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Dealing with uncertainty in a complicated thermodynamic world

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Cette thèse intitulée:

Dealing with uncertainty in a complicated thermodynamic world

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Nowhere can one see more clearly illustrated what may be called the sensibility of such an organic complex—impressed by the fact that whatever affects any species belonging to it, must speedily have its influence of some sort upon the whole assemblage. He will thus be made to see the impossibility of studying any form successfully out of relation to the other forms—the necessity for taking a comprehensive survey of the whole as a condition to a satisfactory understanding of any part.

S. A. Forbes 1880

RÉSUMÉ

Il est très difficile d'extrapoler l'approche réductionniste des mécanismes locaux aux écosystèmes naturels à cause de la complexité des réseaux écologiques et leur nature multi-causale. Pourtant, la plupart des manipulations et des interventions humaines sur notre environnement sont de nature réductionniste, ce qui, par conséquent, nous a conduit à des problèmes de plus grande envergure, plutôt qu'à leur résolution. Une solution plausible à ce problème de complexité consiste à utiliser la théorie thermodynamique pour mieux orienter les questions que nous nous posons. Cette possibilité a été reconnue depuis longtemps (Lotka 1922, Odum and Pinkerton 1955, Margalef 1963, Legendre 1971, Johnson 1994), mais deux facteurs ont entravé sa réalisation: (1) l'incapacité d'analyser et traiter la complexité des réseaux naturels que sont les écosystèmes; et (2) l'absence de données empiriques nécessaires pour confirmer ou réfuter l'utilité de l'approche thermodynamique. Ma recherche aborde ces deux questions.

Le développement théorique nécessaire au succès de l'exploitation de la théorie thermodynamique (thermodynamique linéaire loin des points d'équilibre, telle que développée par Prigogine et ses collègues) devient possible lorsqu'on la combine avec le formalisme de l'analyse des réseaux (network theory, développée par Patten et ses collègues). Une telle démarche permet une définition précise de plusieurs concepts écologiques fondamentaux qui étaient jusqu'alors demeurés vagues et indéfinissables:

(1) la nature de l'état d'équilibre; (2) la distance par rapport au point d'équilibre (*i.e.*, perturbation); et (3) la stabilité relative des systèmes.

Les développements empiriques qui permettent de vérifier les résultats théoriques décrits ci-dessus ont été rendus possibles grâce (1) à la nature allométrique des taux éco-physiologiques, (2) à la nature allométrique de la relation entre la taille et l'abondance des organismes, et (3) à la pléthore des perturbations d'origine anthropique et non-anthropique des écosystèmes. L'utilité de ces résultats théoriques a été validée à l'aide de ces relations empiriques.

La principale contribution de cette recherche consiste, par conséquent, la mise au point d'une mesure simple de la perturbation des systèmes dont le fondement est à la fois théorique et empirique. L'extension de ces idées permet aussi la compréhension et la résolution de plusieurs sujets d'envergure fondamentale: (1) l'omniprésence de la relation entre la taille et l'abondance des organismes; (2) la nature de la relation entre la diversité et la stabilité; et (3) la pertinence du paradoxe de l'enrichissement [par les éléments nutritifs] des écosystèmes et par extension la notion du développement durable. Des études ultérieures continueront d'explorer les limites d'une telle approche et permettront de développer un contexte empirique et théorique encore plus général.

SUMMARY

It is very difficult to extrapolate reductionistic understandings of proximate, causal mechanisms to complex, inter-woven, multi-dimensional and multi-causal systems. An appreciation of this limitation of the reductionistic method in studying complex ecological systems is important. However, the dominant reductionistic bias of most human manipulations or interventions of our environment have lead to the generation of greater ecological uncertainty rather than their successful resolution.

