

Effects of food limitation and emigration on self-thinning in experimental minnow cohorts

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Summary

1. The theory of food-regulated self-thinning (FST) for mobile animals predicts population density (N) to be an inverse function of mean body mass (W) scaled to an exponent (b), such that $N = k W^{-b}$, where k is a constant. FST also predicts energy requirements (or energy flow) to remain constant over time (termed energetic equivalence) as losses to cohorts (e.g. emigration and mortality) are balanced by increased growth of surviving individuals.

2. To test these predictions, we analysed the dynamics of six experimental minnow cohorts. Replicate populations of fish were held under identical conditions with a constant and limited supply of food over a 126-day period. Half of the cohorts were open to emigration, and half were closed so that fish could only be lost through starvation mortality.

3. Patterns of self-thinning indicated non-linear changes in population density and energy flow in relation to changes in mean body mass and time, respectively. Non-linear patterns of self-thinning were probably due to a delayed growth response to changes in population density effected through mortality and/or emigration. Contrary to results of similar experiments on other fish, emigration did not have a significant influence on the pattern of self-thinning.

4. These results may be attributed to trophic interactions within cohorts and the importance of social behaviour to cohort dynamics. Both population density and energy flow in our experimental populations appeared to cycle, with episodes of starvation and mortality alternating with food recovery and weight gain, as predicted by recent models of stepwise die-off and stunted growth in animal cohorts.

5. Most of the support for FST in mobile animals comes from observational data on mean body mass and population density. Potentially important mechanisms, including the manner in which individuals are lost or retained in populations, are usually not investigated directly. Such tests of FST can only provide equivocal support. Detailed observational study and controlled experiments are needed to understand casual mechanisms.

Key-words: animal energetics, cohort dynamics, density dependence, energetic equivalence population regulation, self-thinning, social behaviour.

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Introduction

Self-thinning refers to a pattern of density-dependent growth and survival commonly observed in plants and animals (Begon, Firbank, & Wall 1986; Fréchet & Lefaire 1995; Sackville Hamilton,

Matthew & Lemaire 1995). As individuals in a cohort grow over time, increasing per capita resource demands lead to a shortage of resources. This shortage leads to mortality and/or emigration, and population density declines accordingly. Self-thinning relationships are generally represented by simple power functions such as:

where N is equilibrium population density, W is mean body size (usually mass), and k and b are intercept and slope parameters, respectively. For mobile animals, self-thinning is generally thought to occur through food-regulated growth and mortality (Begon *et al.* 1986; Bohlin *et al.* 1994), but competition for space may also lead to self-thinning (Grant *et al.* 1998). If resource availability is constant over time, this leads to an inverse linear relationship (thinning line) between population density and mean body size on a logarithmic scale.

The theoretical basis for food-regulated self-thinning (hereafter referred to as FST; Fréchette & Lefavre 1995) is derived from energetics allometries (Begon *et al.* 1986; Bohlin *et al.* 1994). Per capita energetic requirements increase as individual body mass (w) increases, according to the relationship:

$$M = a w^b \quad \text{eqn 2}$$

where M is metabolic rate ($\text{mg O}_2 \text{ h}^{-1}$), and a and b are regression coefficients as in equation 1. It can be shown that the relationship between body mass and population density (equation 1) is the inverse of that relating body mass and metabolic rate by combining equations 1 and 2 to represent population energy flow. Average energy flow per individual can be represented by substitution of mean mass (W) for individual body mass (w) in equation 2. The total energy flow through a population (F) may then be estimated by the product of average energy flow per individual ($a W^b$) and population density (N):

$$F = N a W^b \quad \text{eqn 3}$$

which can be rearranged to express population density in relation to average body mass:

$$N = F/a W^{-b} \quad \text{eqn 4}$$

where $F/a = k$, the intercept of equation 1. Thus, at equilibrium, food-limited cohorts should show a negative relationship between population density and body mass with a slope of $-b$. This implies a linear relationship between log body mass and log population density with slope $-b$.

