

*Full Length Research Paper*

# Non-harmonic covariation among life-history traits in amphipods (*Hyalella azteca*) and crayfish (*Orconectes virilis*) in Canadian boreal lakes

R. L. France

<sup>1</sup>Integrated Environmental Management, Department of Engineering, NSAC, Truro, Nova Scotia, Canada.

<sup>2</sup>Faculty of Graduate Studies, Dalhousie University, Halifax, Nova Scotia, Canada.

<sup>3</sup>Center for Technology and the Environment, Harvard University, Cambridge, Massachusetts, USA.

E-mail: [rfrance@nsac.ca](mailto:rfrance@nsac.ca).

Accepted 19 May, 2011

**Principal components analysis was used to determine the degree of covariance among life-history traits in eight populations of the amphipod *Hyalella azteca* and four populations of the crayfish *Orconectes virilis* inhabiting Canadian boreal lakes. Assumptions of tightly coupled traits which vary unidimensionally as a single fixed unit or "tactic" are untenable for these organisms. Instead, populations are characterized by an independence among demographic traits which contradict some established beliefs in life-history trade-offs. The degree to which organisms display traits which can vary independently will influence the resulting phenotypic flexibility of life history responses to varying environmental conditions and may dictate ranges of latitudinal distribution.**

**Key words:** Amphipod *Hyalella azteca*, crayfish *Orconectes virilis*, life-history traits, independent variation.

## INTRODUCTION

Life-history theory involves the study of compromises among a set of traits operating through natural selection through the differential allocation of energy between somatic and reproductive activities (Stearns, 1976; Fenwick, 1984) and is a current field of popular study on a wide variety of organisms (for example, Wellington and Robertson, 2001; Purchase et al., 2005; Ljubisavljevic et al., 2007; Lardies and Bozinovic, 2008; Castaneda et al., 2010). It is the particular combination of traits, adjusted in response to prevailing environmental conditions that is important in defining a specific life-history (Trendall, 1982). In this respect, a life-history "tactic" or "strategy" may be envisioned as a tightly integrated assemblage of such traits functioning together as a coadapted whole. Although there has generally been little work on the adaptive value of life-history traits in freshwater invertebrates relative to that on other taxa, most such research has followed the aforementioned theory (Strong, 1972; Calow and Woolhead, 1977; Browne and Russell-Hunter, 1978; Brown, 1979, 1983; Lynch, 1980;

Schwartz, 1984; Bailey and Mackie, 1986; Etter, 1989; Chung et al., 2008). Work by Trendall (1982) on the mosquito fish *Gambusia affinis*, however, has questioned some assumptions implicit in life-history theory and instead demonstrated a degree of independence in the variability of specific traits for this particular species. Such a mechanism of variable, rather than fixed, relationships would of course put fewer restrictions on the patterns of grouped traits, thereby increasing the range of possible life-history expressions. Haukoja and Hakala (1978) and Kllgour and Mackie (1991) both showed that the inter-correlations among demographic traits for populations of freshwater clams occurred in some circumstances opposite to that expected by theory. As Trendall (1982) stated: "Defining the extent to which traits are connected by fixed relationships is therefore a means of defining life history variation".

Despite the statement by Stearns (1976) that life-history has been regarded for over fifty years as "a set of adaptive traits connected by relations that can be

mathematically analyzed", few either before or since have actually attempted to define the mathematical interdependency of such traits (Pease and Bull, 1988). Later, Stearns (1980), recognizing the paucity of potentially falsifiable empirical evidence on life-history theory, highlighted the need to use "appropriate statistical procedures, such as factor analysis (to observe) the clustering of traits in phenotype space". Unfortunately, studies of phenotypic variation in demographic traits have generally been restricted to analysis of unilateral changes in specific traits or at best to correlating pairs of traits (Saether, 1987, 1988; Harvey and Clutton-Brock, 1985; Trendall, 1982; Brown, 1983; Stearns, 1983, 1984; Dunham and Miles, 1985; Dodson and Murie, 1987; Gaillard et al., 1989). In contrast, the present study, like that of Trendall (1982), uses principal component analysis to examine the degree of covariance among life-history traits, in this case, for populations of the amphipod *Hyalella azteca* (Saussure) and the crayfish *Orconectes virilis* (Hagen) inhabiting Canadian boreal lakes.

