutt & Porter [1983]**)
   d. Temporal and geographic variability in some species. These species provide clues as to the origins and causal mechanisms {Endler's book}
      i. *Calanus pacificus*
      ii. **Koslow & Ota (1981)**, food availability determines vertical migration
      iii. **Enright & Honegger (1977)**
         strong vertical migration of CV and adults in late spring and early summer.
3. Materials and methods
   a. quantitative paired zooplankton hauls
   b. Chl *a*
   c. egg production rate
   d. Gulf of Alaska populations

4. Results
a. seasonal and interannual variability in diel vertical migrations
i. spring females were migratory or non-migratory
ii. summer always vertically migratory.

Fig. 1. vertical distribution of adult females in 1985 and 1986

Fig. 2. Vertical distribution of adult females in 1979 and 1982

iii. variable spring pattern
b. Vertical distributions in spring
i. no association with food availability (Table 1)
ii. no association with thermal stability

Fig. 3. Vertical structure of *Calanus* pacificus females and Chl *a* and vertical structure

c. Vertical distribution in summer and autumn
i. strong subsurface Chl maximum
ii. migrated whether food is high or low
iii. females always vertically migrate no matter what the food or thermal stratification.

Fig. 4. Vertical distribution of adult *C. pacificus* in 4 years

Fig. 5. vertical temp. distribution. Vertical migration even though the water column was isothermal.

d. Vertical distribution in the Gulf of Maine.
\- remained in the upper mixed layer day and night (Fig. 6)

Fig. 6. Vertical distribution in the Gulf of Me.

e. Model of population growth
i. Behavior is not genetically fixed
ii. simple life table approach
iii. r of 0.149 d^{-1} for non-migrant, 0.103 for migrant due to delay in development time.

Table 4. Life Table analysis.

iv. Assumptions
(1) Vidal 1980a used to calculate adult body size at different temperatures.
(2) Clutch size related to prosome length using range 1980, 1984.
(3) For migrant:
(a) females are nonmigratory until CIII
(b) CIV on migrate
(c) Development time according to Thompson's equations.
(4) realized rate of increase is 0.141 per day
v. *"the nearly 3-day delay in development more than counterbalances their increased body size and fecundity."*
vi. differences in r are not particularly great, therefore, enhanced population growth of the migrators at the expense of the non-migrators

Table 5. The value of r was calculated over 10 clutches as described in Table 4.

assuming simple exponential growth, stable age distribution and equal initial populations, after only 30 days, the migratory population would be more than twice as large as the non-migratory population. A 12% reduction in adult mortality will give the migrant the same population growth as the non-migrant.

5. Discussion
a. predation can not be discounted:
b. predation removes nonmigratory genotypes
c. replacement rates could be very rapid
d. phenotypic responses of prey to predator contact
e. thermal retardation of development time
f. Food availability hypotheses
i. starvation-enhanced ingestion
nocturnal feeders have the same ration
ii. assimilate ingested food with high efficiency
iii. Energetic costs of swimming and feeding
g. Life-table assumptions.
i. 10-day spawning. increasing this has little effect on r.
ii. 50:50 sex ratio.
h. nocturnal occupation of the surface layer.
-Enright's model provided for nocturnal ascent.

i. *deus ex machina* explanations of predator abundance.

j. Why does the population continue to have vertical migration response.

Gliwicz, M. Z. 1986. Predation and the evolution of vertical migration in zooplankton. Nature *320*: 746-748[3, 7]

I. Abstract

A. Hypotheses for vertical migration

B. Does predation select for traits of migratory behavior?

II. **Figure 1: a) non migratory population in Lake Czarny and Morskim [no salmon] b) migratory population in lake Mrskie Oko**

III. Predation hypothesis:

A. exploitation of rich food at night

B. predator avoidance during the day

C. Fitness of a migratory individuals should be enhanced

D. Migratory behavior should be of selective advantage in habitats where food resources are significantly higher in the upper strata and where predation is higher in the upper strata

IV. **The presence of *C. abyssorum* in lakes with different fish stocking histories provided an opportunity to study the effects of predation and the length of time that vertical migration behavior takes to evolve.**
-Migration is most pronounced in lakes with natural fish populations.

V. The evolution of migratory behavior combined with the evolution of resistance of eggs to digestion might explain why *Cyclops* is the sole crustacean survivor in lakes stocked with planktivorous fish.

McLaren, I. A. 1974. Demographic strategy of vertical migration by a marine copepod. American Naturalist *108*: 91-102.[4, 6, 7, 17, 22, 25]

I. History of adaptive explanations for vertical migrations:

A. [Wynne-Edwards, V.C.] Animal dispersion in relation to social behavior]

B. **McLaren (1963)** proposed that there was a metabolic advantage from life at cold temperatures.

C. Prudent grazing hypothesis of **McAllister (1969)**

-*"study suggests that vertical migration may give the additional advantage of better utilization of the growth potential of the phytoplankton, as well as permitting the unimpeded growth of plants during the daylight hours."*

a. implies group selection

b. invertebrate predators migrate too

D. **Kerfoot's (1970)** explanation: vertical migration optimizes the transfer of phytoplankton production to zooplankton population

1. Criticized by **Miller *et al.* (1972)** as implying group selection and not being supported by field data.

2. **Kerfoot's (1972)** response.

E. Avoidance of visual predators, **Hutchinson (1967)**, **Zaret & Suffern (1976)**. Predator avoidance.

F. Navigation hypothesis (**Hardy 1958**) Problems: no test.

G. Demographic energetic advantage from living in cold water. McLaren **1963** & **1974**

1. The earlier hypothesis was energetic rather than demographic.

2. The McLaren effect: lowered metabolism in deeper, colder water.

3. The present model operates on realized rates of increase involving natural mortality.

4. The energetic costs of vertical migration are minimal

5. Required no feeding at depth

6. Ignored increased development times.

II. Experimental methods:

1. *Pseudocalanus minutus* is the test organism

2. Females collected near Halifax Nova Scotia.

B. **Effects of temperature on the development rate of P. minutus**

1. All organisms development times can be described by **Belehradek's temperature function**

$$D = a(T-\alpha)^{-b}$$

where, D is the development time to hatching.

a. fit by least squares.

b. **the Isochronal rule** Development time to any given younger stage occupies the same proportion of the time taken to reach adulthood at all temperatures. (see critique by Landry)

Figure 1: Development time a decaying exponential function of temperature

C. **Effects of temperature on the size of *Pseudocalanus* minutus**

1. Size differences controlled by temperature but not food

2. Field data: Field-caught stage III copepodites much larger at lower temperatures (**Lock & McLaren 1970**)

Figure 2: Effects of temperature on the size of adult female P. minutus.

a. At lower temperature, larger body sizes of *P. minutus*

b. However, this was not found in lab populations (Table 1)

Table 1: It was somewhat surprising to find no effect of temperature on size of stage II animals raised in the laboratory from eggs.

D. **Effects of temperature on fecundity.**

Corkett & McLaren (1970)

1. established the characteristics of egg production.

2. **Fig. 3. Mean egg number per clutch and body size of adult females. $E = 20.78(L)^{3.58}$**

- Egg number a positive function of body size **(Fig. 3).**

III. **The model**

A. Assumptions:

1. Number of eggs produced is predictable from cephalothorax length.

2. length predictable from temperature during development from stage III through maturity

3. time to reach stages or maturity and production of 10 successive clutches, can also be determined from temperature.

4. 50:50 sex ratio

5. Model assumes that migration does not begin until CIII

B. The demographic model (P. 97)

1. **$r : \Sigma e^{-rx} mx = 1$**

a. assumes no mortality

b. temperature-dependent egg production and development

2. **$m * \Sigma e^{-rx} = 1$**

a. assumes egg production constant for females of age x raised at a given temperature

b. r increases monotonically with temperature.

c. adding mortality leads to different conclusions.

C. (p. 98) If the non-migrant population is at equilibrium, the instantaneous mortality matches the potential rate of increase and we may write:

$$m \Sigma e^{-dx} = 1$$

1. solve for d as a constant mortality rate

2. Because of delayed development times, a migrant population will experience more mortality and decline.

D. Further assumptions required.

1. Model assumes that migration does not begin until CIII (observed for *P. minutus*)

2. egg bearing females nonmigratory

a. egg development times are therefore not retarded

b. subject to faster developmental rates

3. Juveniles experience higher mortality.

-Two mortality rates d_1 (before CIII) and d_2 (after CIII). d_1 is up to 4 x d_2.

IV. *"A worked example, with some steps added for easier consideration is given in the Appendix."*

A. **Even though he uses the Euler-Lotka equation, which implies he is working with** r, **McLaren plots the rate of increase per generation (=R_o= net replacement rate) in Figure 4.**

B. Solutions expressed as rates of increase per generation of migrants compared with non-migrants.

C. **Figure 4:** **Effects of lower temperature on rate of increase per generation.**

Top panel, 2° temperature difference. 2.5 x mortality required.

Bottom panel. With a 4x difference in mortality, the effects on finite rate of increase of different temperature changes.

V. The assumption of equilibrium over 1 generation can be relaxed. Adding variability in mortality can increase the demographic advantage of the migrating individuals.

VI. Small temperature differences may be quite important in nature.

VII. **Summary**

- A. Demographic advantage if early mortality >> later
- B. Demographic advantage if there are temperature differences.