One potential approach to this problem of extending small-scale mechanisms to understand large-scale patterns is the exploitation of thermodynamic theory to guide the development of questions that are pertinent and answerable. Numerous people have appreciated such a possibility (Lotka 1922, Odum and Pinkerton 1955, Margalef 1963, Legendre 1971, Johnson 1994) however, the useful development of such an approach has been hampered by two factors: (1) our inability to embrace the complexly inter-woven nature of natural systems, and (2) a lack of empirical data to verify the utility of a thermodynamic approach. During the course of this research project, these two lacunae have been addressed with some degree of success.

The theoretical developments that allow the successful exploitation of thermodynamic theory (linear, non-equilibrium, as developed by Prigogine and colleagues) are made possible by combining it with network theory (as developed by Patten and colleagues).

The useful result of this course of analysis is that several key ecological concepts that have historically remained vague and indefinable become more precisely defined: (1) the nature of the steady state condition; (2) the distance from the steady state (*i.e.*, an index of perturbation); and (3) the relative stability of systems.

The empirical developments that allow the verification of this theoretical approach are made possible by: (1) the now well-known allometric nature of eco-physiological rates; (2) the allometric nature of the size-abundance relationships; and (3) the plethora of anthropogenic and non-anthropogenic perturbations. These empirical relations were used to test the utility of some of these theoretical approaches.

The most important contribution of this research is perhaps the description of a theoretically and empirically sound and easily measured index of perturbation. The extension of these ideas allows the understanding and resolution of several other fascinating and pressing issues: (1) the ubiquity of the size-abundance relationship; (2) the nature of the relationship between diversity and stability; and (3) the relevance of the "paradox of [nutrient] enrichment" to ecological systems and by extension the notion of "sustainable development". Future work will continue to explore the utility and limits of such an approach and to develop further their theoretical and empirical foundations.

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The work itself is dedicated to our beloved son, *Liam*, who was born in the midst of its chaos.

A NOTE TO THE READER

Due to the nature of this thesis, being in the form of papers and the synthetic nature of its content, it is advised that the Introductory and Concluding chapters (1 and 6, respectively) be read prior to the rest of the thesis.

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— Chapter 1 —

INTRODUCTION

> *Body size has long been thought to influence both the distribution and abundance of animal species, but we are only just beginning to discern the overall role that size plays in organising the Earth's biota. ... {It} hints at there being as yet undiscovered patterns involving size, energy distribution and abundance ...*
>
> *Damuth 1991*

ABSTRACT

The ubiquity of the size-abundance relationship noted by Damuth (1991, quoted above) is reviewed. The great number of mechanisms that may be responsible for this relationship renders its study difficult. This is especially the case as these numerous mechanisms extend across a huge range of spatial, temporal and organisational scales (*e.g.*, Williams 1964:1-4). This intrinsic difficulty of studying macroscopic patterns and processes (*i.e.*, the size-abundance relationship) from a microscopic approach is better known in other scientific circles as the holistic and reductionistic dialectics. The two main (inter-related) reasons why it is so difficult to extrapolate local mechanisms to explain and predict global patterns include: (1) the complexity of ecological systems, and (2) the self-referential nature of ecological concepts.

Understanding the origins and implications of the size-abundance patterns requires that we go beyond a strictly holistic or strictly reductionistic approach and so address the difficulties inherent in multi-scale and multi-causal patterns and processes. The solution

that is entertained is a scale-free (*i.e.*, fractal-like) approach that can simultaneously encompass the full complexity of real systems and go beyond the self-referential and context dependent nature of ecological logic. For this purpose, the foundations of a thermodynamic analysis of the patterns of size and abundance are introduced and an outline of how the chapters that follow relate to this purpose.

A REVIEW OF THE SIZE-ABUNDANCE RELATIONSHIP

Regularities in the patterns of abundance and size have been appreciated for a long time. One of the earliest references to this pattern was made by Elton (1927). He named this pattern of decreasing numbers of organisms and energy use with increasing trophic level, the "Pyramid of Numbers and Energy", and attributed it to the sequential loss of energy at each step of consumption along the trophic chain (*i.e.*, metabolic heat and waste). While the explanation is not entirely correct, as it does not account for the recycling of biomass (*e.g.*, cannibalism, decomposition, microbial activity; Patten 1985), the empirical pattern itself remains one of the very few well-established ecological regularities.