## METHODS

The approach taken in the present study was to examine the microgeographic variation in, and correlations among, life-history traits of conspecific populations inhabiting contrasting environments. The boreal lakes sampled are located in two locations on the Canadian Shield of central and northwestern Ontario, are contained within small, glacially-formed basins, and are ice-covered from November to March. Lakes were selected to reflect a gradient in two major anthropogenic influences - cottage development and concomitant increase in system productivity, and elevated hydrogen ion deposition and resulting lake acidification.

Consensus has yet to be reached with regard to which particular life-history traits best encompass a "tactic", and how to best go about measuring these. As Haukoja and Hakala (1978) and Hedges (1985) found careful attention must be paid to the particular parameters used. For example, because of confounding with body size, the regression statistics from fecundity relationships are superior to simple measures of mean brood size; due to size-specific mortality, adult body size may not be closely related to the average somatic growth rate of the population; age at maturity is really but a poor requisite relative to the statistical derivation of mean size/age at onset of sexual maturity (Wenner et al., 1974); and longevity estimated from a few old individuals may be an imprecise reflection of the true rate of population mortality (Krementz et al., 1989). The present study circumvented these problems wherever logistically possible.

Ecological data on the *H. azteca* populations are contained in France (1987a, b, 1992a, b, 1993a, b, 1996), France and LaZerte (1987) and France and Stokes (1988). Briefly, from 500 to 2000 amphipods were collected monthly from 8 lakes (little clear, red chalk bay, red chalk main, blue chalk, gullfeather, dickie, crosson, hene) during the ice-free seasons of two years. Sampling was conducted in shallow macrophyte stands with use of a simple coring device. Growth rates were calculated for young, juveniles and adults based on analyses of population length-frequency distributions (Mathias, 1971). Because the increase in size in *Hyalella* is approximately linear, rates of growth were obtained from the slopes of the least-squares regressions of mean head lengths against time in weeks (ranges across populations = young: 0.005 to 0.017 mm; juvenile: 0.001 to 0.005 mm; adult: 0.003 to 0.013 mm). Mean size at maturity for females ranged from 0.452 to 0.593 mm

across the populations. Fecundities are expressed as mean number of eggs per mm head length (population range = 12.8 to 16.5). Preamples values (Strong, 1973) are log transformed proportions for each population (range = 2.30 to 4.49). Mortality rates were calculated as the slopes of the least-squares regressions of  $\ln + 1$  proportional densities per gram macrophyte biomass against time in days for both adults and juveniles. Mortality rates for adults are averaged for two summers (range = 0.009 to 0.018,) while those for juveniles were calculated for the inter-winter period (range = 0.006 to 0.013). Mortality of young was calculated as the difference between total expected recruitment and the juvenile standing crop after recruitment had ceased (range = 27.0 to 63.9). Sample sizes ranged from 65 for the mean fecundity calculations to over 6000 for the growth rate derivations.