VIII. **Appendix**: the mortality rates are right but the survivorship l_{vI} is wrong.

Ohman, M. D. 1990. The demographic benefits of vertical migration by zooplankton. Ecol. Monogr. *60*: 257-281.*[This paper is a detailed version of the arguments presented in Ohman et al.'s Science paper. The demographic arguments are presented in more detail and the field data supporting these arguments are fleshed out.]*[3, 4]

1. Abstract
    - a. 3 types of diel vertical migration in *Pseudocalanus* newmani
        - i. reverse
        - ii. normal
        - iii. none
    - b. reverse only at 185 m deep station containing predators *Euchaeta elongata*, *Sagitta elegans* and *Euphausia pacifica*
    - c. At 55-m station, no reverse migration
    - d. normal migration observed at shallow station.
    - e. theoretical life-table analyses.
    - f. vertical migration is a dynamic trait.
2. Introduction.
    - Tolstoy (1889)

Fig. 1. Temporal variation of *Pseudocalanus* and predators.

Fig. 2. Bathymetric map and sample locations.

- a. hypotheses tested by natural experiment.
- b. review of **McLaren (1974)**

3. Methods
    - a. Sampling
    - b. Life-table analyses
        - i. Embryonic development time
            - (1) Inverse function of temperature (Corkett & McLaren 1978)

$$ED=1845(T+11.45)^{-2.05} \quad (1)$$

            - (2) Expected development time as a function of DT, day temperature and night temperature.

$$EDAV=1/[(0.5/EDDT)+(0.5/EDNT)] \quad (2)$$

        - ii. equiproportional rule = isochronal rule, a given developmental stage occupies the same proportion of the total development time at any constant temperature (Corkett *et al.* 1986)
        - iii. $PL=0.597[1+10.82*(13.4+T)^{-0.99}]$ (3)
        - iv. Fecundity $-=10.39*PL^{3.58}$ (4)
            - (1) This is a slightly higher fecundity than McLaren's
        - v. Mortality rates.
            - (1) d_1 from NI to CIII
            - (2) d_2 from CIII to adults
        - vi. 10 successive clutches
        - vii. Euler equation solved:

$$\Sigma_x\, e^{-rx} l_x m_x$$

4. Results
    - a. Comparison of Station D and Station S

Fig. 4 Temperature profiles: surface temperature increased to 20°C

- i. SCM from May to September.
- ii. predators excluded from the shallow station.
    - (1) Each *Euchaeta* can eat 16-19 *Pseudocalanus* (Yen 1983)
    - (2) *S. elegans* can eat 5 *Pseudocalanus* females per day
    - (3) *Euphausia pacifica* can eat 2.4 females /d
- iii. Fish more abundant in shallow station.
    - 3-spine stickleback eat *Pseudocalanus*, which would be among the larger zooplankton at the shallower station.

- b. Comparative migrations.

Fig. 5. Reverse migration of *Pseudocalanus* females at Station D on 1 August. No evidence for reverse diel vertical migration in September even though the temperature gradient was nearly as large [3.9ºC]. The females remained in the surface in September *[note that Pseudocalanus* overwinters as CV. Are these Mangel & Clark's foragers risking all to get a final clutch in. Note the low abundances.]

Fig. 6 No reverse diel vertical migration ever at Station S. At Station S, classic normal vertical migration pattern. In the spring of the next year, the population remained at the surface during January through March *[Note low abundance of predators during this period]*

Fig. 7. Classic reverse diel vertical migration at station D by July through August

Fig. 8 Normal vertical migration pattern at station S in July

Fig. 9 Summary figure.

c. Predator migration patterns at Station D

Fig. 11. Vertical migration patterns of Sagitta and Euphausia.

d. Food limitation effects.

- i. **Ohman (1985)**: Chl *a* met or exceeded P_{max}
- ii. Food limitation during period of pronounced reverse migration, but as food concentration increased reverse migration persisted.

e. Variations in migration behavior by developmental stages and by other species.

- i. Most adult male and CV stages migrated, but little evidence for reverse migration of CIII, CII or CI.

Fig. 15. Developmental stages stay in the surface. CV stages and adults migrate.

f. *Life table analyses*

- i. Most of the assumptions made by **McLaren (1974)** have been borne out by subsequent data.
- ii. Mortality higher in younger stages.
- iii. d1:d2 is 2, **Ohman *et al.* (1983)** used 4.
- iv. Eggs borne on a sac cross the thermocline.
- v. non-migrant population is at equilibrium, $R_o = 1$

Fig. 17. Migrants have a disadvantage compared to non-migrants.

- vi. p. 274 left. Ohman's explanation of the demographic advantage of a migrant using little r is not quite right. A migrant can have a higher r even though R_o ($=\Sigma_x\, l_x\, m_x$) is lower than the non-migrant.

Fig. 18.

Fig. 19. A 12% reduction in mortality at 4° C produces a demographic advantage for the migrant.

5. Discussion.

a. Predatory zooplankton don't track *Pseudocalanus* at the deep station because they have alternative food.

b. **Enright (1977)**: migrants reduce diurnal grazing pressure on phytoplankton to permit maximal photosynthesis and prey growth by day.

c. Life table analyses

- i. the 3 phenotypes may represent different genotypes
- ii. **Ohman (1985)** found that as many as 8-9 generations of *Pseudocalanus* may occur during a year.

References

GENERAL VERTICAL MIGRATION

Hutchinson, G. E. 1967. Treatise on limnology, Vol. 2.

Longhurst, A. R. 1976. Vertical migration. Pp. 116-140 in D. H. Cushing and J. J. Walsh, eds., The ecology of the seas.

Mauchline, J., and L. R. Fisher. 1969. The biology of euphausids. Adv. Mar. Biol. 7: 1-454.

ADAPTIVE SIGNIFICANCE OF VERTICAL MIGRATION

Aarseth, K. A. , and T. A. Schram. 2003. Susceptibility to ultraviolet radiation in *Calanus finmarchicus* and *Lepeophtheirus salmonis* and the adaptive value of external filtering (Crustacea: Copepoda) J. Plankton Res. 24: 661-679. *["Copepods were exposed to UVB with a spectral irradiance maximum at 313 nm and* *additional visible light. In the holopelagic Calanus finmarchicus, with a carotenoid concentration of 0.85 µg mg^{-1}, the LD50 dose was 29 kJ m^{-2} whereas in the parasitic copepod Lepeophtheirus salmonis the LD50 was 84 kJ m^{-2}. The ability to photorepair was demonstrated for both species...The adaptive value associated with behavioural avoidance of toxic radiation, and the implications relative to vertical migration are discussed."]* {**7**}

Bollens, S. M. and B. W. Frost. 1989. Zooplanktivorous fish and variable diel vertical migration in the marine planktonic copepod *Calanus pacificus*. Limnol. Oceanogr. *34*: 1072-1083.*[Strenght of vertical migration is positively correlated with planktivorous fish abundance]{}*

Bollens, S. M. and B. W. Frost. 1993. Vertical distributions and susceptibilities to vertebrate predation of the marine copepods *Metridia lucens* and *Calanus pacificus*. Limnol. Oceanogr. 38: 1827-1837. *[2 years of field & lab studies used to show that the more pronounced diel vertical migration pattern of Metridia relative to Calanus pacificus is NOT due to greater vulnerability to fish. Fish don't selectively ingest Metridia]*

Clark, C. W. and D. A. Levy. 1988. Diel vertical migrations by juvenile sockeye salmon and the antipredation window. Amer. Natur. *131*: 271-290.

Conover, R. J. 1968. Zooplankton life in a nutritionally dilute environment. Amer. Zool. 8: 107-118.{**23**, **26**}

Dagg, M. J. 1985. The effects of food limitation on diel migratory behavior in marine zooplankton. Arch. Hydrobiol. Beih. Ergebn. Limnol. *21*: 247-255.

Dagg, M. J., B. W. Frost and J. A. Newton. 1997. Vertical migration and feeding behavior of *Calanus pacificus* females during a phytoplankton bloom in Dabob Bay, U.S. Limnol. Oceanogr. *42*: 974-980. *[During March phytoplankton bloom copepods had full guts only at night. The majority of copepods remained at depth apparently because there was sufficient food sinking to them]*

David, P. M. 1961. The influence of vertical migration on speciation in the oceanic plankton. Syst. Zool. *10*: 10-16.

Dawidowicz, P. And C. J. Loose. 1992. Metabolic costs during predator-induced diel vertical migration of Daphnia. Limnol. Oceanogr. *37*: 1589-1595. *[A lab setup with temperature-stratified tubes used to demonstrate vertical migration in response to fish karomone. Populations that vertically migrate have a much lower growth 0.21 d^{-1} than those that remain in the warm surface 0.57 d^{-1}]*[?]

Dumont, H. J. 1972. A competition-based approach to the reverse vertical migration in zooplankton and its implications, chiefly based on a study of the interactions of the rotifer *Asplanchna priodonta* (Gosse) with several crustacea enotmostraca. Int. Rev. Ges. Hydrobiol. *57*: 1-38.