For mobile animals, the most extensive body of evidence in support of self-thinning comes from observational data on body size and abundance of stream-living salmonid fish (reviewed by Grant *et al.* 1998). Changes in population density of salmonid fish related to increased body size may be due to increasing per capita resource demands for food, space or both. Salmonids in streams often defend territories, and space requirements increase predictably as individuals grow larger (Grant & Kramer 1990). Slopes of thinning lines predicted for space vs. food limitation are potentially distinguishable with observational data (Keeley & Grant 1995;

Dunham & Vinyard 1997; Keeley 1998; Steingrims-son & Grant 1999).

Outside of salmonid fish, data can be found to support FST in mobile animals (Begon *et al.* 1986; Latto 1994) but the generality of this proposed rule has yet to be demonstrated. Furthermore, to our knowledge, there are few experimental data available to evaluate self-thinning in mobile animals (but see Keeley 1998). Experiments designed to identify causal mechanisms are badly needed because patterns of self-thinning in mobile animals may be complicated by factors unrelated to competition for food (Fréchette & Lefavre 1995). Here, we present experimental evidence for self-thinning in food-regulated populations of juvenile fathead minnows (*Pimephales promelas* Rafinesque). We maintained six fish cohorts for over 4 months with a constant and limited food supply. If the FST is correct, we predicted an equilibrium relationship between mean body mass and population density with slope $-b$ (equation 1).

A second prediction from FST is that total energy flow through a population (F) at equilibrium will be constant over time (termed energetic equivalence; Bohlin *et al.* 1994). During self-thinning, losses through death or emigration reduce energy flow through a population. As population density declines, however, increased individual growth results from the concomitant per capita increase in food resources. Energy flow through a population is predicted to be constant over time because losses to a population are balanced by individual growth. Regression slopes of estimated energy flow (F) in relation to time should thus be zero. We tested this prediction with an individual-based estimate of total energy flow (Dunham & Vinyard 1997). This test of FST may be more robust because information on individual variation is not lost through averaging body mass within a cohort (Lømnicki 1988).

We also examined how patterns of self-thinning were effected through mortality or emigration. The mechanism by which individuals are lost from a cohort or population, either via mortality or emigration, may have important effects on population structure and dynamics (MacMahon & Tash 1988). The design of our experiments was similar to the study reported by MacMahon & Tash (1988). In closed cohorts, losses can only occur as individuals die *in situ*. In open cohorts, individuals facing a shortage of food may emigrate before they die of starvation. Accordingly, we predicted thinning lines should develop more rapidly in open cohorts. Closed cohorts should show a delayed response if mortality acts more slowly to remove individuals. In closed cohorts, delayed or cyclic die-offs from starvation mortality also may occur (cf. Scheffer *et al.* 1995), while such patterns should be less pronounced in those open to emigration.

Finally, we were interested in contrasting patterns of self-thinning observed in a species with social behaviour that differs dramatically from more commonly studied salmonid fish (Grant *et al.* 1998). Unlike territorial salmonids, fathead minnows often exhibit strong conspecific attraction, such as schooling behaviour in response to predation risk (Theodorakis 1989; Hager & Helfman 1991). In contrast to other groups (e.g. plants and sedentary invertebrates) where self-thinning has been applied, self-thinning in mobile animals should consider the relative roles of social behaviour, emigration and mortality. These potentially important influences have been generally ignored in past treatments of self-thinning in mobile animals.

Methods

EXPERIMENTAL DESIGN AND MAINTENANCE

Self-thinning was compared between groups of fish held in three closed tanks and in three tanks open to emigration from 21 May to 22 September 1996. Individual closed and open tanks were paired to form three experimental blocks. Each block consisted of one closed and one open tank with water flowing from a common sump. Tanks were rectangular plastic tubs (55 × 38 × 22 cm) filled with 28 L of dechlorinated tap water. Nylon mesh covers prevented fish from jumping out of the tanks. Each sump was a plastic tub (60 × 40 × 23 cm) filled with 33 L of dechlorinated tap water. This design ensured constant water volume in tanks. All tanks were placed together indoors on the University of Nevada Reno campus (Nevada, USA).

