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Advances in
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VOLUME 17

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Preface

This very full volume of six reviews contains two follow-on papers by previous contributors to the series. Professor J. A. Kitching's earlier paper (in collaboration with F. J. Ebling, Vol. 4, pp. 198–291, 1967) on Lough Ine summarised work up to that date on factors determining the distributions of marine organisms in a unique locality which, although sheltered and with limited tidal range enjoys normal marine salinity conditions. The current paper, using the more correct name of L. Hyne, covers progress over two further decades and extends to further localities within and outside the Lough which provide a greater range of combinations of environmental factors. Field observations have now been supplemented by experimental studies including the transplantation of organisms between habitats and some fascinating studies on migratory movements. Insight into recent geological history has been gained by bottom mud sampling.

Dr Waloff's first paper (Volume 11, pp. 82–215, 1980) brought together studies, mainly at Silwood Park, on grassland leafhoppers (Auchenorrhyncha) which affect grasses both directly through feeding and also by disease transmission. The new paper with Dr M. A. Jervis, extends the field to Auchenorrhyncha throughout Europe and concentrates on parasite/parasitoid complexes. The practical importance of this work for biological control, especially in the context of "green revolution cereals" cannot be over-emphasised. The paper will be of general interest to ecologists also for its account of the subtle ways in which resources are divided between closely related species apparently exploiting the same resources.

The first paper in the volume by P. H. Crowley and others builds on nearly two decades' work on Damselflies at York and elsewhere and develops a most ambitious and successful multi-factor model of population regulation in these freshwater insects. They exhibit particularly complex life histories with quite different regulating factors in the different stages, and factors promoting or suppressing asynchrony of sub-populations receive special attention. Analogies emerge from this work which remind one of the non-linear and threshold functions which are well known in epidemiology.

Insect-plant relationships have been the subject of much attention over the past two decades and more. The nematodes, which rival insects in terms of the number of individuals on the Earth if not in their diversity of species have had far less attention, especially as regards the effects of plants on their

populations. The practical importance of such effects is demonstrated by the limited success of campaigns against potato-root eelworm, for instance. Dr G. W. Yeates' paper helps to rectify the situation by reviewing the many kinds of effects which plants have on vital nematode functions and life stages and the great range of nematode responses in return. Parallels are drawn with plant-insect relationships to the advantage of workers in both fields.

The Terrestrial Isopod Crustacea seem to the outsider to be quite anomalous. Members of a primarily aquatic group, they nevertheless thrive under surprisingly dry conditions, and are of major importance as decomposers of certain soils. Dr Warburg's article demonstrates how their success on land is ensured by combinations of features of anatomy, physiology and behaviour and life history strategy. Moisture, however, proves to remain the ultimate constraint to their range. This is a good example of the growing recrudescence of functional studies in ecology and the contribution they can make to population ecology.

Before dismissing the paper by M. J. Tegner and P. K. Dayton as yet another on the El Niño phenomenon, the reader must realize that their paper concerns effects far North of the Equator, in fact the specific effect on Kelp beds in the Bay of California. Although the ultimate cause of the effects described is oceanographic these are modified and amplified in a most revealing way by biological factors which act sometimes reversibly, sometimes in an irreversible manner. A point of interest is that both here and in Professor Kitching's studies a critical role is played by Sea Urchins and by the effects of temperature on seaweed physiology and development.

Once again the papers in this volume demonstrate the vital importance of longer term studies in ecology. Few of the principles which emerge here could have been unearthed by studies lasting less than a decade: which is a very sobering thought at a time of curtailment of funding both to individual projects and to whole institutions which are not solely committed to short term research.

AMYAN MACFADYEN

Contents

Contributors to Volume 17	v
Preface	vii

Population Regulation in Animals with Complex Life-histories: Formulation and Analysis of a Damselfly Model

P. H. CROWLEY, R. M. NISBET, W. S. C. GURNEY and J. H. LAWTON

I. Summary	1
II. Introduction	3
A. Overview	3
B. Damselfly Life-histories	4
III. Regulatory Factors and Processes	5
A. Larval Growth	5
B. Larval Mortality	9
C. Emergence	10
D. The Immature Adult Stage	12
E. The Mature Adult Stage	13
F. The Egg Stage	14
IV. The Model	14
A. Derivation	15
B. Steady States	25
C. Dynamics	35
V. Discussion	45
VI. Tests and Hypotheses	47
A. In Search of Data	47
B. Some Testable Hypotheses	49
Acknowledgements	50
References	51