Enright, J. T. 1977. Diurnal vertical migration: adaptive significance and timing. Part 1. Selective advantage: a metabolic model. Limnol. Oceanogr. *22*: 856-872. *[Presents a model, based on* ***Conover 1968****, that copepods vertically migrate to maximize energy intake, rising in time to reach their maximum daily ration {rather than avoiding predation}, tested in* ***Enright & Honegger (1977)****, criticized by* ***Pearre (1979)*** *and* ***Miller (1979)****, which is rebutted by* ***Enright (1979)****. See* ***Frost's (1988)*** *analysis of the effects of delayed development]{**6**, **7**, **22**, **23**, **24**, **26**}*

Enright, J. T. 1979. The why and when of up and down. Limnol. Oceanogr. *24*: 788-791. *[A response to* ***Miller's(1979)*** *vicious attack]* {**23**}

Enright, J. T. and H.-W. Honegger. 1977. Diurnal vertical migration: adaptive significance and timing. Part 2. Test of the model: details of timing. Limnol. Oceanogr. *22*: 873-886. *[Field data to test* ***Enright (1977)****]* *{**6**, **23**}*

Fiksen, O. and J. Giske. 1995. Vertical-distribution and population-dynamics of copepods by dynamic optimization. ICES J. Marine Science *52* (3-4): 483-503. *[Abstract: "Vertical distribution and population dynamics of copepods are viewed as a consequence of individual maximization of reproductive value (RV)...The optimal copepod response (vertical migration) to increased density of planktivores is to seek less risky habitats, and therefore the predation risk of copepods is a non-linear function of planktivore density. The model suggests that optimal diel migration intensity is changed with food density from no migration at low food levels, reaches a maximum at intermediate levels, but is reduced again at high algal concentrations."]*

Fiksen, O. and F. Carlotti. 1998. A model of optimal life history and diel vertical migration in *Calanus finmarchicus*. Sarsia *83*: 129-147. *[Abstract: "...copepods face a trade-off between survival and growth, as surface waters generally are more risky and productive than the dark refuges at greater depths, both in the diel and annual temporal scale. The model suggests an explanation for observations of absence of vertical migration during spring bloom and before descent to overwintering, and it suggests 1-2 successful generations per year in its basic version. It shows that migratory strategies are not similar between stages and strongly depend on the level of accumulated reserves, that the risk of predation can affect growth, distribution and number of generations and that one should expect phenotypic plasticity in DVM patterns."]*

Frost, B. W. 1988. Variability and possible adaptive significance of diel vertical migration in *Calanus pacificus*, a planktonic marine copepod. Bull. Mar. Sci. *43*: 675-694. *[Contains many vertical migration profiles, shows the flaws in **Enright's (1977)** starvation response model, and provides a more sophisticated demographic model for the 'predation-avoidance' explanation than found in **Ohman et al. (1983)**]* {**3**, **4**, **6**}

Frost, B. W. and S. M. Bollens. 1991. Variability of diel vertical migration in the marine planktonic copepod *Pseudocalanus newmani* in relation to its predators. Can. J. Fish. Aquat. Sci. *49*: 1137-1141.

Gabriel, W. and B. Thomas. 1988. Vertical migration of zooplankton as an evolutionary stable strategy. Amer. Natur. *132*: 199-216.

Hairston, N. G. 1976. Photoprotection by carotenoid pigments in the copepod *Diaptomus nevadensis*. Proc. Nat. Acad. Sci. USA 73: 971-974.

Han, B. and M Straskraba. 1998. Modeling patterns of zooplankton diel vertical migration. J. Plankton Res. 20: 1463-1487.*["This work supports the assumption that minimizing changes in sensed predation pressure can explain the wide variation in the vertical profile of zooplankton"]{}*

Hardy, A. C. 1958. The open sea: its natural history Part 1: the world of plankton. Collins London.

Harvell, C. D. 1990. The ecology and evolution of inducible defenses. Q. Rev. Biol. *65*: 323-340.

Hays, G. C. 2003. A review of the adaptive significance and ecosystem consequences of zooplankton diel vertical migrations. Hydrobiologia *503*: (1-3): 163-170.

Iwasa, Y. 1982. Vertical migration of zooplankton: a game between predator and prey. American Naturalist *29*: 915-921.

Kerfoot, W. B. 1970. Bioenergetics of vertical migration. American Naturalist *104*: 529-546. *[A model viciously attacked by **Miller et al.(1972)**]*

Kerfoot, W. B. 1972. Reply to Miller *et al.*'s letter. Amer. Natur. *106*: 548-553. *[In response to **Miller et al. 1972)**]*

Kimmerer, W. J., J. R. Burau, and W. A. Bennett. 1998. Tidally oriented vertical migration and position maintenance of zooplankton in a temperate estuary. Limnol. Oceanogr. *43*: 1697-1709. *[All zooplankton in an estuary vertically migrated with the tide, but the copepod migration was insuffficient to keep the population from being swept seaward]*[?]

Lampert, W. 1989. The adaptive significance of diel vertical migration of zooplankton. Functional Ecology *3*: 21-27.

Lane, P. A. 1975. The dynamics of aquatic systems: a comparative study of the structure of four zooplankton communities. Ecol. Monogr. 45: 307-336.

Liu, S.-H , Song Sun , and Bo-Ping Han. 2003. Diel vertical migration of zooplankton following optimal food intake under predation. J. Plankton Res. *25*: 1069-1077. *[Abstract: "The 'venturous revenue' (VR) is used as the criterion for optimal trade-offs. It is a function of environmental factors and the age of zooplankter. During vertical migration, animals are assumed to check instantaneously the variations of environmental parameters and thereby select the optimal behavioral strategy to maximize the value of VR, i.e. taking up as much food as possible with a certain risk of mortality. The model is run on a diel time scale (24 h) in four possible scenarios during the animal's life history. The results show that zooplankton can perform normal DVM balancing optimal food intake against predation risk, with the profile of DVM largely modified by the age of zooplankte"]*

Lock, A. R. and I. A. McLaren. 1970. The effect of varying and constant temperatures on size of a marine copepod. Limnol. Oceanogr. *15*: 638-640. *[Provides a refutation of the assumption of* ***Mclaren's 1963*** *adaptive model.]*

Loose, C. J. and P. Dawidowicz. 1994. Trade-offs in diel vertical migration by zooplankton: the costs of predator avoidance. Ecology *75*: 2255-2263.

Mackintosh, N. A. 1937. The seasonal circulation of the Antarctic macroplankton. Discovery Report *16*: 365-412.

Mangel, M. and C. W. Clark. 1988. Dynamic modeling in behavioral ecology. Princeton University Press, Princeton. *[Includes a model of the zooplankton vertical migration pattern described by* ***Ohman et al. (1983)****]* [**7**, **8**]

McLaren, I. A. 1963. Effects of temperatures on growth of zooplankton and the adaptive value of vertical migration. J. Fish. Res. Board Can. *20*: 685-727. *[An energetic model, energy accumulated per day, is proposed to explain the adaptive value of vertical migration. Vertical migrants have lower respiration rates and can accumulate more energy. This model was recast in* ***McLaren (1974)*** *as a demographic model, including the effects of development time on mortality.]*

McLaren, I. A. 1978. Generation lengths of some temperate marine copepods: estimation, prediction, and implications. J. Fish. Res. Board Can. *35*: 1330-1342. *[Zooplankton are apparently not food-limited (according to I.A.M., anyway). They may be limited by predation. Thus, energetic arguments based on increased food gathering abilities would not work.]* {}

Miller, C. B. 1979. Comments from a nominate referee on an exchange of notes. Limnol. Oceanogr. *24*: 785-787. *[This is a funny, cynical and troubling insight into how papers are treated in the review process. Miller was a reviewer of* ***Enright (1977)*** *and* ***Enright & Honegger's (1977)****.]* {**6**, **23**}

Miller, C. B., W. G. Pearcy, and M. H. Schonzeit. 1972. Comments on Kerfoot's paper. Amer. Natur. *106*: 545-547. *[A devastating critique of* ***Kerfoot's (1970)*** *model of vertical migration Kerfoot's paper is a perfect example of how a natural phenomenon can be explained if the explainer can design his or her own natural phenomenon.]*

Moore, H. B. and E. G. Corwin. 1956. The effects of temperature, illumination and pressure on the vertical distribution of zooplankton. Bull. Mar. Sci. Gulf Caribbean *6*: 273-287.

Neill, W. E. 1990. Induced vertical migration in copepods as a defense against invertebrate predation. Nature *345*: 524-525.

Ohman, M. D. 1988. Behavioral responses of zooplankton to predation. Bull. Mar. Sci. *43*: 530-550.

Ohman, M. D. 1990. The demographic benefits of vertical migration by zooplankton. Ecol. Monogr. *60*: 257-281.

Orcutt, J. D. and K. G. Porter. 1983. Diel vertical migration by zooplankton: Constant and fluctuating temperature effects on life history parameters of *Daphnia*. Limnol. Oceanogr. *28*: 720-730.

Pearre, S. 1973. Vertical migration and feeding in *Sagitta elegans* Verrill. Ecology *54*: 300-314.

Pearre, S. 1979. On the adaptive significance of vertical migration. Limnol. Oceanogr. *24*: 781-782. *[Commentary on* ***Enright's (1977)*** *model, which is based on* ***Conover's (1968)*** *hypothesis that copepods migrate & feed until their ration is met, rather than to avoid visual predators. Pearre argues that rising before dark isn't sufficient to rule out the predation hypothesis]* {?}

Stich, H.-B. and W. Lampert. 1984. Growth and reproduction of migrating and non-migrating *Daphnia* species under simulated food and temperature conditions of diurnal vertical migration. Oecologia (Berl.) *61*: 192-196.

Vuorinen, I. 1987. Vertical migration of *Eurytemora* (Crustacea, copepoda): a compromise between the risks of predation and decreased fecundity. J. Plankton Res. *9*: 1037-1046.

Williamson, C. E., R. W. Sanders, r. E. Moeller, and P. Stutzman. 1996. Utilization of subsurface food resources for zooplankton reproduction: implications for diel vertical migration theory. Limnol. Oceanogr. *41*: 224-233.

Wright, D., W. J. O'Brien, and G. L. Vinyard. 1980. Adaptive value of vertical migration: a simulation model argument for the predation hypothesis. Pp. 138-147 *in* W. C. Kerfoot, *ed*., Evolution and ecology of zooplankton communities. University Press of New England, Hanover, New Hampshire, U.S.A.