A 3.8-cm diameter outlet was attached to a 67-cm long piece of polyvinyl chloride (PVC) pipe, the bottom of which was located 2 cm below the water surface in each tank. Water was pumped, via the filter, from the sump into the tanks, creating flow (0.01 L s⁻¹) through the outlets. Open tanks differed from closed tanks in that this outlet was left open to allow for emigration. Outlets in open tanks flowed into a 67-cm long by 7.6 cm wide by 2 cm deep PVC emigration channel that drained into a small net pen. To leave a tank, fish had to swim into the outlet pipe, through the emigration channel, and into the net pen. Water velocity was low enough to allow (healthy) fish the opportunity to explore the emigration channel and either return to the main tank or emigrate into the net pen.

Juvenile fathead minnows were collected in May 1996 from Little Washoe Lake, Washoe County, Nevada, USA. Prior to experimentation, fish were maintained in two 76-L filtered and aerated aquaria for 1 week and fed commercial sinking pellet food *ad libitum*. Information from the manufacturer (Tetra Sales USA, Blacksburg, VA) indicated the

food was composed of approximately 45% crude protein and 8% crude fat, with the remaining fraction consisting of ash and moisture.

On 18 May 1996, 100 randomly sampled minnows were introduced into each experimental tank. Both open and closed tank outlets were left closed and fish were fed *ad libitum* for 3 days to allow for acclimation to experimental conditions. After this acclimation period, excess food was removed and mesh covers on outlets of the open tanks were removed. For the duration of the experiment, cohorts in each tank were fed a constant daily ration of 0.25 g of the sinking pellet food, about 4% of the average initial dry weight of the cohorts. Food was delivered in the morning (09.00–10.00) in a single batch. This method of feeding was employed to minimize the ability of individuals to monopolize access to food. During feeding we did not observe attempts by fish to monopolize or defend food, rather it appeared feeding was best described by 'scramble' or exploitative competition (J. Dunham, personal observations).

Dechlorinated tap water was added to the sumps as needed to maintain water levels. Filters containing ammonia chips and activated carbon were changed every 2 weeks. Aeration was provided by natural mixing of turbulent flows in tank outlets. These simple conditions are more than sufficient to maintain fathead minnows, which are extremely tolerant of adverse environmental conditions in the wild (Moyle 1976). During the experiments, no fish were observed to exhibit any behaviour or signs of disease indicating poor health due to conditions other than starvation.

DATA COLLECTION

All fish were weighed on day 0 of the experiment and every 2 weeks thereafter, beginning with week 4 (day 28) of the experiment, allowing enough time for self-thinning to occur. Fish were netted from tanks, individually weighed to the nearest 0.01 g, and then returned. On days when body masses were recorded, fish were not fed until after measurements were completed. Within minutes of being returned to the tanks, fish resumed normal feeding behaviour. All tanks were closed to emigration overnight (*c.* 8 h) after the fish were returned, however, to minimize any possible effects of handling on emigration behaviour. Stress due to handling was determined to be minimal, with only one or two mortalities per weighing event across all six tanks. Mortalities and emigrants in tanks were removed twice daily, and immediately enumerated and weighed. Frequent monitoring of mortalities and moribund fish prevented cannibalism, which may complicate analyses of self-thinning (Fr chet te & Lefai vre 1995).

Previous workers (Latto 1994; Fr chet te & Lefaivre 1995) have emphasized the importance of choosing an appropriate b -value for prediction of slopes for thinning lines. Fr chet te & Lefaivre (1995) suggested that ontogenetic changes in the value of b may be important. For cyprinid fish, values of b were previously thought to be 0.80 (Wieser 1991), but Post & Lee (1996) found a biphasic metabolism–mass relationship in common carp (*Cyprinus carpio*). Their analysis suggested a relatively flat (mass-independent) relationship for individuals up to 0.29 g, and a steeper mass-specific ($\text{mg O}_2 \text{g}^{-1} \text{h}^{-1}$) slope of -0.179 for larger fish. The latter value corresponds closely to a value of 0.80 for whole body metabolism–mass relationships (expressed in terms of $\text{mg O}_2 \text{h}^{-1}$; Wieser 1991). Because the mean mass of individuals in this study was always greater than 0.29 g, we used a value of 0.80 as the expectation for b under the hypothesis of food-regulated self-thinning (equation 4).

Statistical analysis of relationships between body size and population density is another controversial issue in the literature on self-thinning (Sackville Hamilton *et al.* 1995). We used a double logarithmic transformation of equation 1 to permit an analysis of the linear relationship between mean body size and population density. Analyses proceeded with ordinary least squares regression, but we soon determined that linear models were inappropriate (see the Results). Fit of the linear model to the data was evaluated by examining residual deviations.