Ecological data for *O. virilis* are contained in France (1985, 1987c, 1993c), France and Graham (1985) and France et al. (1989). From 68 to 200 crayfish were collected monthly from 4 lakes (Lake 224, 239, 240, and experimentally acidified Lake 223) during the ice-free seasons of two years. Sampling was conducted in the littoral zone with SCUBA. Growth rates are expressed as the relative percentage increase in size based on length-frequency analysis (France et al., 1989) (range across populations = 195.7 to 227.4 mm). Mean sizes at onset of sexual maturity were obtained with the method of Wenner et al. (1974) (population ranges = females: 19.2 to 21.8 mm; males: 21.8 to 23.6 mm). Instantaneous rates of mortality were computed using catch curve procedures described in Ricker (1975) (range = 0.95 to 1.44). Other life-history data included: maximum size (range = 29.3 to 33.5 mm), mean egg weight (range = 1.48 to 1.55 ug), mean ovarian fecundity range = 77.7 to 98.1 eggs/g, and slopes (that is relative) and intercepts (that is absolute) of the size-specific fecundity regressions (ranges = relative: 7.83 to 10.93), absolute: -108.3 to -191.6). Sample sizes ranged from 178 for ovarian fecundity to over 4000 for the growth rate derivations.

Principal component analysis (PCA) was used to test whether the life history traits were either tightly coupled as an integrated unit displaying unidimensional change or rather whether they displayed independent flexibility in their patterns of variation. PCA is a relatively objective procedure which provides insight into relationships among individual traits by fitting a series of composite axes in ordinate space (Gauch, 1982). This ordination in a small number of dimensions emphasizes the major patterns of variation and co-dependence among characters (Digby and Kempton, 1987). The percentage of variation explained by each component measures the relative strength of that component. Traits which are associated occur together and provide interpretation of the particular component in which they occur. Individual character loadings reflect the strength of association. As per established procedure (Trendall, 1982), PCA was run using life-history traits scaled with means = 0 and standard deviations = 1. Standardization was important because of differences among the traits with respect to measures of quantification and variability.

## RESULTS

In the PCA for amphipods (Table 1), the first three components explained almost 80% of the variation, but only three of the 9 traits had character loadings over 0.70. Juvenile and young mortality rates and young growth rate were positively associated with PC 1. Mean female size at maturity and juvenile growth rate were negatively associated with PC 2 and 3, respectively.

For crayfish, the first two components explained over 80% of the variation, with all 9 character traits displaying loadings over 0.70 in one of the three principal

**Table 1.** Loadings of scaled life history traits for *Hyalella azteca* on principal components (PC) 1 to 3.

	PC 1	PC 2	PC 3
Fecundity	0.32	-0.69	-0.56
Preamplexus	0.50	0.50	0.69
Female size maturity	0.29	-0.74	0.45
Young growth	0.70	-0.63	0.10
Juvenile growth	0.03	0.62	-0.74
Adult growth	0.51	0.46	0.06
Young mortality	0.83	0.15	0.29
Juvenile mortality	0.92	0.13	-0.31
Adult mortality	-0.33	-0.33	-0.01
% of variation	38.6	24.4	16.7

**Table 2.** Loadings of scaled life history traits for *Orconectes virilis* on principal components (PC) 1 to 3.

	PC 1	PC 2	PC 3
Relative fecundity	-0.09	0.14	-0.99
Absolute fecundity	0.12	-0.03	0.99
Ovarian fecundity	0.98	-0.08	0.17
Egg weight	0.32	0.79	-0.53
Female size maturity	0.92	-0.36	-0.14
Male size maturity	0.96	-0.25	0.15
Growth	0.97	0.03	-0.24
Maximum size	0.97	0.22	-0.10
Mortality	0.17	0.91	0.38
% of variation	54.1	28.1	17.8

components (Table 2). Growth rate, mean sizes at onset of sexual maturity and mean ovarian fecundity were all positively associated with PC 1. Grouped on the second component were mortality rate and mean egg weight. Relative and absolute fecundity were strongly associated with PC 3.