Wroblewski, J. S. 1982. Interaction of currents and vertical migration in maintaining *Calanus marshallae* in the Oregon upwelling zone – a simulation. Deep-Sea Research *29*: 665-686.

Wynne-Edwards, V. C. 1962. Animal dispersion in relation to social behavior. Oliver and Boyd, Edinburgh. *[A massive tome providing anecdotal evidence for how animals use social (epideictic) displays to assess population size and curtail reproductive output if necessary to avoid overshooting the habitat's carrying capacity. Wynne-Edwards' theory requires group selection. The prudent reproduction phenotype could not be an evolutionary stable strategy — a cheater, or Don Juan, phenotype would always increase in frequency]*

Zaret, T. M. and J. S. Suffern. 1976. Vertical migration as a predator avoidance mechanism. Limnol. Oceanogr. *21*: 804-813.

PREDATION AND VERTICAL MIGRATION

Bollens, S. M. and B. W. Frost. 1989. Zooplanktivorous fish and variable diel vertical migration in the marine planktonic copepod *Calanus pacificus*. Limnol. Oceanogr. *34*: 1072-1083.

Carter, J. C. H. and K. H. Goudie. 1986. Diel vertical migration and horizontal distributions of *Limnocalanus macrurus* and *Senecella calanoides* (Copepoda, Calanoida) in lakes of southern Ontario in relation to planktivorous fish. Can. J. Fish. Aquat. Sci. *43*: 2508-2514. *[Shallower distribution in lakes with lower transparency]*

Clark, L. W. and D. H. Levy. 1988. Diel vertical migration by juvenile sockeye salmon and the antipredation window. Amer. Natur. *131*: 271-290.

Decaestecker E, L. De Meester L, and D. Ebert. 2002. In deep trouble: habitat selection constrained by multiple enemies in zooplankton. Proc. Natl. Acad. Sci. USA 99: 5481-5485 *[Vertically migrating Daphnia magna pick up a bacterial endoparasite from sediments, which kills the host for release, a cost of vertical migration]*

Dini, M. L. and S. R. Carpenter. 1991. The effect of whole-lake fish community manipulation on *Daphnia* migratory behavior. Limnol. Oceanogr. *36*: 370-377.

Falkenhaug, T., K. S. Tande, and T. Semenova. 1997. Diel, seasonal and ontogenetic variations in the vertical distributions of four marine copepods. Mar. Ecol. Prog. Ser. *149*: 105-119. *[Abstract: "Diel and seasonal variations in the vertical distributions of Calanus finmarchicus, Metridia longa, M. lucens and Chiridius armatus in Malangen, northern Norway, were determined..vertical distribution of C. finmarchicus was dominated by seasonal rather than diel vertical migration, and this species was found in surface waters during the spring phytoplankton bloom (March to May), and at the bottom of the fjord in the fall and winter ... While seasonal variations in vertical behaviour are related to variations in food and light conditions, inter- and intraspecific differences may be due to life history, diet and susceptibility to predation. "]*

Fiksen, Ø, S. Eliassen, and J. Titelman. 2005. Multiple predators in the pelagic: modelling behavioural cascades . Journal of Animal Ecology *74*: 423-429.

Frost, B. W. 1988. Variability and possible adaptive significance of diel vertical migration in *Calanus pacificus*, a planktonic marine copepod. Bull. Mar. Sci. *43*: 675-694.

Frost, B. W. and S. M. Bollens. 1992. Variability of diel vertical migration in the marine planktonic copepod *Pseudocalanus newmani* in relation to its predators. Can. J. Fish. Aquat. Sci. *49*: 1137-1141. *[Abstract "We report results of a 3-yr field study of the vertical distributions and diel vertical migration (DVM) of Pseudocalanus newmani in the central basin of Dabob Bay...relationship exists between strength of DVM in P. newmani and the potential predation impact of its planktonic invertebrate predators. Second, a strong "normal" DVM (up at night, down during the day), unique for P. newmani in 5 yr of sampling at this locale, occurred at a time when the zooplanktivorous fish Ammodytes hexapterus was unusually abundant and preying on the copepod; this DVM may have been induced by the fish. DVM behavior of P. newmani was highly variable, with changes in behavior commonly occurring on a time scale of weeks; in one case the copepod switched from a normal migration pattern to a reverse migration pattern (down at night, up during the day) in less than 5 wk."]*

Gabriel, W. and B. Thomas. 1988. Vertical migration of zooplankton as an evolutionary stable strategy. Amer. Natur. *132*: 199-216.

Gliwicz, M. Z. and J. Pihanowsk. 1988. Effect of predation and resource depth distribution on vertical migration of zooplankton. Bull. Mar. Sci. *43*: 695-709.

Hays, G. C. 1995. Zooplankton avoidance activity. Nature 376: 650. {**27**}

Hays, G. C., A. J. Warner, and D. Lefevre. 1996. Long-term changes in the diel vertical migration behaviour of zooplankton. Mar. Ecol. Prog. Ser. 141: 149-159. *[Hardy continuous plankton recorder data used to argue that increased herring leads to increased diel vertical migration. **Hirst & Batten 1998** criticize the methods and conclusions arguing no association between fish and vertical migration]* {**27**}

Hirst, A. G. and S. D. Batten. 1998. Long-term changes in the diel vertical migration behaviour of Calanus finmarchicus in the North Sea are unrelated to fish predation. Mar. Ecol. Prog. Ser. *171*: 307-310. *[**Hays (1995) & Hays et al. (1996)** using Hardy continuous plankton recorder data had argued that vertical migration of C. finmarchicus is related to herring abundance. These authors found problems with the classificaiton of night & day in the Hays studies and problems with the index used to distinguish diel vertical migration. They find no association between vertical migration and herring abundance in the Hardy continuous plankton recorder data]*

Iwasa, Y. 1982. Vertical migration of zooplankton: a game between predator and prey. American Naturalist *29*: 915-921.

Leibold, M. A. 1990. Resources and predators can affect the vertical distribution of zooplankton. Limnol. Oceanogr. *35*: 938-944.

Levy, D. A. 1990. Reciprocal diel vertical migration behavior in planktovores and zooplankton in British Columbia lakes. Can. J. Fish. Aquat. Sci. *47*: 1755-1764.

Levy, D. A. 1990. Sensory mechanism and selective advantage for diel vertical migration in juvenile sockeye salmon, *Oncorhynchus nerko*. Can. J. Fish. Aquat. Sci. *47*: 1796-1802.

Mangel, M. and C. W. Clark. 1988. Dynamic modeling in behavioral ecology. Princeton University Press, Princeton. *[Includes a model of the zooplankton vertical migration pattern described by **Ohman et al. 1983**]*

Neill, W. E. 1990. Induced vertical migration in copepods as a defense against invertebrate predation. Nature 345: 524-525.

Ohman, M. D. 1986. Predator-limited population growth of the copepod Pseudocalanus sp. J. Plankton Res. 8: 673-713.

Ohman, M. D. 1988. Behavioral responses of zooplankton to predation. Bull. Mar. Sci. *43*: 530-550.

Ohman, M. D. 1990. The demographic benefits of vertical migration by zooplankton. Ecol. Monogr. *60*: 257-281.

Ohman, M. D. and S. N. Wood. 1996. Mortality estimation for planktonic copepods: *Pseudocalanus newmani* in a temperate fjord. Limnol. Oceanogr. *41*: 126-135.

Tarling, G. A. , Jarvis T. , Emsley S. M., Matthews, J.B.L. 2002. Midnight sinking behaviour in *Calanus finmarchicus*: a response to satiation or krill predation? Mar. Ecol. Prog. Ser. 240: 183-194. *[An acoustic doppler current profiler used in the Clyde Sea to document the vertical migration & krill. The midnight sinking appears to be due to the appearance of krill in the surface]* {?}

Tjossen, S. F. 1990. Effects of fish chemical cues on vertical migration patterns of *Chaoborus*. Limnol. Oceanogr. *35*: 1454-1468.

Wright, D., W. J. O'Brien, and G. L. Vinyard. 1980. Adaptive value of vertical migration: a simulation model argument for the predation hypothesis. Pp. 138-147 in W. C. Kerfoot, ed., Evolution and ecology of zooplankton communities. University Press of New England, Hanover, New Hampshire, U.S.A.

Zaret, T. M. and J. S. Suffern. 1976. Vertical migration as a predator avoidance mechanism. Limnol. Oceanogr. *21*: 804-813.

DEEP SCATTERING LAYERS & MIGRATION AND SUBMARINE ILLUMINATION

Alldredge, A. L., and J. M. King. 1980. Effects of moonlight on the vertical migration patterns of demersal zooplankton. Journal of Experimental Marine Biology and Ecology *44*: 133-156.

Barham, E. G. 1966. Deep scattering layer migration and composition: observations from a diving saucer. Science *151*: 1399-1402.

Kampa, E. M. 1975. Observations of a sonic-scattering layer during the total solar eclipse, 30 June 1973. Deep-Sea Research *22*: 417-424.

Rimmer, D. W. and B. F. Phillips. 1979. Diurnal migration and vertical distribution of phyllosoma larvae of the western rock lobster *Panulirus cygnus*. Marine Biology *54*: 109-124.

ENDOGENOUS RHYTHMS AND VERTICAL MIGRATION

Cronin, T. W. and R. B. Forward. 1979. Tidal vertical migration: an endogenous rhythm in estuarine crab larvae. Science *205*: 1020-1022. *[Crab larvae utilize estuarine circulation to move upstream in bottom waters.]*

Enright, J. T. and W. M. Hamner. 1967. Vertical diurnal migration and endogenous rhythmicity. Science *157*: 937-941.