Sheldon *et al.* (1972, 1977) were among the first to systematically quantify this pattern for marine plankton when they noted that the biomass in logarithmically-scaled body size categories from plankton to whales seemed to be a flat function (slope = 0, although a great deal of spatio-temporal variation was also observed). Another representation of this pattern is the "normalised biomass size spectrum" (Platt and

Denman 1978), which represents this pattern in terms of numerical abundance (rather than biomass) as a function of the size of the organisms, both on logarithmic scales. This latter, “size-abundance” relationship has been found to have slopes with values near –1.

In the intervening years, numerous other systems have been explored and this pattern has been repeatedly confirmed: a log-linear form of the size-abundance relationship with slopes near –1. Finer-scaled patterns exist (*e.g.*, Gasol *et al.* 1991, Thibeaux and Dickie 1992, Sprules and Goyke 1994), termed "secondary" scalings (Boudreau *et al.* 1991), but the "primary" scaling of a log-linear form between size and abundance remains consistent (Boudreau and Dickie 1992, Sprules and Goyke 1994). For example, in examining the plankton (10 μm to 8 mm length scales) of the North Pacific Central Gyre, Rodriguez and Mullin (1986) described the slope of the size-abundance relationship to range from –1.34 to –1.07. In studies of the Laurentian Great lakes and some smaller inland lakes, Sprules and Munawar (1986) and Sprules and Goyke (1994) found the slopes, for organisms ranging from phytoplankton to fish, to also range between –1.24 to –0.62. In lake Constance, Gaedke (1992) found the slopes to seasonally range from –1.3 to –0.9 for a size range from bacteria to zooplankton; while in an examination of organisms ranging from bacteria to zooplankton (0.2 to 1600 mm length scale) in smaller Québec lakes, Ahrens and Peters (1991a,b) found the slopes to range from –1.01 to –0.75. Garcia *et al.* (1995) report an average slope of –1.06 for a shallow saline lake for plankton with length scales ranging from 2 to 4000 mm. These results indicate that the size-abundance relationship is a robustly stable state that extends across a huge range in organism sizes in the pelagic environment.

In the terrestrial literature, these patterns have been independently elucidated by the work of Mohr (1940) and Damuth (1981) for mammals, Nee *et al.* (1991) for birds, and Yoda *et al.* (1963) for plants. Studies of benthic ecosystems have also found similar allometric patterns (slopes ranging between –0.97 and –0.81; Schwinghamer 1981, Cattaneo 1993), although there is some uncertainty as to whether there are discontinuities in this pattern (see Cattaneo 1993). These patterns also exist at a global scale (Peters 1983), an ecosystem scale (Marquet *et al.* 1990, Morse *et al.* 1985) as well at the population/cohort scale (Yoda *et al.* 1963, Bohlin *et al.* 1994). The slopes reported vary greatly, generally ranging between –0.62 and –1.3, but its average form is consistently a value near –0.75 to –1. The recurrence of this pattern has sparked a number of debates, such as what is the "correct" value of the exponent, or is the quantity of energy flowing through a species the same for all species (Damuth 1991, Nee *et al.* 1991); these questions are yet to be resolved.