If an organism's life-history evolved as a single coadapted unit, the great majority of variation would be expected to be explained solely through a single PCA axis. Clearly this is not true for either *H. azteca* or *O. virilis*. In both cases, a substantial portion of the total life-history variation among populations is explained by each of the three principal components. The high loadings of preamplexus and juvenile growth for *H. azteca*, and of relative and absolute fecundity for *O. virilis*, on the third component suggests that PC 3 measures previously non-described variation rather than being merely the third step of a general summary (Trendall, 1982). Such results refute the hypothesis of unidimensional change along a single axis, the basis for much life-history theory (Stearns, 1984). In contrast, relationships among life-history traits for these organisms do not appear to be rigidly fixed. In other words, proximally situated

populations of crayfish and amphipods in Canadian boreal lakes display a marked degree of phenotypic plasticity in their expression of life-history. Predetermined "tactics" do not exist for these north-temperate, boreal populations. The three principal components are independently associated most strongly with traits representing mortality and young growth, reproduction and maturation, and reproductive activity and juvenile growth, respectively for *H. azteca*; and are associated with growth, maturation and ovarian fecundity, mortality and egg weight, and absolute fecundity, respectively for *O. virilis*.

## DISCUSSION

Life-history theory is often based on belief in the expression of certain relationships among traits as general principles (Stearns, 1976). In PCA, the loadings of individual traits enables examination for the presence of these general principles (Trendall, 1982). Covarying traits will be associated with the same component. Positive relationships are reflected by both traits having

the same sign. Opposite signs denote trade-offs between traits. Trade-offs between somatic growth and fecundity in these populations of amphipods and crayfish do not occur. Likewise, trade-offs between fecundity and mortality rate do not occur. The hypothesis of Strong (1973) concerning increased amphipod precomplexus under conditions of high mortality was not supported. An inverse relationship between somatic growth and relative fecundity does not exist for these populations. A strong trade-off between egg weight and number (Stearns, 1980) also did not occur. Maximum adult size was independent of embryo weight. In conclusion, the traits characterizing mortality, growth, and reproduction for these two species were not closely interrelated. These findings are in support of contentions by Haukoja and Hakala (1978), Trendall (1982) and Brown (1983) that tight couplings of life-history traits at the intraspecific level, although they certainly may exist, should not be invoked "a priori" as a general principle.

Stearns (1980) questioned whether life history "tactics" as such are real in an evolutionary sense, or rather whether they exist as emergent epiphenomena through collapsing taxonomic hierarchies. The present work, together with that of Trendall (1982), Brown (1983) and Stearns (1983), supports the contention that what we perceive of as being a life-history "strategy" [implications involved in use of such a noetic metaphor notwithstanding, (Chapleau et al., 1988)] being based on a number of covarying traits, is probably less likely to be recognized within species than among species or even higher taxa.

Unfortunately, studies of the variation in demographic traits among conspecific populations inhabiting different environments are much less common than are those based on comparisons among different species. As a result, unless the research emphasis is shifted toward the former, empirical tests of the predictions of life-history theory will remain sorely lacking (Stearns, 1976, 1983; Fenwick, 1984). It is extremely time consuming to obtain the comprehensive data needed to examine intraspecific variability in life-history, however. In consequence, studies have been limited to comparing, for example, 2 (Brown, 1983), 3 (Ljubisavljevic et al., 2007; Landies and Bozinovic, 2008), 4 (Trendall, 1982), 6 (Dobson and Murie, 1987), 8, 13 (Haukoja and Hakala, 1978) or 17 (Kilgour and Mackie, 1991) populations.

What this means is that Stearns (1976, 1980) clarion call for the need for mathematical testing of life-history theory is compromised whereas in the present study using PCA, the number of variables being examined is greater than the number of replicate populations. This weakness has to be acknowledged. Life-history theory, based on an assumption of fixed relationships between traits, limits both the degree and direction of phenotypic variation possible toward environmental change (Trendall, 1982). The present results indicate that for the species *H. azteca* and *O. virilis*, populations even within a