Gliwicz, Z. M. 1986. A lunar cycle in zooplankton. Ecology *67*: 883-897.

Kimerer, W. J. and A. D. McKinnon. 1987. Zooplankton in a marine bay. II. Vertical migration to maintain horizontal distributions. Mar. Ecol. Prog. Ser. *41*: 53-60.

SWIMMING SPEED OF VERTICAL MIGRATORS

Ashjian C. J., S. L. Smith, C. N. Flagg, and C. Wilson. 1998. Patterns and occurrence of diel vertical migration of zooplankton biomass in the Mid-Atlantic Bight described by an acoustic Doppler current profiler. Cont. Shelf Res. *18*: 831-858.

Enright, J. T. 1977. Copepods in a hurry: sustained high-speed upward migration. Limnol. Oceanogr. *22*: 118-125.

Rippeth, T. P. And J. H. Simpson. 1998. Diurnal signals in vertical motions on the Hebridean Shelf. Limnol. Oceanogr. 43: 1690-1696. *[Vertical swimming speed measured using ADCP]*

Torres, J. J. and J. J. Childress. 1983. Relationship of oxygen consumption to swimming speed in Euphausia pacifica. I. Effects of temperature and pressure. Marine Biology *74*: 79-86.

ENERGETIC COST OF MIGRATING

Foulds, J. B. and J. C. Roff. 1976. Oxygen consumption during simulated vertical migration in *Mysis relicta* (Crustacea, Mysidacea). Can. J. Zool. *54*: 377-385.

Klyashtorin, L. B. 1978. Estimation of energy expenditures for active swimming and vertical migrations of planktonic crustaceans. Oceanology *18*: 91-94.

Swift, M. C. 1976. Energetics of vertical migration in *Chaoborus trivittatus* larvae. Ecology *57*: 900-914.

Torres, J. J. and J. J. Childress. 1983. Relationship of oxygen consumption to swimming speed in Euphausia pacifica. I. Effects of temperature and pressure. Marine Biology *74*: 79-86.

GENETIC VARIATION AND DIEL VERTICAL MIGRATION

De Meester, L and H. J. Dumont. 1988. The genetics of phototaxis in *Daphnia magna*: existence of three phenotypes for vertical migration among parthenogenic females. Hydrobiologia *162*: 47-55.

De Meester, L and H. J. Dumont. 1989. Phototaxis in Daphnia: on the interaction of hunger and genotype Limnol. Oceanogr. *34*: 1322-1325.

Dumont, H. J., Y. Guisez, I. Carels, and H. M. Verheye. 1985. Experimental isolation of positively and negatively phototactic phenotypes from a natural population of *Daphnia magna* Strauss: a contribution to the genetics of vertical migration. Hydrobiologia *126*: 121-127.

Weider, L. J. 1984. Spatial heterogeneity of *Daphnia* genotypes: Vertical migration and habitat partitioning. Limnol. Oceanogr. *29*: 225-235.

RELATIONSHIP TO FOOD CONCENTRATION

Dagg, M. J. 1985. The effects of food limitation on diel migratory behavior in marine zooplankton. Archiv for Hydrobiologie Egebnisse der Limnologie *21*: 247-255.

Dagg, M. J., B. W. Frost, and W. E. Walser. 1989. Copepod diel migration, feeding and the vertical flux of pheopigments. Limnol. Oceanogr. *34*: 1062-1071.

Dagg, M J. , B. W. Frost, and J. A. Newton. 1997. Vertical migration and feeding behavior of Calanus pacificus females during a phytoplankton bloom in Dabob Bay, U.S. Limnol. Oceanogr. *42*: 974-980. *[During a March bloom, 58% of phytoplankton ingestion occured at depth (25-50 m) on sinking phytoplankton. More than 50% of the copepods remained at depth during the night]*

Geedey, C. K, A. J. Tessier and K. Machledt. 1996. Habitat heterogeneity, environmental change, and the clonal structure of *Daphnia* populations. Functional Ecology 10: 613-621. *[Clonal diversity changes during the season both horizontally and vertically, with selection due to competition and seasonal anoxia]*

King, C. E. and M. R. Miracle. 1995. Diel vertical migration by *Daphnia longispina* in a Spanish lake: genetic sources of distributional variation. Limnol. Oceanogr. 40: 226-231. *[1st clear demonstration for 2 genetic clones of Daphnia with different depth distributions]*

Koslow, J. A. and A. Ota. 1981. The ecology of vertical migration in three common zooplankters in the La Jolla Bight, April-August 1967. Biological Oceanography *1*: 107-134. *[Food availability controls vertical migration]*

Huntley, M. and E. R. Brooks. 1982. Effects of age and food availability on diel vertical migration of Calanus pacificus. Marine Biology *71*: 23-31.

Napp, J. M, E. R. Brooks, F. M. H. Reid, P. Matrai and M. M. Mullin. 1988. Vertical distribution of marine particles and grazers. I. Vertical distribution of food quality and quantity. Mar. Ecol. Prog. Ser. *50*: 45-58. II. Relation of grazer distribution to food quality and quantity. Mar. Ecol. Prog. Ser. *50*: 59-72.

Simard, Y., G. Lacroix, and L. Legendre. 1985. In situ twilight grazing rhythm during diel vertical migration of a scattering layer of *Calanus finmarchicus* Limnol. Oceanogr. *30*: 598-606. *[Calanus individuals swim to the surface, fill their guts, exhibit a midnight sinking, evacuation of guts and return to the surface]*

Stich, H.-B. and W. Lampert. 1984. Growth and reproduction of migrating and non-migrating *Daphnia* species under simulated food and temperature conditions of diurnal vertical migration. Oecologia (Berlin) *61*: 192-196.

REVERSE DIEL VERTICAL MIGRATION

Båmstedt, U. 2000. Life cycle, seasonal vertical distribution and feeding of *Calanus finmarchicus* in Skagerrak coastal water. Marine Biology *137*: 279-289. *[A vertical migration index is developed to graphically display patterns of diel and reverse diel migration. From Nov. To March, adult males undergo a reverse diel vertical migration.]*

Ohman, M. D., B. W. Frost, and E. B. Cohen. 1983. Reverse diel vertical migration: an escape from invertebrate predators. Science *220:* 1404-1407. *[Diel and reverse diel vertical migration by Pseudocalanus in Dabob Bay WA.]*

VERTICAL MIGRATION IN THE GULF OF MAINE

Durbin, E. G., R. G. Campbell, S. L. Gilman, A. G. Durbin. 1995. Diel feeding-behavior and ingestion rate in the copepod *Calanus finmarchicus* in the southern Gulf of Maine during late spring. Continental Shelf Research *15*: 539-570.*[Abstract: "In situ feeding was measured on late stage C. finmarchicus in S. Gulf Maine... a spring feeding ground for the planktivorous right whale...ingestion rates ranged from 30.2% body C d^{-1} at a spring bloom station to 0.6% body C d^{-1} after stratification....C. finmarchicus food-limited after stratification. ...Diel feeding rhythms and vertical migration absent during the bloom, but developed as the bloom declined. During the post-bloom stratified conditions, diel feeding rhythms continued but vertical migration ceased. ..a small population of nonmigratory individuals resided at depth feeding upon sedimented spring bloom diatoms. At the spring bloom station C. finmarchicus ingested only a small proportion of the phytoplankton standing stock in the >7 µm size fraction (2.9% d^{-1}), reflecting the high biomass of phytoplankton and the stage composition of the C. finmarchicus population, dominated by early copepodite states with low biomass...at the post-bloom stations, dense surface aggregations of [late copepodite] C. finmarchicus consumed a significantly larger fraction of the >7 µm phytoplankton standing crop (up to 62.5% d^{-1}."]*

DIAPAUSE & SEASONAL MIGRATIONS

Hairston, N. G. and W. R. Munns. 1984. The timing of copepod diapause as an evolutionary stable strategy. Amer. Natur. *123*: 733-751. *[FORTRAN simulation of the switch from subitaneous eggs to diapause eggs. With a catastrophe eminent, diapause eggs should be equal to the time to first reproduction PLUS the time needed to obtain an R_o of 1.0 {1 female replacing itself}]* {?}

Osgood, K. E. and D.M. Checkley. 1997. Observations of a deep aggregation of Calanus pacificus in the Santa Catalina basin. Limnol. Oceanogr. 42: 997-1001. *[Diapausing C. pacificus CV individuals trapped between the sill depth and a layer of anoxic waters, attaining 6900 individuals m^{-3}]*

Ślusarczyk, M. 1995. Predator-induced diapause in *Daphnia*. Ecology 76: 1008-1013. *[In a cleverly designed laboratory system, the addition of karomones from fish induced the production of ephippia (overwintering eggs) in Daphnia magna]*

MODELS OF VERTICAL MIGRATION

Dodson, S. 1990. Predicting diel vertical migration of zooplankton. Limnol. Oceanogr. *33*: 1195-1200. *[84% of the variation in amplitude of vertical migration in lakes predicted using Secchi depth; residuals linearly related to moonlight]*[?]

Fiksen, Ø. 1997. Allocation patterns and diel vertical migration: modeling the Daphnia optima. Ecology *78*: 1446-1456. *[Model of Daphnia magna using dynamic programming compared to experiments. The use of R_o compared to r, and the latter gives better estimates of real data.]*[?]