How Plants Affect Nematodes

G. W. YEATES

I. Summary	61
II. Introduction	62
III. Ecosystem Productivity	63
IV. Plant Quality	66
V. Fertiliser Response	68

VI. Grazing or Pruning Responses	72
VII. Rooting Patterns	74
VIII. Root Exudates and Nematode Activity	79
A. Hatching	79
B. Egg Hatch	80
C. Moulting	80
D. Toxic Exudates	81
IX. Nematode : Nematode Interactions within Roots	81
X. Host Plant and Nematode Morphometrics	86
XI. Nematode Reproductive Strategies	87
XII. Sex Ratios	90
XIII. Nematode Races and Plant Cultivars	93
XIV. Plant Resistance Mechanisms	96
XV. The Plant–Bacterial–Nematode Pathway	99
XVI. Conclusions	100
Acknowledgements	100
References	100

Ecological Studies at Lough Hyne

J. A. KITCHING

I. Summary	115
II. Historical Note	119
III. The Rocky Sea Coast	120
A. Supralittoral and Littoral	120
B. The Rocky Sublittoral	124
C. Tide Pools	128
D. The Bullock Island Cave	134
IV. The Rocky Shore of the Lough	140
A. Littoral	140
B. Shallow Sublittoral	148
C. Sublittoral Cliffs	157
V. The Deep Water of the Lough	158
A. Stratification	158
B. Effects of Anoxia	165
C. Benthos of the Soft Sediment	167
D. Plankton	169
VI. Special Features of the Flora and Fauna	172
VII. Geological History	177
Acknowledgements	180
References	181

Isopods and Their Terrestrial Environment

M. R. WARBURG

I. Summary	188
II. Introduction	188

III. Anatomical Adaptations of Isopods Settling on Land	189
A. The Respiratory Organs	189
B. The Integument	189
C. The Digestive Organs	189
D. The Excretory Organs	192
E. The Reproductive System	195
IV. Behavioural Adaptations in Isopods	196
A. Receptors and Perception	198
B. Orientation	203
C. Rhythmic Activity	204
V. Physiological Adaptations of Isopods	205
A. The Water Balance	205
B. The Thermal Balance	209
VI. How Isopods Utilize Their Food Resources	211
A. Feeding Habits	211
B. Food Preferences	211
C. Food Consumption	213
D. Energy Expenditure	214
VII. Isopod Habitat Selection and Dispersal Patterns	214
A. Habitat Selection	214
B. The Role of Climatic Factors in the Distribution of Isopods	215
VIII. Reproductive Patterns, Energetics and Strategies	215
A. Ovarian Oocytes and Marsupial Eggs	215
B. Gestation and Reproductive Period	217
C. Factors Affecting Breeding	217
D. Numbers of Oocytes, Eggs and Larvae	224
E. Mortality of Eggs and Embryos	224
F. The Energy Spent on Egg Production	225
G. Reproductive Strategies in Isopods	225
IX. Population Structure and Fluctuations	226
X. Discussion and Conclusions	227
Acknowledgements	229
References	229

**El Niño Effects on Southern California
Kelp Forest Communities**

MIA. J. TEGNER AND PAUL. K. DAYTON

I. Introduction	243
II. Southern California Kelp Forest Communities	245
III. The Physical Environment: Relationship of the California Current to ENSO Events	250
IV. The 1982–1984 El Niño in California	251
V. Storm Effects on Kelp Forests	253
VI. Events Subsequent to the Storms	255
VII. Effects on Higher Trophic Levels	259
VIII. Prospects for Recovery	266
IX. Discussion	267
Acknowledgements	274
References	274