In contrast to the extensive empirical work described above, the theoretical understanding of the mechanisms that cause these patterns has progressed little beyond Elton's simple explanation (1927). The few theoretical models that exist still exclusively adopt Elton's paradigm and try to explain the empirical patterns through mass transfer and energy loss from small to larger organisms or from lower to higher trophic levels (*i.e.*, predator-prey interactions; Platt and Denman 1978, Borgmann 1987, Thibeaux and Dickie 1992, Sprules and Stockwell 1995). Using such an argument, the scaling exponent in steady state was predicted to be near –1.2 by Platt and Denman (1978). Unfortunately, these models apply only to large heterotrophic consumers (zooplankton and fish), as they do not explain the presence of this pattern amongst autotrophs and heterotrophic bacteria where matter and energy flows are much more complex. Further, these models do not account for the reverse transfers (*i.e.*, feedback cycles) of mass and energy from larger to smaller organisms (*e.g.*, decomposers, parasites or detrital system), which can account for the bulk of the metabolic activity in aquatic systems (> 50%; Winberg 1972, Pomeroy 1974, Williams 1984, Platt *et al.* 1984, Cole *et al.* 1988, Strayer 1986, Jahnke and Craven. 1995). The extremely important role of the input of organic carbon (dissolved and particulate) from the littoral zone, the watershed runoff, the resuspension of sedimented organics by abiotic (storms) and biotic (vertically migrating zooplankton and fish) factors, and the internal recycling of carbon in lake ecosystems are also ignored, making this approach a tenuous one at best. Silvert (1982), one of the pioneers of these models, also notes that these simple models are inappropriate as the same size-abundance patterns are also found in more physically structured terrestrial and benthic environments.

At a population level of description, other mechanisms have been proposed to explain this phenomenon. When a cohort is followed through time, a self-thinning of population size occurs, as individuals grow larger. In plant populations, the "self-thinning" rule has been attributed to <u>intra-specific competition</u> for space or resources (light, water, nutrients) and is commonly referred to as the "self-thinning rule" (exponent ≈ –0.67;

Yoda *et al.* 1963). The same pattern, although considerably more variable, has been demonstrated by Bohlin *et al.* (1994) for cohorts of Atlantic salmon, brown trout and sea trout in Swedish rivers (slopes ranging from ≈ –0.9 to –1). Thus, strong intra-specific competition causing self-thinning of populations over time represents an important mechanism that may potentially generate the patterns of size and abundance that we observe.

A similar competitive mechanism but at an inter-specific level, was suggested by Morse *et al.* (1985) when examining the abundance of arthropods in vegetation. They attributed the log-linear form of the pattern to the fractal-like nature of habitat space as a limiting resource. Unfortunately, this explanation does not account for the presence of these patterns in physically less structured environments such as, for example, the pelagic system. Nor does it (nor do the other explanations, being based solely upon competitive or predatory relations) account for other important interactions such as parasitism, disease, mutualisms/synergisms and the profoundly complex and intricate nature of spatial, temporal and biological organisation found in real systems.

The widespread nature of these patterns in pelagic, terrestrial and benthic systems and across many different spatio-temporal scales suggests the presence of some very fundamental and general mechanisms that interact to create these patterns of size and abundance. Unfortunately, as with most other ecological concepts, no consensus is emerging as to how or why these patterns come to be.

THE LIMITS TO REDUCTIONISM: COMPLEXITY AND CIRCULARITY

Clearly, there are numerous ecological mechanisms working at many different spatial-temporal-organisational scales that delimit the size-abundance relationship. However, an understanding of the reductionistic (idealised) relationships or interactions do not help us understand how they integrate and interact to create these recurrently emergent (realised) log-linear patterns. This incompatibility between reductionistic mechanisms and emergent patterns is a limitation that has been repeatedly expressed (*e.g.*, Forbes 1880, Bertalanffy 1968:89-119; Allen and Starr 1982; McIntosh 1985:193-233, Ricklefs 1987, Yodzis 1988, Patten 2000) and may be attributed to two main (related) reasons:

(1) The complexity of real ecological systems, and
(2) The circularity of ecological concepts.

COMPLEXITY

The problem of complexity, that is, the difficulty in harmonising numerous and intertwined local mechanisms to provide an understanding of globally emergent patterns and processes, is a recurrent one that is commonly described by holists with the mantra, "The whole is greater than the sum of its parts". The reductionists unfortunately do not subscribe to such folk wisdom and continue to search for an even smaller part/mechanism that, when added to the model, will explain the whole. In the classical reductionist approach, local, binary (or even unary) interactions between systems are studied under controlled (*i.e.*, isolated) conditions. The object of such analyses is to qualify, quantify and classify the feedback interactions, *i.e.*, as deviation-amplifying or deviation-reducing feedbacks.