localized region can display a flexibility of life-history responses impossible under a system based on a single, coadapted package of rigid trade-offs. Such a result is perhaps not surprising considering that *H. azteca* and *O. virilis* are the most ubiquitous species of freshwater amphipods and crayfish in the Western Hemisphere (Bousfield, 1958; Crocker and Barr, 1968). Both species therefore have a wide "ecological amplitude" or tolerance, enabling their successful colonization and occupation of a vast variety of habitats (France, 1989e). Trendall (1982) in *G. affinis* also has a ubiquitous natural distribution and has been easily spread worldwide for mosquito control (Stearns, 1977). Conceivably, all such wide ranging species will display patterns of independent variation among their life-history traits. Indeed, it is likely that it is precisely just such an uncoupling of tight linkages among traits that actually enables ubiquitous distributions to occur in the first place. Alternatively, those species constrained ecologically or physiologically to limited distributional ranges at lower latitudes [that is Rapoport's Rule (Stevens, 1989)] may display a strong canalization among their life-history parameters. Whether this is a result of (a) higher structural complexity of habitats which precludes expression of colonizing or independently varying traits, (b) a greater temporal period for cohesion to develop among individual traits, or (c) stronger competitive pressure pigeonholing organisms to specialized, individual packages (or "tactics") of traits, all of which are more likely to characterize low latitude environments (France, 1989e), is unknown. Such answers might go far in helping to provide insight into the species-richness gradient, which, because it currently "mocks our ignorance", has been referred to as "the major, unexplained pattern in natural history" (Levin, 1989). Further, understanding patterns of variability among life-history traits will aid in the assessment of how different species might respond to, and possibly recover from, anthropogenic stress, such as, for example, the influence of climate change on species range extensions or restrictions (France, 1991).

## REFERENCES

- Bailey RC, Mackie GL (1986). Reproduction of a fingernail clam in contrasting habitats: life-history tactics. *Can. J. Zool.*, 64: 1701-1704.
- Bousfield EL (1958). Freshwater amphipod crustaceans of glaciated North America. *Can. Field Nat.*, 72: 55-113.
- Brown KM (1979). The adaptive demography of four freshwater pulmonate snails. *Evolution*, 33: 417-432.
- Brown KM (1983). Do life history tactics exist at the intraspecific level? Data from freshwater snails. *Am. Nat.*, 121: 871-879.
- Browne RA, Russell-Hunter WD (1978). Reproductive effort in molluscs. *Oecologia*, 37: 23-27.
- Calow R, Wodlhead AS (1977). The relation between predation, reproductive effort and age-specific mortality in the evolution of life history strategies - some observations on freshwater triclads. *J. Anim. Eco.*, 46:765-782.
- Castaneda LE, Sandrock C, Vorburger C (2010). Variation and covariation of life history traits in aphids are related to infection with the facultative bacterial endosymbiont *Hamiltonella defensa*. *Biol. J.*