**Communities of Parasitoids Associated with
Leafhoppers and Planthoppers in Europe**

N. WALOFF and M. A. JERVIS

General Introduction	282
Part 1 General Biology, Systematics and Taxonomy of Parasitoids	284
I. Introduction	284
II. Egg Parasitoids	285
A. Mymaridae	285
B. Other Egg Parasitoids	297
III. Parasitoids of Nymphs and Adults	299
A. Dryinidae	299
B. Pipunculidae	313
C. Strepsiptera	322
D. Other Parasitoids of Nymphs and Adults	328
IV. Hyperparasitism and Multiple Parasitism of Auchenorrhyncha	330
A. Hyperparasitism	330
B. Multiple Parasitism	330
Part 2 Ecological and Experimental Studies	332
V. Introduction	332
VI. Mymaridae, Trichogrammatidae and Eulophidae	338
A. Field Levels of Parasitism	338
B. Functional Response to Host Density	338
C. Spatial Variations in Levels of Parasitism	339
D. Temporal (Intergeneration) Variation in Parasitism	343
E. <i>Polynema striaticorne</i> , an Introduced Parasitoid Species	343
F. Impact of <i>Tetrastichus mandanis</i> on Host Populations	343
VII. Dryinidae	343
A. Effects of Dryinid Parasitism on Host Populations	343
VIII. Pipunculidae	347
A. Effects of Pipunculid Parasitism on Host Populations	347
IX. Strepsiptera	351
A. Effects of Strepsipteran Parasitism on Host Populations, and Other Field Observations	351
X. Hyperparasitoids	354
XI. General Discussion	354
A. Host Range Among Parasitoids	354
B. Leafhopper-Parasitoid Population Dynamics	355
C. Interactions Between the Communities of Auchenorrhyncha and Those of Their Parasitoids	358
D. Parasitoids as Potential Biological Control Agents	361
Acknowledgements	362
References	362
Appendices	
I. Mymaridae	378
II. Dryinidae	382
III. Pipunculidae	391
IV. Strepsiptera	398
V. Hosts of European <i>Ismarus</i> spp.	402
Subject Index	403

Population Regulation in Animals with Complex Life-histories: Formulation and Analysis of a Damselfly Model

P. H. CROWLEY, R. M. NISBET, W. S. C. GURNEY,
and J. H. LAWTON

I. Summary	1
II. Introduction	3
A. Overview	3
B. Damselfly Life-histories	4
III. Regulatory Factors and Processes	5
A. Larval Growth	5
B. Larval Mortality	9
C. Emergence	10
D. The Immature Adult Stage	12
E. The Mature Adult Stage	13
F. The Egg Stage	14
IV. The Model	14
A. Derivation	15
B. Steady States	25
C. Dynamics	35
V. Discussion	45
VI. Tests and Hypotheses	47
A. In Search of Data	47
B. Some Testable Hypotheses	49
Acknowledgements	50
References	51

I. SUMMARY

The complex life-histories of taxa such as damselflies (Odonata: Zygoptera) obscure the mechanisms of population regulation. Most of the available data are for the family Coenagrionidae, and its best-known member is the British and European species *Ischnura elegans*. This information suggests four

plausible mechanisms of damselfly population regulation: food availability; feeding-related intraspecific interference; mortality-related intraspecific interference; and density-dependent predation.

We derive a mathematical model of a damselfly population and obtain parameter values largely based on *I. elegans*. The model represents six damselfly life-stages and their interactions with a population of aquatic prey, using coupled ordinary and delay-differential equations, which are solved numerically. Also incorporated are seasonal driving functions, one modifying feeding and mortality parameters according to temperate-zone temperature oscillations, and the other controlling emergence as if by photoperiod or temperature cues. We analyze the model's behavior both in steady state and dynamically with our literature-derived parameter values, and perform sensitivity analyses.

The resulting larval densities, larval stage durations, emergence rates, and general emergence pattern for the standard parameter values are in good agreement with those in the literature: the generation time slightly exceeds one year, and the emergence pattern is strongly bimodal, as observed for some *I. elegans* populations in the British Midlands. Varying the size needed to achieve emergence strongly influences these patterns and densities, emphasizing the need for more data on the body sizes of emerging damselflies.

Varying the carrying capacity of the prey assemblage demonstrates a threshold below which damselflies are unable to persist, and a general increase in densities and decrease in stage durations of larval damselflies with increasing carrying capacity. Stage durations rapidly approach their minimum at and above intermediate prey levels, but larval densities continue to rise even at high carrying capacities. Despite this apparent food-limitation of damselfly larvae, they are generally unable to deplete their prey substantially, and are thus seemingly unable to compete with each other for food. They should nevertheless be susceptible to such competition from other animals such as fish that may be capable of substantially reducing prey densities. Feeding-related interference has essentially no effect on the damselfly population.

The damselfly population is sensitive to changes in the larval and adult mortality parameters: particularly at low prey levels, threefold increases in one of the density-independent mortality parameters generally resulted in extinction of the damselflies. The effectiveness of mortality-related interference and density-dependent predation in regulating the model population is clearly indicated in the stage-by-stage damping of shifts in fecundity: small larvae responded strongly, large larvae weakly, and subsequent emergence rates hardly at all.

Emergence patterns produced by the model seem to reflect the balance between forces promoting and opposing the coexistence of the asynchronous

subpopulations that produce separate emergence peaks; promoting coexistence are density-dependent predation and intra-stage, mortality-related larval interference, and opposing it is interstage interference.