The maintenance of a stable ecological community (*i.e.*, some *locally quasi-steady state*) is usually attributed to the dominance of these local, deviation-reducing ("negative") feedback mechanisms (*e.g.*, density-dependent mortality, natality, immigration/emigration and behavioural factors) relative to local, positive-feedback mechanisms (*e.g.*, sexual selection, co-evolution, mutualism; Wiener 1962, Wynne-Edwards 1966, Patten and Odum 1981). However, in natural systems, the relationships between systems are quite numerous and complexly intertwined in their extent (spatially, temporally and organisationally). In such systems, knowledge of the local binary relationships between systems is insufficient to understand the behaviour of the whole system. This intrinsic difficulty of understanding complex systems has been appreciated for a long time in the mathematical/astronomical domain, under the guise of the "three-body" problem, which relates to the difficulty of predicting the time evolution of orbital motions when there are more than two interacting systems (Poincaré 1892).

A more tangible example may be found in our personal experiences with the difficulty in moving a cup filled with water, without spilling the water. This is due to the presence of time lags between movement of water, observation of movement, response to movement and the consequent movement of water, *etc.* Such temporal-spatial-organisational decouplings between action and reaction can result in an amplification of over-compensations, even though the negative feedback mechanisms involved generally provide functional, deviation-reducing results under other conditions. When muscles are fatigued, over-compensation becomes stronger still. Similar effects are observed in humans that have had neural damage (*e.g.*, cerebral palsy, muscular dystrophy) or simple muscle fatigue (*e.g.*, trembling after holding a heavy load). The amplification of over-compensations or "overshoots" of movement, due to physiological limitations in the firing rate of neurons or contraction of muscles (*i.e.*, spatial-temporal-organisational complexity) are thought to be responsible for the trembling response (Wiener 1962, Beuter *et al.* 1993).

In ecological systems, the capricious nature of complex biological interactions is better known as "indirect effects" or "higher-order effects" (*e.g.*, Forbes 1880, Patten 1983, Smith *et al.* 1997; see Figure 1.1). As an example, we can look at the concept of competition, one of the reductionistic explanations of the size-abundance relationship (mentioned above). Competition is a cornerstone of mainstream *reductionistic* ecology; it finds its origins in the works of Malthus, Darwin and Wallace and its formalisation in the classic reductionistic work of Gause (1934, who paradoxically subscribed to a holistic point of view). However, its influence upon natural systems at spatial-temporal-organisational scales larger than that of two species interactions in microcosms still remains a contested subject. Criticisms focus upon the importance of other biological factors such as predation (Paine 1966, 1974), parasitism, disease, mutualism, co-operation, dispersion (Kropotkin 1902, Wynne-Edwards 1966) and perturbations such as climatic fluctuations and natural catastrophes that keep a system from reaching an internal “equilibrium” (Andrewartha and Birch 1954).

Even for rather simple systems, it has been shown that indirect effects are quite important relative to the direct effects between systems (Patten 1983, 1985). Further complicating the situation is the virtual impossibility of perfect information of the present, past and future states of all simultaneously occurring interactions between systems (Smith *et al.* 1997), which generates an uncertainty or unpredictability of cause-effect (input-output) relationships that has been called a “pseudo-nonlinearity” (Patten 1983). The spatially, temporally and organisationally varying nature of the systems and their interactions add another layer of complexity that makes any attempt to understand a whole system via the extension of binary interactions quite an impossible task.