- Linn. Soc., 1000: 237-247.
- Chapleau F, Johanson PH, Williamson M (1988). The distinction between pattern and process in evolutionary biology: The use and abuse of the term "strategy". *Oikos*, 53:136-138.
- Chung PP, Hyne RV, Mann RM, Ballard JW (2008). Genetic and life-history trait variation of the amphipod *Melita plumulosa* from polluted and unpolluted waterways in eastern Australia. *Sci. Total Environ.*, 403: 222-229.
- Crocker DW, Barr DW (1968) Handbook of the crayfishes of Ontario. Univ. of Toronto Press.
- Digby PGN, Kempton RA (1987). Multivariate analysis of ecological communities. Chapman and Hall Publ.
- Dodson FS, Murie JO (1987). Interpretation of intraspecific life history patterns: evidence from Columbian ground squirrels. *Am. Nat.*, 129: 382-397.
- Dunham AE, Miles DB. (1985). Patterns of covariation in life history traits of squamate reptiles: the effects of size and phylogeny reconsidered. *Am. Nat.*, 126: 231-257.
- Etter RJ (1989). Life history variation in the intertidal snail *Nucella lapillus* across a wave-exposure gradient. *Ecology*, 70: 1857-1876.
- Fenwick GD (1984). Life-history tactics of brooding crustacea. *J. Exp. Mar. Biol. Ecol.*, 84: 247-264.
- France RL (1985). Relationship of crayfish (*Orconectes virilis*) growth to population abundance and system productivity in small oligotrophic lakes in the Experimental Lakes Area, northwestern Ontario. *Can. J. Fish. Aquat. Sci.*, 42: 1096-1102.
- France RL (1987a). Test of biotic and abiotic environmental determinants of amphipod (*Hyalella azteca*) pre-emptus. *Can. J. Fish. Aquat. Sci.* 49: 478-482.
- France RL (1987b). Aggregation in littoral amphipod populations: transformation controversies revisited. *Can. J. Fish. Aquat. Sci.*, 44: 1510-1515.
- France RL (1987c). Reproductive impairment of the crayfish *Orconectes virilis* in relation to experimental lake acidification. *Can. J. Fish. Aquat. Sci.*, 44(Suppl. 1): 107-113.
- France RL (1991). Empirical methodology for predicting changes in species range extension and richness through climate warming. *Internat. J. Biometeorol.*, 34: 211-216.
- France RL (1992a). Biogeographical variation in size-specific fecundity of the amphipod *Hyalella azteca*. *Crustaceana* 62: 240-248.
- France RL (1992b). Use of sequential sampling of amphipod abundance to classify the biotic integrity of acid-sensitive lakes. *Environ. Manage.*, 16: 157-166.
- France RL (1992c). The North American latitudinal gradient in species richness and geographical range of freshwater crayfish and amphipods. *Amer. Nat.*, 139: 342-354.
- France RL (1993a). Production and turnover of *Hyalella azteca* in central Ontario, Canada compared with other regions. *Freshw. Biol.*, 30: 343-349.
- France RL (1993b). Inter-relationships among variables comprising amphipod production. *Hydrobiology*, 271: 71-74.
- France RL (1993c). Effect of experimental lake acidification on crayfish *Orconectes virilis* population recruitment and age composition in northwestern Ontario, Canada. *Biol. Conserv.*, 63:53-59.
- France RL (1996). Biomass and production of amphipods in low alkalinity lakes affected by acid precipitation". *Environ. Pollut. Ser. A*, 94: 189-194.
- France RL, Graham L (1985). Increased microsporidian parasitism of the crayfish *Orconectes virilis* in an experimentally acidified lake. *Water Air Soil Pollut.*, 26: 129-136.
- France RL, LaZerte BD (1987). Empirical hypothesis to explain the limited abundance of *Hyalella azteca* (Amphipoda) in anthropogenically acidified lakes. *Can. J. Fish. Aquat. Sci.*, 44: 112-1121.
- France RL, Stokes PM (1988). Isoetid-zoobenthos associations in acid sensitive Ontario, Canada lakes. *Aquat. Bot.*, 32: 99-114.
- France R, Holmes J, Lynch A (1991). Use of size-frequency data for estimation of the age composition of crayfish populations. *Can. J. Fish. Aquat. Sci.*, 48: 2324-232.
- Gaillard JM, Pontier D, Allaine D, Lebreton JD, Trouvillez J, Clobert J (1989). An analysis of demographic tactics in birds and mammals. *Oikos*, 56: 59-76.