Mangel, M. and C. W. Clark. 1988. Dynamic modeling in behavioral ecology. Princeton University Press, Princeton. *[Includes a model of the zooplankton vertical migration pattern described by* ***Ohman et al. (1983)****]* [**7**, **8**]

EFFECTS OF VERTICAL MIGRATION ON CARBON FLUX

Bradford-Grieve, J. M. , S. D. Nodder , J. B. Jillett , K. Currie , and K. R. Lassey. 2001. Potential contribution that the copepod Neocalanus tonsus makes to downward carbon flux in the Southern Ocean J. Plankton Res. 23: 963-975. *[“We estimate that Neocalanus tonsus makes a contribution to downwards carbon flux of 1.7–9.3 g C* m^{-2} *year*$^{-1}$*, in subantarctic waters, the Subtropical Front and waters immediately to the north, based on its ontogenetic vertical migration minus the biomass of eggs, the products of which are returned to the surface the following season. This flux is an order of magnitude greater than that estimated (0.27 g C* m^{-2} *year*$^{-1}$*) for vertical migration of large copepods in the North Atlantic...”]*{}

Morales, C. 1999. Carbon and nitrogen fluxes in the oceans: the contribution by zooplankton migrants to active transport in the North Atlantic during the Joint Global Ocean Flux Study. J. Plankton Res. 21: 1799-1808. *[“The role of vertical migrant zooplankton, with both seasonal/ontogenetic and daily strategies, in the active transport of carbon and nitrogen out of the surface layer in the North Atlantic is analysed. The data used were obtained mainly during the Joint Global Ocean Flux Study (JGOFS)-North Atlantic Bloom Experiment (NABE) (1989-1990) ...The contribution of seasonal migrants to carbon export flux, however, has been considerably underestimated before, although it appears to be significantly lower compared to that of diel migrants... ”]{}*

DEMOGRAPHY

Life Tables (general):

Birch, L. C. 1948. The intrinsic rate of natural increase of an insect population. Journal of Animal Ecology *17*: 15-26. *[How to calculate r]*

Caswell, H. 1978. A general formula for the sensitivity of population growth rate to changes in life history parameters. Theor. Pop. Biol. *14*: 215-230.

Caswell, H. 1980. On the equivalence of maximizing reproductive value and maximizing fitness. Ecology *61*: 19-24.

Caswell, H. 1989. Matrix population models. Sinauer Assoc., Sunderland MA *[The best available reference on matrix models]*

Caswell, H. 2001. Matrix Population Models: construction, analysis and interpretation, 2nd Edition. Sinauer Associates, Sundereland MA. 722 pp. *[The definitive treatment of matrix-based population models]*[]{}

Charnov, E. L. and D. Berrigan. 1990. Dimensionless numbers and life history evolution: age of maturity versus the adult lifespan. Evol. Ecol. 4: 273-275. *[{Age of maturity/lifespan}≈constant}]*

Deevey, E. S. 1947. Life tables for natural populations of animals. Quarterly Review of Biology *22*: 283-314. *[The Type I, II, and III mortality curves are introduced. Now, the Type I and II curves might be modeled using the Weibull distribution. A Weibull* γ *parameter corresponds to a Deevey Type II curve with a constant mortality (or constant hazard rate).]*[5]

Emlen, J. M. 1984. Population Biology. Macmillan Publishing, New York. *[A superb textbook]*

Groenendael, J., H. deKroon, and H. Caswell. 1988. Projection matrices in population biology. Trends in Evolution and Ecology *3*: 264-269.

deKroon, H, A. Plaiser, J. van Groendendael and H. Caswell. 1986. Elasticity: the relative contribution of demographic parameters to population growth rate. Ecology *67*: 1427-1431. *[Elasticities, the normalized partial differentials of* λ *to demographic rates, are defined and utilized]*

Leslie, P. H. 1945. On the use of matrices in certain population mathematics. Biometrika *33*: 183-312. *[Leslie introduced the use of matrix algebra to analyze age specific fecundity and survivorship. Emlen’s book provides a nice summary of the approach.]*

Leslie, P. H. 1958. A stochastic model for studying properties of certain biological systems by numerical methods. Biometrika *45*: 16.

Lewontin, R. C. 1965. Selection for colonizing ability. Pp. 79-94 *in* H. G. Baker and G. L. Stebbins, *eds*. The Genetics of Colonizing Species. Academic Press, New York, USA. *[Describes graphically the importance of early reproduction.]*

Manly, B. F. J. 1974. Estimation of stage-specific survival rates and other parameters for insect populations developing through several stages. Oecologia (Berl.) *15*: 277-285. *[The model applied by* ***Sonntag & Parslow (1981)*** *to marine populations.]*

Manly, B. F. J. 1974. A comparison of methods for the analysis of insect stage-frequency data. Oecologia (Berl.) *17*: 335-348.

Schaffer, W. M. and M. D. Gadgill. 1975. Selection for optimal life histories in plants. Pp. 142-147 *in* M. L. Cody and J. M. Diamond, *eds*, Ecology and Evolution of Communities. Belknap Press, Cambridge. *[Using simple models, they expand on Lamont Cole's work on when reproducing more than once (iteroparity) leads to higher growth rates.]*

Sibly, R. M. and P. Calow 1989. A life-cycle theory of responses to stress. Biol. J. Linn. Soc. *37*: 101-116.

Stearns, S. C. 1976. Life-history tactics: a review of the ideas. Quart. Rev. Biol. *51*: 3-47.

Stearns, S. C. 1977. The evolution of life history traits. a critique of the theory and a review of the data. Ann. Rev. Ecol. Syst. *8*: 145-171. *[An important review of r- & K-selection and bet-hedging]*

Werner, P. A. and H. Caswell. 1977. Population growth rates and age vs. stage distribution models for teasal (*Dipsacus sylvestris* Huds.) Ecology *58* 1103-1111. *[Introduced size-or stage-specific projection matrices. The techniques are reviewed in Emlen and Caswell (1989)]*

Wilson and Bossert. A primer on population biology.

Wood, S. N. S. P. Blythe, W. S. C. Gurney, and R. M. Nisbet. 1989. Instability in mortality estimation schemes related to stage-structure population models. IMA Journal of Mathematics applied in Medicine and Biology *6*: 47-68.

Confidence limits for life-history parameter estimates

Efron, B. 1982. The jackknife, the bootstrap and other resampling plans. SIAM, Philadelphia.

Meyer, J. S., C.-G. Ingersoll, L. L. McDonald and M. S. Boyce. 1986. Estimating uncertainty in population growth with jackknife vs. bootstrap techniques. Ecology *67*: 1156-1166.

Life tables and life cycles for benthic populations

Akesson, B. 1982. A life table study on three genetic strains of *Ophryotrocha diadema* (Polychaeta Dorvilleidae). International Journal of Invertebrate Reproduction *5*: 59-69. *[One of the few polychaete life tables. Provides a nice example of the advantages of early reproduction]*

Ayal, Y. and U. N. Safriel. 1982. r-curves and the cost of the planktonic stage. Amer. Natur. *119*: 391-401. *[The inability to estimate mortality in the planktonic stage limits the application of demographic theory to most benthic populations.]*

Caswell, H. 2001. Matrix Population Models: construction, analysis and interpretation, 2nd Edition. Sinauer Associates, Sundereland MA. 722 pp. *[The definitive treatment of matrix-based population models]*[]

Fauchald, K. 1982. Life diagram patterns in benthic polychaetes. Proc. Biol. Soc. Wash. *96*: 160-177.

Feller, R. J. 1980. Quantitative cohort analysis of a sand-dwelling meiobenthic harpacticoid copepod. Est. Coast. Mar. Sci. *11*: 459-476. *[One of the few life tables for meiofaunal populations.]*

Grahame, J. 1977. Reproductive effort and r- and K-selection in two species of *Lacuna* (Gastropoda: prosobranchia). Marine Biology *40*: 217-224. *[Reproductive effort measured as total spawn weight: body weight]*

Gremare, A., A. G. Marsh, and K. R. Tenore. 1988. Short-term reproductive responses of *Capitella* sp. I (Annelida: Polychaeta) fed on different diets. J. exp. mar. Biol. Ecol. *123*: 147-162.

Gremare, A., A. G. Marsh, and K. R. Tenore. 1988. Fecundity and energy partitioning in *Capitella capitata* type I (Annelida: Polychaeta) Marine Biology *100*: 365-372.

Gremare, A., A. G. Marsh, and K. R. Tenore. 1989. Secondary production and reproduction of *Capitella capitata* Type I (Annelida: Polychaeta) during a population cycle. Mar.

Ecol. Prog. Ser. 51: 99-105.

Gudmondsson, H. 1985. Life history patterns of polychaete species of the family Spionidae. J. mar. biol. Assoc. U.K. *65*: 93-111.

Levin, L. A. 1984. Multiple patterns of development in *Streblospio benedicti* Webster (Spionidae) from the three coasts of North America. Biol. Bull. *166*: 494-508. *[Planktotrophic and lecithotrphic phenotypes — both phenotypes found on Boston's Savin Hill Cove]*

Levin, L. A. 1986. Effects of enrichment on reproduction in the opportunistic polychaete *Streblospio benedicti* (Webster): a mesocosm study. Biol. Bull. *171*: 143-160.

Levin. L. A., H. Caswell, K. D. DePatra and E. L. Creed. 1987. Demographic consequences of larval development mode: planktotrophy vs. lecithotrophy in *Streblospio benedicti*. Ecology *68*: 1877-1886.

Levin, L. A. and D. V. Huggett. 1990. Implications of alternate reproductive modes for seasonality and demography in an estuarine polychaete. Ecology *71*: 2191-2208. *[Includes an analysis of the seasonal variability of populations as a function of development mode, elasticity analyses, and production]*

Levinton, J. S. and S. Stewart. 1988. Effects of sediment organics, detrital input and temperature on demography, production and body size of a deposit feeder. Mar. Ecol. Prog. Ser. *49*: 259-266.