Population energy flow was estimated by summing individual energetic requirements (Dunham & Vinyard 1997). Taking w as individual body mass and summing for $i=1$ to n , the number of individuals in a cohort, total energy flow (F , expressed in units of $\text{mg O}_2 \text{h}^{-1}$) was calculated as follows:

$$F = \sum a w^b \quad \text{eqn 5}$$

Values of b were converted from biphasic mass-specific estimates for common carp, with b -values of -0.051 for fish less than 0.29 g and -0.179 for fish larger than 0.29 g (Post & Lee 1996).

We analysed temporal trends to determine if energy flow was constant over time, as predicted by FST (Bohlin *et al.* 1994). Changes in population energy flow in relation to time (day) and treatment (open vs. closed tanks) were analysed with a repeated measures analysis of variance (SAS MIXED procedure) with a first-order autoregressive covariance structure (Littell *et al.* 1996). We considered linear, quadratic, cubic and quartic day effects in the model, plus interaction terms and block effects. No reduced major axis slope adjustments were made (McArdle 1988; Sackville Hamilton *et al.*

1995) because we were only interested in whether or not slopes were significantly different from zero.

Body masses of fish that died or emigrated during the course of the experiment were compared to resident fish by first-order autoregressive models with linear, quadratic and cubic time effects (Littell *et al.* 1996). Regressions of median body size vs. time for each of the six tanks were used to predict expected body masses of fish on the day each individual died or emigrated (assuming they were similar in size to resident fish). Choice of the mean or median as a measure of central tendency did not affect the outcome of the analysis. The difference between predicted median body mass of resident fish and individual mortalities or emigrants was compared with an expected value of zero (no difference) for both treatments (open and closed tanks) by means of a Wilcoxon non-parametric rank sum test.

Results

BODY SIZE, ABUNDANCE AND ENERGY FLOW

We attempted to fit a linear (log-transformed) self-thinning model to the relationship between population density and body size (mass), but residual deviations clearly indicated a non-linear (piecewise or stepwise) pattern (Fig. 1). In each case, an initially steep decline in population density was followed by an abrupt decrease in slope (Fig. 1), and we were confident in rejecting the hypothesis of a constant linear relationship between body mass and population density with slope $-b$ (-0.80). This result was independent of the choice of b because a linear model was not plausible, even with a logarithmic transformation.

A plot of total energy flow in relation to time similarly suggested a non-linear relationship (Fig. 2). Analyses of population energy flow in relation to time (day) revealed significant linear (RMANOVA $F_{1,39} = 48.52$, $P < 0.0001$), quadratic (RMANOVA $F_{1,39} = 38.04$, $P < 0.0001$) and cubic (RMANOVA $F_{1,39} = 5.56$, $P < 0.024$) day effects. Linear, quadratic and cubic day by treatment interactions, block effects, treatment effects and quartic day effects were not significant. In summary, energy flow within cohorts was not related to whether cohorts were open or closed to emigration, but energy flow changed significantly over time (Fig. 2).

EMIGRATION, MORTALITY AND COHORT STRUCTURE

Fish began emigrating almost immediately from open tanks, while mortality did not occur until day

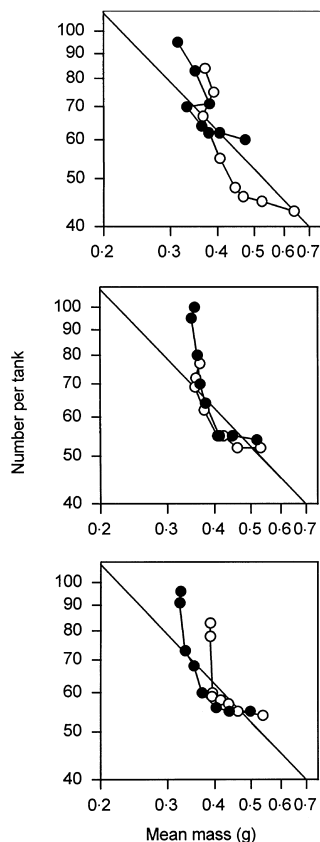


Fig. 1. Number of fish per tank in relation to mean body mass for each of three experimental blocks. Data points represent mass recorded at 2-week intervals, ranging from day 28 to day 126. Solid diagonal lines have slopes equal to -0.80 , the slope of thinning lines predicted by FST. Filled circles represent closed tanks; unfilled circles represent open tanks.