Our attempts to use chemical pesticides as a means of controlling pests represents another rather pointed example of the distinction that needs to be made between feedback mechanisms (in an ideal reductionistic world where only binary mechanisms are important) and feedback effects (in a real experiential world where indirect effects are also important). After an initial period of success in controlling pest organisms, there invariably results an explosion of the abundance of the pest species. This is frequently due to the adaptive response of the pests that develop resistance and the co-incident removal of other previously developed mechanisms of biological control (*e.g.*, predators). Thus, even though the (binary) feedback *mechanism* was designed to control (stabilise or diminish) the pest population, the feedback *effect* was to act as a destabilising, deviation amplifier. The reason for this complex behaviour is due to the inherent spatial-temporal-organisational complexity of real systems ("pseudo-nonlinearity", "nonlinearity", "multi-causality" (networked) and context-dependent nature of ecological interactions).

Another well-known example of the importance of the complexity of real systems and the associated indirect effects is the predation by starfish upon the invertebrates of the inter-tidal community (Paine 1966, 1974). Starfish predation upon any particular species can be devastating, however, in the presence of multiple prey species, this effect is highly modulated. Watson and Lovelock's (1983) daisy-world model represents another well-known example of the importance of complexity and indirect effects. Many other examples of the importance of complexity and indirect effects exist: the frequent outbreaks of pest populations (*e.g.*, spruce-budworm) and their modulation by climatic variations, food availability and predation; social, cultural, economic and environmental modulations of the expressions of complex diseases such as HIV, influenza, tuberculosis (Lewontin 1991:43), plague, Lymes disease (Barbour and Fish 1993), chronic fatigue syndrome and even stomach ulcers (Marshall and Warren 1984, NIH 1994, Hamilton 2001).

To summarise, because their relationship is not a simple one, a clear distinction must be made between (local, controlled) feedback *mechanisms* that are identified via reductionistic analyses and the actually realised (global, integrated) feedback *effects* that are identified via empirical observations. In other words, it is not enough to reductionistically determine the nature and strength of pairwise feedback mechanisms if one's goal is to understand real systems because the realised ecological feedback effects can and do switch between positive and negative feedbacks in rather complex and unpredictable ways.

CIRCULARITY

The second major (and related) cause of the difficulty in going "from the local to the global", circularity, is epistemological in nature—dealing with the problem of the relativistic nature of knowledge, a problem that has been appreciated for quite some time. For example, Xenophanes (VI Century B.C.) distinguished between the intelligible world that could be understood by science and the physical world that could only be imperfectly known by our senses. Another well-appreciated example comes from Plato's *Republic*: people in a cave, with only glimpses of distorted forms as shadows on the cave walls from which to learn about the external world.

Our incapacity to verify the veracity of our knowledge represents a rather daunting limitation, a limitation that ecology shares with all other sciences of nature. To illustrate this point, I borrow from Gödel's *Incompleteness Theorem* (1931):

> *In any formal system S, which is consistent, there can be a proposition which denies the provability of that proposition (of itself) within the system; i.e., the statement "this statement cannot be proven within S" can exist within S. Since this proposition can exist then it must be true, which denies its 'not provable' status, and therefore*

> *produces an inconsistency within what is supposed to be a consistent system. Thus no formal system of propositions can be complete.*

That is, any self-consistent axiomatic system (*i.e.*, a symbolic system of thought such as logic, mathematics, language and ecological theory) contains axioms whose truth is undecidable within that system and its consistency is, hence, not provable within that system. This means that, no such system can consistently and completely describe/explain all phenomena—there exist circular or self-referential or paradoxical loops that bounds such systems.

For example, in linguistic systems, every word or idea is in some way related to another as they are referenced to each other. This self-reference implies a circular system. Thus, when we examine what is meant by the word "cat", we get a series of different words that describes the word "cat". These words are referenced to other words that are referred to other related words and so on, until finally one returns to the word "cat". It is a circular, self-referential, symbolic system. There is no ultimate or ideal archetypical (in the Platonic sense) "cat" that exists outside of the system that can be unambiguously defined.