Muus, K. 1973. Settling, growth, and mortality of young bivalves in the Oresund. Ophelia *12*: 79-116. *[Muus's study contains detailed analyses of the mortality of bivalve cohorts over several years.]*

Roughgarden, J, Y. Iwasa, and C. Baxter. 1985. Demographic theory for an open marine population with space-limited recruitment. Ecology *66*: 54-67. *[A stage-projection matrix.]*

Strathman, R. R. and M. F. Strathmann. 1982. The relationship between adult size and brooding in marine invertebrates. Amer. Natur. *119*: 99-101.

Weinberg, J.R., H. Caswell, and R. B. Whitlatch. 1986. Demographic importance of ecological interactions: how much do statistics tell us? Marine Biology *93*: 305-310. *[This is a poor title for conveying the main theme: measuring relative fecundity or (even worse) the size of individuals may not be informative in assessing relative effects on the population growth rate. Juvenile survival rate is the key parameter for Gemma gemma. The elasticity concept introduced by Caswell is nicely applied]*

Life tables for pelagic populations

Aksnes, D. L. 1996. Natural mortality, fecundity and development time in marine planktonic copepods — implications of behavior. Mar. Ecol. Prog. Ser. *131*: 315-316 .

Aksnes, D. L, and T. J. Hoisaeter. 1987. Obtaining life table data from stage-frequency distributional statistics. Limnol. Oceanogr. *32*: 514-516.

Asknes, D. L. and M. D. Ohman. 1996. A vertical life table approach to zooplankton mortality estimation. Limnol. Oceanogr. *41*: 1461-1469. *[Horizontal=time series of abundance, Vertical=stage distributions at 1 time. Simulation compared to horizontal data, showing that the vertical approach can work]*

Asknes, D. L., C. B. Miller, M. D. Ohman, and S. N. Wood. 1997. Estimation techniques used in studies of copepod population dynamics — a review of underlying assumptions. Sarsia *82*: 279-296.

Allan, J. D. 1976. Life history patterns in zooplankton. American Naturalist *110*: 165-180. *[Applies a general model, based on* ***Lewontin (1965)*** *to analyze the per capita growth of different zooplankton groups]*

Ang, P. A. and R. E. DeWreed. 1990. Matrix models for algal life history stages. Mar. Ecol. Prog. Ser. *59*: 171-181.

Corkett, C. J. and I. A. McLaren. 1970. Relationships between development rate of eggs and older stages of copepods. J. Mar. Biol. Assoc. U. K. *50*: 161-168. *[Provides data for McLaren's demographic models of vertical migration.]*

DeMott, W. R. 1980. An analysis of the precision of birth and death rate estimates for egg-bearing zooplankters. Pp. 337-345 *in* W. C. Kerfoot, *ed*., Evolution and ecology of zooplankton communities. University Press of New England, Hanover, New Hampshire, U.S.A.

Dorazio, R. M. 1986. Estimating population birth rates of zooplankton when rates of egg deposition and hatching are periodic. Oecologia (Berlin) *69*: 532-541.

Dorazio, R. M. and J. T. Lehman. 1983. Optimal reproductive strategies in age-structured populations of zooplankton. Freshwater Biology *13*: 157-175.

Edmondson, W. T. 1960. Reproductive rates of rotifers in natural populations. Mem. Ist. Ital. Idrobiol. *12*: 21-77.

Edmondson, W. T. 1968. A graphical model for evaluating the use of the egg ratio for measuring birth and death rates. Oecologia *1*: 1-37.

Edmondson, W. T. 1972. Instantaneous birth rates of zooplankton. Limnol. Oceanogr. *17*: 792-795.

Eiane, K, D. L. Asknes, M. D. Ohman, S. Wood, and M. B. Martinussen. 2002. Stage-specific mortality of Calanus spp. under different predation regimes. Limnol. Oceanogr. *47*: 636-645. *[Two different fjords with different predation regimes (invertebrate and vertebrate) sampled, producing drastic differences in stage-specific mortality]*

Eiane, K. And M.D. Ohman. 2004. Stage-specific mortality of *Calanus finmarchicus*, Pseudocalanus elongatus and Oithona similis on Fladen Ground, North Sea, during a spring bloom. Mar. Ecol. Prog. Ser. *268*: 183-193. *[Pseudocalanus undergoes a DVM, but larger Calanus finmarchicus stay deep day and night. The small Oithona don't vertically migrate but they aren't experiencing much mortality because of their small size and lack of mechanical signature make them difficult to detect by visual and invertebrate predators using mechanoreceptors.]*

Fager, E. W. 1973. Estimation of mortality coefficients from field samples of zooplankton. Limnol. Oceanogr. *18*: 297-301. *[A critique of Mullin and Brooks methods with some advice]*

Fujiwara, M. and H. Caswell. 2001. Demography of the endangered North Atlantic Right Whale Nature 414: 537-541. *[Mortality is the major cause of low numbers and saving 2 whales per year could lead to the survival of the species]* {}

Fulton, J. 1973. Some aspects of the life history of *Calanus plumchrus* in the Strait of Georgia. J. Fish. Res. Board Can. *30*: 811-815.

Gabriel, W., B. E. Taylor, and S. Kirsch-Prokosch. 1987. Cladoceran birth and death rate estimates: experimental comparisons of egg-ratio methods. Freshwater Biology *18*: 361-372.

Gehrs, C. W. and A. Robertson. 1975. Use of life tables in analyzing the dynamics of copepod populations. Ecology *56*: 665-672. *[This is the first life table analysis for a marine copepod population.]*

Hairston, N. G. and S. Twombly. 1985. Obtaining life table data from cohort analyses: a critique of current methods. Limnol. Oceanogr. *30*: 886-893.

Hairston, N. G., M. Braner and S. Twombly. 1987. Perspective on prospective methods for obtaining life-table data. Limnol. Oceanogr. *32*: 517-519.

Hairston, N g. , T. A. Dillon, B. T. De Stasio. 1990. A field test for the cues of diapause in a freshwater copepod. Ecology *71*: 2218-2223.

Hay, S. J., G. T. Evans, and J. C. Gamble. 1988. Birth, growth and death rates for enclosed populations of calanoid copepods. J. Plankton Res. *10*: 431-459. *[Using the* ***Sonntag & Parslow (1981)*** *technique the effects of pollution on P. elongatus, A. clausi, and Temora lonigicornis are assessed. A very nice paper.]*

Landry, M. R. 1975. The relationship between temperature and the development of life stages of the marine copepod *Acartia clausi* Giesbr. Limnol. Oceanogr. *20*: 854-857.

Landry, M. R. 1978. Population dynamics and production of a planktonic marine copepod, *Acartia clausi*, in a small temperate lagoon in San Juan Island, Washington. Int. Revue ges. Hydrobiol. *63*: 77-119.

Landry, M. R. 1983. The development of marine calanoid copepods with comment on the isochronal rule. Limnol. Oceanogr. *28*: 614-624.

Lynch, M. 1980. The evolution of cladoceran life histories. Q. Rev. Biol. *55*: 23-42.

Lynch, M. 1983. Estimation of size-specific mortality rates in zooplankton populations by periodic sampling. Limnol. Oceanogr. *28*: 533-545.

Lynch, M. 1984. The limits to life history evolution in *Daphnia*. Evolution *38*: 465-482.

Marcus, N. H. 1984. Recruitment of copepod nauplii into the plankton: importance of diapause eggs and benthic processes. Mar. Ecol. Prog. Ser. *15*: 47-54.

McLaren, I. A. 1978. Generation lengths of some temperate marine copepods: estimation, prediction, and implications. J. Fish. Res. Board Can. *35*: 1330-1342.

McLaren, I. A. 1986. Is "structural" growth of *Calanus* potentially exponential" Limnol. Oceanogr. *31*: 1342-1345.

McLaren, I. A. and C. J. Corkett. 1981. Temperature-dependent growth and production by a marine copepod. Can. J. Fish. Aquat. Sci. *38*: 77-83.

Miller, C. B., J. K. Johnson, and D. R. Heinle. 1977. Growth rules in the marine copepod genus *Acartia*. Limnol. Oceanogr. *22*: 326-335. *[The 'isochronal rule' of copepod development is proposed.]*

Miller, C. B., M. E. Huntley, and E. R. Brooks. 1984. Post-collection molting rates of planktonic, marine copepods: measurement, applications and problems. Limnol. Oceanogr. *29*: 1274-1289.

Miller, C. B., B. W. Frost, H. P. Batchelder, M. J. Clemons, and R. E Conway. 198 . Life histories of large, grazing copepods in a subarctic Ocean gyre: *Neocalanus bungii* in the Northeast Pacific. Prog. Oceaong. *13*: 201-243.

Myers, R. A. and J. A. Runge. 1983. Predictions of seasonal natural mortality rates in a copepod population using life-history theory. Marine Ecology Progress Series *11*: 189-194.

Neill, W. E. 1975. Experimental studies of microcrustacean competition, community composition and efficiency of resource utilization. Ecology <u>56</u>: 809-826. *[Includes life tables of competing populations.]*

Ohman, M. D. 1985. Resource-satiated population growth of the copepod *Pseudocalanus* sp. Arch. Hydrobiol. *21*: 15-32. *[In Dabob Bay, <u>Pseudocalanus</u> per capita growth controlled by predation, not food. The developmental rate is fast, the egg production is high, and the food availability is in the saturating range]*

Ohman, M. D. 1986. Predator-limited population growth of the copepod *Pseudocalanus* sp. J. Plankton Res. *8*: *673-713. [<u>Pseudocalanus</u> isn't food limited: generation times rapid, egg production high, and food abundant. Therefor, must be limited by predators]*

Ohman, M. D., B. W. Frost, and E. B. Cohen. 1983. Reverse diel vertical migration: an escape from invertebrate predators. Science *220*: 1404-1407.