14 (Fig. 3). By the end of the experiment, however, cumulative total losses were not related to treatment effects (heterogeneity $\chi^2 = 5.65$, d.f. = 3, NS).

Median fish mass and biomass of cohorts increased over time in a non-linear fashion (Fig. 4). Median body masses of residents on each day were predicted for each tank by first-order autoregressive models with linear, quadratic and cubic time effects (results not shown). All regressions had high coefficients of determination, ranging from 0.86 to 0.98.

Individual fish that died or emigrated during the course of the experiment were smaller than fish that remained alive in the tanks (residents). Predicted median mass of residents was significantly larger than observed masses of emigrants ($n = 104$) and mortalities ($n = 170$) (Wilcoxon non-parametric rank sum test, $P < 0.0001$). On average, emigrants were 0.08 g smaller than residents, while mortalities were 0.13 g smaller, but these values were not significantly different from each other.

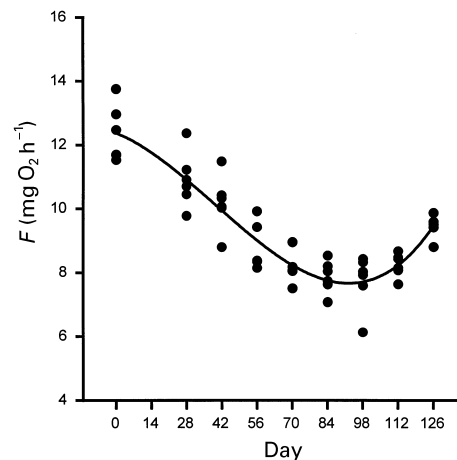


Fig. 2. Energy flow (F) in six experimental cohorts from day 28 to day 126. The fitted regression line represents an average for all cohorts.

Discussion

POPULATION DENSITY AS A FUNCTION OF BODY MASS

We found little evidence to support predictions for FST (equation 1) of minnow cohorts held in the laboratory with a constant and limited food supply. Population density did decline, however, over the course of the experiment, and many fish died or emigrated in an obvious response to food limitation. The relationship between body mass and population density was clearly non-linear, even after log transformation. While the predicted value of $-b$ used in this study was not derived specifically from fathead minnows, it is clear that a purely linear model of FST was not sufficient to explain the observed patterns of self-thinning.

A non-linear pattern of self-thinning might be expected if initial population densities in this experiment were above equilibrium. In such cases, density is expected to precipitously decline via starvation mortality and/or emigration until the equilibrium thinning line is approached (Bohlin *et al.* 1994). If so, slopes of the relationship between body mass and population density should only approach b after suitable time has passed for a pattern of self-thinning to manifest itself. In our experiments, losses to populations and rapid increases in mean body mass did not occur until after day 84. Therefore, if time lags in the approach to equilibrium occurred, we may only expect thinning lines with slope $-b$ (-0.80) to occur after day 84. However, slope estimates from regressions on the last three sampling periods (days 98–126) ranged from -0.21 to -0.46 , so this explanation seems unlikely.