A more concrete ecological example is found in the concept of *competitive exclusion*. Even when it was experimentally shown that competitive exclusion does not always happen (*e.g.*, for *Drosophila* sp. by Ayala 1970), the competitive exclusion principle was defended with the argument that the organisms tested had different niches and so did not represent a valid test (Gause 1970). This latter statement demonstrates the intrinsic circularity (self-referential nature) of the ecological concept of competitive exclusion, in that it is operationally defined. If competition is not observed, it is because the organisms have different niches (Hardin 1960, McIntosh 1985:186). Thus, it is impossible to prove (or "falsify" in the Popperian sense) the importance of competition. Similar critiques have been laid out for *optimal foraging theory*: a given currency is being optimised by an organism. If the currency is found not to be optimised, that is because the choice of the currency is not appropriate or correct. The correct currency is the one that is optimised! Another famous example of (paradoxical) circularity of thought revolves around the most basic of biological principles, the concept of *natural selection*. The formalism is that what is fittest will survive and reproduce. What is fittest is that which is most adaptive. And that which is most adaptive is that which is most fit to survive. Again, it is impossible to prove what is fit and what is not because fitness and survival refer to each other.

Due to the intrinsic circularity and complexity of ecological/evolutionary ideas and concepts, some have gone so far as to suggest that they serve nothing but to confuse the real issues at hand, which "should be" the development of a "predictive", empirical science (*e.g.*, Rigler 1975).

Such an extreme perspective is not adopted in this thesis. Intrinsic circularity and complexity does not mean that we must abandon all attempts at communication. Language serves a useful, albeit imperfect, function. Similarly, logical systems such as ecological thought also serve a useful, albeit imperfect, function. That is, these circular systems empirically work, even though it stands upon shaky theoretical foundations. Perhaps the more pragmatic stance is to acknowledge that *microscopic (theoretical) concepts are limited if the purpose is to go beyond the logical system to understand macroscopic (empirical) patterns.*

For such a pragmatic purpose, thermodynamic theory provides a consistent frame of reference that no other theory can provide: a generally agreed upon direction of time. This directionality of time allows us to go beyond the constraints imposed by the maze of self-referential *circularity*[1]. Further, thermodynamic analysis is explicitly a macroscopic (probabilistic) approach that embraces the spatial, temporal and organisational *complexity* of systems, and so avoid the majority of difficulties associated with a reductionistic approach. Indeed, using a thermodynamic approach it is possible to not only develop a scale-independent understanding of ecological processes and structures such as the size-abundance relationship but also to clarify a large class of ecological issues that have so far remained controversial and ambiguous. The chapters that follow will build these arguments and develop a few of these clarifications.

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[1] *Thermodynamic analysis and theory are also axiomatic systems and so are also doomed to be self-referential. As such, it cannot for example help us understand the ultimate question of the origin of the universe. However, as the direction of time is in general a mutually accepted and agreed upon concept, it is deemed by the author that it is a sufficiently general axiomatic system to be used as a mutually acceptable "compass" to guide the analysis of more proximate axiomatic systems, such as ecosystem patterns of size and abundance.*

A REVIEW OF THE THERMODYNAMIC APPROACH USED IN THE THESIS

The first well-known attempt at a thermodynamic understanding of ecological patterns and interactions is attributable to Lotka (1922). Lotka's work was based upon the earlier writings of Boltzmann (1905) who had restated the Darwinian principle of Natural selection in energetic terms: that living systems struggle for free energy. Lotka (1922) reformulated this idea further into his "Maximum power principal:"

> *Natural selection* tends *to make the energy flux through the system a maximum, as much as possible.*

In other words, when there is a resource available, it will be used. Organisms are selectively advantaged if they can more efficiently use these resources. The most *probable* consequence of this process was that the total amount of energy passing through the biota would be as large as possible. Of course, one must parenthetically recognise first, the uneasy circular relationship that exists between that which is a resource and that which is selectively advantaged (as mentioned in the previous section); second, the rather open-ended nature of the constraints referred to by the clause, "as much as possible"; and third, the potential for higher-order interactions (indirect interactions; Forbes 1880, Paine 1974, Patten 1983, Smith *et al.* 1997) to modulate such simplistic expectations (*e.g.*, via the extinction or extirpation of a focal or "keystone" species). This general line of reasoning has continued through the work of Margalef (1963), Odum and Pinkerton (1955), Matsumo (1978), Johnson (1981,1994), Odum (1983) and Schneider and Kay (1994); and today persists particularly in the fisheries and bioenergetics literature, as it provides a much-needed integrative and unifying framework (Ware 1982, Bryan *et al.* 1990, Lin 1995).