Ohman, M. D., D. L. Aksnes, and J. A. Runge. 1996. The interrelationship of copepod fecundity and mortality. Limnol. Oceanogr. *41*: 1470-1477. *[Egg production rates doesn't necessarily indicate changes in food supply – they are strongly affected by mortality]*

Ohman, M. D. and S. Wood. 1996. Mortality estimation for planktonic copepods: Pseudocalanus newmani in a temperate fjord. Limnol. Oceanogr. 41: 126-135.

Ohman, M. D. and H.-J. Hirche. 2001. Density-dependent mortality in an oceanic copepod population. Nature 412: 638-641 [Calanus finmarchicus in the Norwegian Sea]

Paloheimo, J. E. 1974. Calculation of instantaneous birth rate. Limnol. Oceanogr. *19*: 692-694.

Paloheimo, J. E. and W. D. Taylor. 1987. Comments on life-table parameters with reference to *Daphnia pulex*. Theor. Pop. Biol. *32*: 289-302.

Parslow, J. and N. C. Sonntag. 1979. Techniques of systems identification applied to estimating copepod population parameters. Journal of Plankton Research *1*: 137-151.

Parslow, J., N. C. Sonntag, and J. B. L. Mathews. 1979. Application of systems identification techniques to estimate copepod population parameters. Journal of Plankton Research {?}

Rigler, F. H. and J. M. Cooley. 1974. The use of field data to derive population statistics of multivoltine copepods. Limnol. Oceanogr. *19*: 636-655.

Runge, J. A. 1984. Egg production of the marine, planktonic copepod, *Calanus pacificus* Brodsky: laboratory observations. J. exp. Mar. Biol. Ecol. *74*: 53-66.

Runge, J. A. 1985. Relationship of egg production of *Calanus pacificus* to seasonal changes in phytoplankton availability in Puget Sound, Washington. Limnol. Oceanogr. *30*: 382-396.*[Copepods isolated in the lab produce eggs proportional to their recent feeding history]*

Runge, J. A. 1987. Measurement of egg production rae of *Calanus finmarchicus* from preserved samples. Can. J. Fish. Aquat. Sci. *94*: 2009-2012.

Runge, J. A., I. A. McClaren, C. J. Corkett., R. N. Boher and J. A. Koslow. 1985. Molting rates and cohort development of *Calanus finmarchicus* and *C. glacialis* in the sea off Southwest Nova Scotia. Marine Biology *86*: 241-246.

Saunders, J. F. and W. M. Lewis. 1987. A perspective on the use of cohort analysis to obtain demographic data for copepods. Limnol. Oceanogr. *32*: 511-513.

Sonntag, N. C. and J. Parslow. 1981. Technique of systems identification applied to estimating copepod production. Journal of Plankton Research *3*: 461-473. {**32**, **34**}

Taylor, B. E. 1988. Analyzing population dynamics of zooplankton. Limnol. Oceanogr. *33*: 1266-1273.

Threlkeld, S. T. 1979. Estimating Cladoceran birth rates: the importance of egg mortality and the egg age distribution. Limnol. Oceanogr. *24*: 601-612.

Estimating Secondary Production:

Crisp, D. J. 1984. Energy flow measurements. Pp. 284-372 *in* N. A. Holme and A. D. McIntyre, *eds*., Methods for the study of Marine Benthos. Blackwell, Oxford.

Downing, J. A. and F. H. Rigler. 1984. A manual for the assessment of secondary productivity in fresh waters, 2nd Ed. Blackwell.

Kimmerer, W. J. 1987. The theory of secondary production calculations for continuously reproducing populations. Limnol. Oceanogr. *32*: 1-13.

Landry, M. R. 1978. Population dynamics and production of a planktonic marine copepod, *Acartia clausi*, in a small temperate lagoon in San Juan Island, Washington. Int. Revue ges. Hydrobiol. *63*: 77-119. *[Reduced dispersal in an enclosed population allows the determination of field demographic rates.]*

McLaren, I. A. 1969. Population and production ecology of zooplankton in Ogac Lake, a landlocked fiord on Baffin Island. J. Fish. Res. Board Can. *26*: 1485-1559.

Mullin, M. M. and E. R. Brooks. 1970. Production of the planktonic copepod, *Calanus helgolandicus*. Bull Scripps Instn. Oceanogr. *17*: 89-103.

Oyenekan, J. A. 1983. Production and population biology of *Capitella capitata*. Arch. Hydrobiol. *98*: 115-126.

Romanovsky, Y. E. and L. V. Polischuk. 1982. A theoretical approach to calculation of secondary production at the population level. Int. Revue ges. Hydrobiol. *67*: 341-359. *[They clearly distinguish between germinated vs somatic production.]*

GROUP SELECTION

Maynard Smith, J. and M. Slatkin. 1973. The stability of predator-prey systems. Ecology *54*: 384-391. *[Contains the criticism that Slobodkin had invoked group selection in his discussion of prudent predation, rebutted by* ***Slobodkin 1974****]*

Nunney, L. 1985. Group selection, altruism and structured-deme models. Amer. Natur. *126*: 212-230.

Nunney, L. 1989. The maintenance of sex by group selection. Evolution *43*: 245-257.

Slobodkin, L. B. 1974. Prudent predation does not require group selection. Amer. Natur. *108*: 665-678. *[**Maynard Smith & Slatkin (1973)** had attacked the MacArthur-Slobodkin prudent predator by stating that it tacitly implied group selection. Slobodkin responds with my favorite opening line from a scientific paper, "Interpreting what an author really did or did not "tacitly assume" is a favorite game of literary criticism, but is best undertaken when the author in question is dead or otherwise incapacitated." LBS goes on to present an individual selectionist argument that looks like prudence. He concludes that prey and predator coevolve so that prey make predators look prudent.]*

Wade, M. J. 1978. A critical review of the models of group selection. Quart. Rev. Biol. *53*: 101-114.

Williams, G. C. 1966. Adaptation and Natural selection. *[The major critique of Wynne-Edwards' verbal model group selection]*

Wilson, D. S. 1983. The group selection controversy: history and current status. Ann. Rev. Ecol. Syst. 14: 159-187. *[Group selection can be justified as an extension of Sewall Wright's shifting balance theory of intra- and interdemic selection]*

Wynne-Edwards, V. C. 1962. Animal dispersion in relation to social behavior. Oliver and Boyd, Edinburgh. *[Proposes the incredibly wrong-headed group-selectionist theory that individuals, after epideictic displays, limit their population growth to stay within the carrying capacity]*

ON GAME THEORY

Brown, G. W. 1951. Iterative solutions of games by fictitious play. Pp. 374-376 *in* T. C. Koopmans, *ed.* Activity, analysis of production and allocation. Wiley, New York.

Frank, P. W. 1981. A condition for a sessile strategy. Amer. Natur. *118*: 288-290. [**12**]

Levin, S. A., B. Grenfell, A. Hastings, and A. S. Perelson. 1997. Mathematical and computational challenges in population biology and ecosystems science. Science 275: 334-343. *[Reviews a number of newer models, including Game Theory and ESS's, individual-based models and epidemiological models of disease.]*

Lucas, W. F. 1968. A game with no solution. Bull. Amer. Math. Soc. *74*: 237-239.

Lucas, W. F. 1971. Some recent developments in n-person game theory. SIAM Review *13*: 491-523.

Luce, R. D. and H. Raffa. 1957. Games and Decisions. Wiley, New York.

Maynard Smith, J. 1982. Evolution and the theory of games. Cambridge University Press, Cambridge [*Maynard Smith uses 2-person symmetric games to introduce game theory to evolutionary ecology]*{**7**, **14**, **15**, **16**}

Maynard Smith, J and G. R. Price. 1973. The logic of animal conflict. Nature *246*: *15-18. [For the 1st time, 2-person game theory applied to evolutionary problems and the concept of an evolutionary stable strategy introduced]{**8**}*

von Neumann, J. and O. Morgenstern. 1944. Theory of Games and Economic Behavior. Princeton University Press, Princeton. *[The classic book that created both 2-person and n-person game theory]*

Paulos, J. A. 1995. A mathematician reads the newspaper. Basic Books, New York. 212 pp.*[A collection of short articles about mathematics, probability and statistics]* [**11**]

Schmeidler, D. 1969. The nucleolus of a characteristic function game. S.I.A.M J. Appl. Math. *17*: 1163-1170.

Taylor, P. D. and L. B. Jonker. 1978. Evolutionary stable strategies and game dynamics. Math. Bioscience *40*: 145-156.

COEVOLUTION

Van Valen, L. 1973. A new evolutionary law. Evol. Theory 1: 1-30. *[The Red Queen hypothesis introduced. Like Lewis Carroll's Red Queen, coevolving species must evolve rapidly just to stay where they are on the fitness landscape.] {**15**}*

PHILOSOPHY OF SCIENCE

Kuhn, T. S. 1962. The Structure of Scientific Revolutions. University of Chicago Press, Chicago. *[Paradigms & normal science overthrown by the rare revolution]*

Lakatos, I. 1970. Falsification and the methodology of scientific research programmes. Pp. 91-196. in I. Lakatos and A. Musgrave, eds., Criticism and the Growth of Knowledge. Cambridge University Press . *[(p. 45)...experiments do not simply overthrow theories, ...no theory forbids a state of affairs specifiable in advance. It is not that we propose a theory and Nature may shout NO; rather, we propose a maze of theories, and Nature may shout INCONSISTENT.]*

Index