II. INTRODUCTION

A. Overview

Some populations exhibit wild density fluctuations; others are more tranquil. Population ecologists face the daunting task of explaining how severely fluctuating populations often manage to persist, and how other populations can remain within relatively narrow ranges of density. The typical magnitude and temporal pattern of density in a population are determined by aspects of the biotic environment (e.g., predators, food supply), the abiotic environment (e.g., seasonal cycles), the population itself (e.g., intraspecific competition), and interactions among them. The magnitudes of excursions from typical densities, and the tendency to return, depend strongly on an important subset of these density-determining factors, referred to herein as *regulatory* and characterized by *direct density-dependence*.

Identifying the factors that determine and regulate densities of natural populations becomes even more formidable for organisms with complex life-histories. For these, the relevant physiological and ecological constraints may shift dramatically during post-embryonic development. Thorough investigations of such organisms encompassing all life-stages may encounter serious methodological and logistical problems, which may largely account for the rarity of these studies in the literature. An alternative approach attempts to combine, within a single conceptual framework, results from separate investigations of different life-stages. This at least offers the hope of generating some testable hypotheses about how population densities of organisms with complex life-histories are regulated.

Here we follow the latter approach, synthesizing information on a fascinating group of organisms—the damselflies—in an attempt to understand how their population densities are regulated. Damselflies (Odonata: Zygoptera) are classical examples of animals with complex life-histories. During the relatively long-lived aquatic larval stage, damselflies experience a continuously changing spectrum of enemies, food and environmental stresses; they then metamorphose directly into flying adults, a transformation in morphology, habitat, and behavior as dramatic as any seen in the animal kingdom. The adults live in a world totally unlike that of the larvae. Indeed, the transition from aquatic larva to terrestrial adult can be viewed as a seasonal “migration” by damselflies between two quite different habitats. The population dynamic consequences of such behavior are poorly understood (Fretwell, 1972; Kot and Schaffer, 1984).

Long-term population dynamic studies of damselflies are rare, though extensive natural history observations attest that populations of many species persist within relatively narrow bounds for several years, provided that habitats remain unaltered. Macan (1974) presents data on the number of large larvae of two species (*Pyrrhosoma nymphula* and *Enallagma cyathigerum*) in Hodson's Tarn in northern England, for 17 and 16 years respectively (1955– and 1956–1971). Populations fluctuated rather little at first, with a ratio of maximum to minimum numbers in *Pyrrhosoma* of 2.02 over the 11 years 1955–1965, and 2.51 over the corresponding 10 years for *Enallagma* (coefficients of variation in log-transformed counts of large larvae were 0.054 and 0.067 respectively). Thereafter, numbers of both species declined to lower levels, apparently because of deterioration in *Littorella* and *Myriophyllum* weed beds in the tarn. These data suggest that damselfly populations are relatively stable and well regulated, at least without severe habitat modification (Williamson, 1972; Hassell *et al.*, 1976; Connell and Sousa, 1983).

We begin our attempt to identify the ecological mechanisms responsible for these relatively tranquil population dynamics with a brief description of damselfly life-histories. We then review relevant published observations, hypotheses, and experimental studies, proceeding through the life stages sequentially. Much of this material necessarily focuses on the relatively long larval (or naiad or nymph) stage, for which the most quantitative information is available. Using these ideas and data, we develop and analyze a model incorporating major facets of damselfly life-histories. This exercise illuminates the more glaring deficiencies in our current state of knowledge, and helps us to evaluate some ways that damselfly population densities may be regulated in nature.

B. Damselfly Life-histories

For readers unfamiliar with damselfly biology, this section sketches the bare outline of a much more detailed and informative picture presented by Corbet (1962, 1980). Insects in the ancient hemimetabolous order Odonata, damselflies in the suborder Zygoptera and dragonflies in the suborder Anisoptera, have both aquatic and terrestrial stages. The aquatic larval stage usually lasts considerably longer than the terrestrial adult stage, particularly towards higher latitudes. Following hatching, the aquatic larvae pass through 9–15 instars, the duration of each instar depending on feeding rate and temperature. Severe environmental changes (such as the onset of winter) may halt or drastically slow development. In many species late instar larvae enter diapause in response to temperature or photoperiod cues, or both; but in other species, a simple winter quiescence is apparently induced by low ambient temperatures. The larvae are generalized predators on

invertebrates and occasionally on vertebrates, especially cladocerans and midge larvae; damselfly larvae are themselves common prey of fish and other aquatic vertebrates, as well as bugs, dragonflies, and other damselflies. The larvae are usually ambush predators in shallow water (<2 m deep) and are known to interact aggressively with each other.