- Gauch HG (1982). Multivariate analysis in community ecology. Cambridge Univ. Press.
- Harvey PH, Clutton-Brock TH (1985). Life history variation in primates. *Evolution*, 39: 559-581.
- Haukoja E, Hakala T (1978). Life history evolution in *Anodonta piscinalis* (Mollusca, Pelecypoda). Correlation of parameters. *Oecologia*, 35:253-266.
- Hedges SB (1985). The influence of size and phylogeny on life history variation in reptiles: A response to Stearns. *Am. Nat.*, 126:258-260.
- Kilgour BW, Mackie GL (1991). Relationships between demographic features of a pill clam (*Pisidium casertanum*) and environmental variables. *J. North Am. Benthol. Soc.*, 10: 68-80.
- Krementz DG, Sauer JR, Nichols JD. (1989). Model-based estimates of annual survival rate are preferable to observed maximum lifespan statistics for use in comparative life-history studies. *Oikos*, 56: 203-208.
- Lardies MA, Bozinovic F (2008). Genetic variation for plasticity in physiological and life-history traits among populations of an invasive species, the terrestrial isopod *Porcellio laevis*. *Evolut. Ecol. Res.*, 10: 747-762.
- Levin R (1989). Biologists disagree over bold signature of nature. *Science*, 244: 527-528.
- Ljubisavljevic K, Polovic L, Kolarov NT, Dzucik G, Kalezic ML (2007). Female life-history characteristics of the Mosor rock lizard, *Dinarolacerta mosorensis* (Kolombatovic, 1886) from Montenegro (Squamata: Lacertidae). *J. Nat. Hist.*, 41: 2979-2993.
- Lynch M (1980). The evolution of cladoceran life histories. *Quart. Rev. Biol.*, 55: 538-545.
- Mathias JA (1971). Energy flow and secondary production of the amphipods *Hyalella azteca* and *Cragonyx richmondensis occidentalis* in Marion Lake, British Columbia. *J. Fish. Res. Bd. Can.*, 28: 711-726.
- Pease CM, Bull JJ (1988). A critique of methods for measuring life history trade-offs. *J. Exp. Biol.* 1: 293-303.
- Purchase C, Collins N, Morgan G, Shuter B (2005). Sex-specific covariation among life-history traits of yellow perch (*Perca flavescens*). *Evol. Ecol. Res.*, 7: 549-566.
- Ricker WE (1975). Computation and interpretation of biological statistics of fish populations. *Bull. Fish. Res. Bd. Can.*, p.191.
- Saether BE (1987). The influence of body weight on the covariation between reproductive traits in European birds. *Oikos*, 48: 79-88.
- Saether BE (1988). Pattern of covariation between life history traits of European birds. *Nature*, 331: 616-617.
- Schwartz SS (1984). Life history strategies in *Daphnia*: A review and predictions. *Oikos*, 42: 114-122.
- Stearns SC (1976). Life-history tactics: A review of the ideas. *Quart. Rev. Biol.*, 51: 3-47.
- Stearns SC (1977). The evolution of life history tactics: A critique of the theory and a review of the data. *Ann. Rev. Ecol. Syst.*, 8: 145-171.
- Stearns SC (1980). A review of life history evolution. *Oikos*, 35:266-281.
- Stearns SC (1983). The influence of size and phylogeny on patterns of covariation among life-history traits in the mammals. *Oikos*, 41: 173-187.
- Stearns SC (1984). The effects of size and phylogeny on patterns of covariation in the life history traits of lizards and snakes. *Am. Nat.* 123: 56-72.
- Stevens GC (1989). The latitudinal gradient in geographical range: How so many species coexist in the tropics. *Am. Nat.*, 133: 240-256.
- Strong DR (1972). Life history variation among populations of an amphipod (*Hyalella azteca*). *Ecology*, 53:1103-1111.
- Strong DR (1973). Amphipod amplexus, the significance of ecotypic variation. *Ecology*, 54: 1383-1388.
- Trendall JT (1982). Covariation of life history traits in the mosquitofish *Gambusia affinis*. *Am. Nat.*, 119: 774-483.
- Wellington GM, Robertson DR (2001). Variation in larval life-history traits among reef fishes across the Isthmus of Panama. *Mar. Biol.*, 138: 111-22.
- Wenner AM, Fusaro C, Oaton A (1974). The mean size at onset of sexual maturity as an indication of growth rates in crustacean populations. *Can. J. Zool.*, 52: 1095-1106.