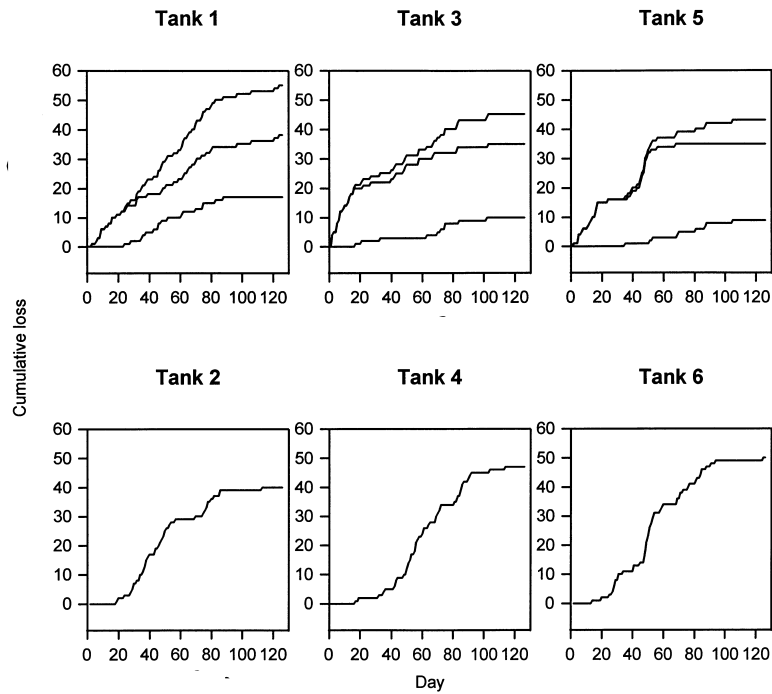


Fig. 3. Cumulative losses (number of individuals) due to emigration and mortality in minnow cohorts during days 0–126. For cohorts in open tanks (top row), solid lines on top represent total losses, and lines in the middle and bottom represent fish that emigrated and died, respectively. Patterns of mortality in closed tanks are shown in the bottom row. Each vertical pair of cohorts represents one experimental block.

Attenuation of mortality and/or emigration, combined with increased growth, resulted in rapid increases in mean body size and population biomass after day 84. Thus, during the initial phase of self-thinning growth did not track changes in population density closely enough to produce the pattern expected from FST. After day 84, increased indivi-

dual growth and lack of losses to cohorts through emigration or mortality led to a relatively shallow thinning trajectory.

An important implication of FST is that regulation of cohorts occurs relatively continuously over an extensive period, rather than during a relatively brief ‘critical period’ for survival (Armstrong 1997). Had we continued the experiment for a much longer time under relatively constant (and notably unnatural) conditions, a thinning trajectory with a slope similar to that proposed by FST may have resulted as the ‘steps’ in the thinning pattern produced an overall slope similar to that predicted by FST. Other investigators have noted stepwise patterns of self-thinning, resulting from predator–prey cycling (Scheffer *et al.* 1995) and from seasonal or ontogenetic changes in limiting resources (Armstrong 1997). Clearly, the timing and time scale of observations on body mass and population density may affect the pattern of self-thinning that is observed (see also Steingrímsson & Grant 1999)

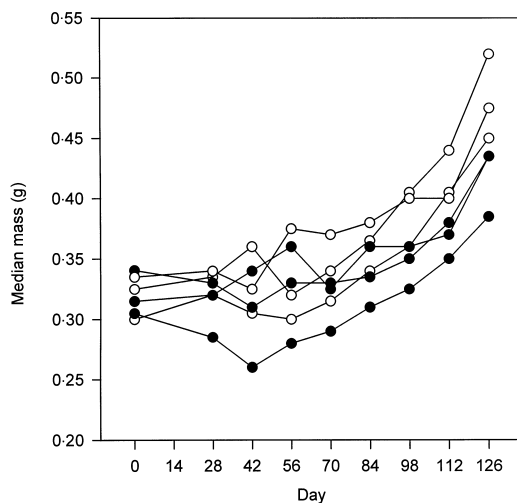


Fig. 4. Median mass over time for six minnow cohorts. Filled circles represent fish from cohorts in closed tanks; unfilled circles represent open tanks.

POPULATION ENERGY FLOW

It could be argued stepwise self-thinning trajectories in this study are a statistical artefact of using mean mass as a measure of central tendency, but individual-based analyses of energy flow through cohorts are in agreement with our interpretations of the data. Population energy flow (F), predicted to be

constant (energetic equivalence), varied significantly over time (Fig. 2).

As individuals were lost to cohorts, either through mortality or emigration, population energy flow declined until the latter part of the experiment (days 84–98), when it began to increase. This increase in energy flow was due to a decrease in mortality and emigration during the end of the experiment (Fig. 3), and growth of surviving individuals (Fig. 4). These qualitative results are independent of the value of b assumed in estimating F because F is predicted to be constant. Changing b would only change the intercept of the F vs. time regression (assuming b is a constant).