Once a larva has developed sufficiently within the final instar, and subject to other constraints imposed by water temperature and photoperiod, it undergoes metamorphosis. Feeding ceases; mouthparts degenerate; and eyes, wings, new mouthparts, and other structures develop rapidly within the larval exoskeleton over several days. Then weather permitting, the larva emerges by climbing up onto the shore or a stalk of vegetation (or some comparable object) and pulls itself out of the exuvia. After a few minutes, when its wings have dried, the new adult can fly. At temperate latitudes, a population may emerge more synchronously early in the year (usually spring); or less synchronously later in the year (summer or autumn); or in multimodal seasonal patterns. Typically, immature adults remain away from water for 1–3 weeks, a period of dispersal, feeding, and reproductive development. Adults eat mainly smaller insects and are frequent prey of birds, fish, frogs, and spiders. Mature adult damselflies return to water to mate, which generally features aggressive interactions among conspecific males. Mated females oviposit in stalks of aquatic or overhanging terrestrial vegetation, or in floating leaves, algal mats, or debris; or, rarely, directly into water. Egg development may proceed immediately to completion and hatching, or there may be a delay of variable duration in response to photoperiod, temperature, or other cues.

III. REGULATORY FACTORS AND PROCESSES

The following sections review many components that impinge upon the complex life-cycles of damselflies, and that might conceivably contribute to population regulation.

A. Larval Growth

1. Prey Availability and Dynamics

Larvae of damselflies and other odonates are generalist predators in the field, consuming cladocerans, larval dipterans, copepods, larval ephemeropterans, ostracods, oligochaetes, larval odonates, and other invertebrates in proportions largely determined by the relative abundances of each kind of prey (e.g., Chutter, 1961; Pritchard, 1964; Pearlstone, 1973; Thompson, 1978b,c). These prey differ considerably in morphology,

behavior, density, distribution, and population growth rates, but relatively little in nutritional content or in the efficiency with which they are assimilated (Lawton, 1970, 1971). Damselflies in intermediate and later instars eat mostly cladocerans and midges (usually the most abundant prey—see above references), and there is good evidence from the work of Macan (1964, 1974), Lawton (1971), Folsom (1980), Pickup *et al.* (1984), and Baker (1986a,b) that these larvae can be food-limited in the field, but Thompson (1982) and Folsom and Collins (1982a,b), were unable to detect food limitation. In contrast, the earliest instars feed on the small end of the prey size-spectrum, including large protozoans, copepod nauplii, rotifers, small cladocerans, and first-instar chironomids (Corbet, 1962; Walker, 1953); these prey may generally be abundant and productive enough to make food limitation less likely.

There is some evidence that anisopteran larvae at natural densities can reduce prey densities in the field (Folsom, 1980; Jeffries, 1984; D. M. Johnson *et al.*, 1987; see also Peckarsky, 1984), but this has not been unequivocally demonstrated for damselflies (Jeffries, 1984). Predators that consume damselflies may also deplete damselfly prey (e.g., fish: Hayne and Ball, 1956; Macan, 1966; Bohanan and Johnson, 1983; Johnson *et al.*, 1983; Morin, 1984b) or otherwise make them unavailable by inducing shifts in prey or damselfly behavior (Macan, 1966). These possibilities for prey depletion and food limitation, except perhaps in the earliest instars, argue that the density and dynamics of prey may be important in damselfly population regulation. Unfortunately, diversity in the damselfly prey assemblage makes evaluation of this view difficult.

2. *Functional Response to Prey Density*

Most damselfly larvae, with the exception of some in the family Lestidae, are classic sit-and-wait predators, moving seldom and slowly, and depending primarily on prey movement to bring them into striking range (Corbet, 1962). In laboratory experiments in structurally simple containers with a single prey type, the relation between killing rate per larva and prey density (i.e., the functional response to prey density) has consistently followed a decelerating rise to a plateau with increasing prey density (e.g., Thompson, 1978a,b), generally known as type II response (Holling, 1959, 1966). It is possible that physical structure (Benke, 1978), density-dependent prey behavior (Crowley, 1975), or presence of alternative prey (Lawton *et al.*, 1974; Akre and Johnson, 1979) could tend to make the functional response sigmoid (i.e., type III) in the field. However, there is evidence that damselfly larvae at higher prey densities hunt less actively or less frequently for prey (Savan, 1979; Thompson, 1975; Wilson, 1982) and kill and consume fewer prey captured (Johnson *et al.*, 1975), which may tend to reverse this effect.