Temporal changes in thinning slopes, mean body mass and F indicate that net energy allocation in the cohorts switched from respiration to production after day 84. Some individuals may have grown rapidly over the entire course of the experiment, but production at the cohort level was not evident until day 84. The timing of this cohort-level shift of energy allocation from respiration to production represents, in principle, the point at which sufficient starvation mortality (or emigration) has occurred to allow increased food access to, and growth of, surviving individuals (Scheffer *et al.* 1995).

EFFECTS OF EMIGRATION

Self-thinning is caused by loss of individuals from cohorts and concomitant increased growth by survivors. We hypothesized that the nature of losses to cohorts, namely emigration vs. mortality, would have an important influence on self-thinning. However, emigration did not have a detectable effect on patterns of self-thinning or energy cycling through cohorts. Furthermore, final densities of fish among treatments were similar, as were body masses of fish that died or emigrated during the experiments.

We modelled our experiments in part after a similar study of desert pupfish (*Cyprinodon macularius*) in closed and open systems (MacMahon & Tash 1988). In that study, emigration had several important effects on pupfish populations. Pupfish in populations closed to emigration attained higher densities, with higher mortality rates, lower body condition and recruitment. MacMahon & Tash (1988) attributed emigration of desert pupfish to food limitation and territorial aggression by breeding males. In this study food limitation was probably an important proximate cause of emigration, but aggressive breeding behaviour was not a factor because fish in the experiment were juveniles. Our finding that body masses of fish that died or emigrated were similar suggests fish did not emigrate until very near death by starvation.

Observations on the behaviour of fathead minnows during the study suggested individuals were aggregated in schools (J. Dunham, personal obser-

vations). Fathead minnows commonly exhibit schooling behaviour as a response to predation risk (Theodorakis 1989; Hager & Helfman 1991). If such was the case in this study, starving minnows may have been reluctant to emigrate and risk exposure to a perceived risk of predation. Further evidence of the importance of social interactions for fathead minnows is suggested by the fact that fish held singly in respirometers have elevated metabolic rates, relative to those held in groups (Escandon 1994).

This interpretation of the results points to the potential importance of social behaviour to self-thinning in mobile animals. If social behaviour has an effect on rates of emigration, then it must certainly have an effect on self-thinning. In the case of territorial species like pupfish (MacMahon & Tash 1988) or salmonids (Grant *et al.* 1998), self-thinning may be strongly affected by territorial behaviour. Unlike territorial salmonids or pupfish, however, patterns of self-thinning we observed in cohorts of juvenile fathead minnows may have resulted, at least in part, from conspecific attraction.

In our experiments, losses to populations through starvation mortality or emigration may not have occurred at rates fast enough to allow a pattern of self-thinning as predicted by FST. Perhaps if predators were included in our experiments (as would be the case in the wild), predation on smaller or starved fish would remove individuals more quickly from cohorts and FST would be more apparent as a continuous process (e.g. constant thinning slope).

Results of this study provide one of the first tests of FST for mobile animals under controlled experimental conditions (see also Keeley 1998). Patterns of self-thinning observed in minnow cohorts were not consistent with the simple predictions of FST. Furthermore, there are many factors not considered herein that may play an important role in self-thinning, such as variation in growth and metabolism (e.g. b -values) related to water temperature, interactions with other species (e.g. predators, competitors and parasites), social interactions with conspecifics, and access to food resources. Clearly FST is a special case of self-thinning that occurs when interactions among a host of other factors are not important.

There are many reported cases where relationships between population density and body size show patterns consistent with FST (Begon *et al.* 1986; Elliot 1993; Grant 1993; Bohlin *et al.* 1994; Latto 1994; Armstrong 1997; Dunham & Vinyard 1997). The existence of such relationships between body size and abundance can provide only equivocal support for FST, however, because it is impossible to exclude the influences of other potentially important factors without supporting data or controlled conditions to exclude alternatives. As we have shown here, social behaviour, emigration and mortality are among the important factors that should

receive consideration for mobile animals. Application of FST to mobile animals is appealing in its logic and simplicity, but we concur with recent criticisms (Fréchette & Lefavre 1995; Armstrong 1997; Dunham & Vinyard 1997; Keeley 1998; Steingrímsson & Grant 1999) that call for more rigorous approaches to understanding important causal mechanisms.

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