Schrödinger (1945) popularised these ideas as the principle of "negative" entropy or “negentropy” when he explicitly pointed out the “anti-entropic” nature of life that was implicit in Boltzmann’s and Lotka’s perspectives. This “negentropic” principle describes the tendency for living organisms to become more ordered and to maintain that order for a time (*i.e.*, decrease their local entropy) against the universal pattern of the Second Law of Thermodynamics for order to be destroyed with time (entropy to increase). Living organisms accomplish this apparently anti-entropic feat (*locally*) by actively “exporting” excess disorder at the expense of the universe (*globally*). That is, living systems “create” a <u>local fluctuation</u> (*i.e.*, a *local reversal*) in the global action of the Second Law of Thermodynamics.

It has now become clear that many non-living dynamical systems (chemical reactions, turbulent mixing, weather patterns) also demonstrate such local fluctuations in the action of the Second Law—like the small eddies that flow counter to the currents in flowing waters. While these patterns are empirically (*i.e.*, phenomenologically) well known, it is not at all clear what may be *causing* these local fluctuations in the action of the Second Law

Prigogine (1947) was one of the first to suggest a formal (mathematical) cause of this anti-entropic tendency of some systems—the “<u>Least specific dissipation</u>” (**LSD**; see

Appendices 1 and 2C) principle. However, the dependence of this principle upon a linearised description of thermodynamic processes infinitesimally close to "thermodynamic equilibrium," limited the scope of its application and so its general acceptance.

Continuing to explore these lines of the Darwinian-Boltzmann-Lotka school, Glansdorff and Prigogine (1971) suggested that this *local* fluctuation in the action of the Second Law is attributable to the presence of *local* fluctuations of free energy densities (*i.e.*, statistical asymmetries or inhomogeneities) that become coherent flows of energy and matter. They called this mechanism for this autocatalytic creation of ordered "dissipative structures" (*e.g.*, the "anti-entropic" eddies, above)—the "Order through fluctuation" (**OTF;** see Chapter 2) scenario. Such ordered flows are never completely efficient due to the Second law of thermodynamics and so they act to dissipate the very same thermodynamic gradients that gave rise to them (and thus the name, "Dissipative structures"). As such, Glansdorff and Prigogine (1971) suggested the OTF scenario to be a *phenomenological mechanism for the creation of order* (*e.g.*, the "anti-entropic" eddies, above) and the consequential maintenance of some local quasi-steady state where LSD-like conditions apply.

In other words, the local fluctuations in the action of the Second Law are attributed to local fluctuations in free energy gradients. What causes these fluctuations in free energy gradients is of course not addressed in any detail beyond attributing them to chance anomalies, as any such attempt would lead to another circular/self-referential loop in causation: local fluctuations in the Second Law are caused by local fluctuations in free energy gradients which are in turn caused by local fluctuations in the Second Law, *etc.* This question is taken up again in Chapters 3 and 6, where an alternate (hierarchical, fractal-like) framework is used in an attempt to lessen this circularity of causation.

LINEAR THERMODYNAMICS

The linear nature of Prigogine's (1947) original proof mentioned above represents a point of concern that needs clarification. The main limitation to this approach is the formal (mathematical) requirement of linearisability of the thermodynamic flows and fluxes and the use of the "Onsager reciprocity relations" which requires a microscopic reversibility of interactions.

The basis of the "Onsager reciprocity relations" is the assumption of microscopic reversibility of molecular processes (*i.e.*, a time *symmetry* of statistical microscopic fluctuations). However, in its application to generalised compartmentalised systems (so called, "black boxes" in ecological modelling) this reversibility can be assured by a judicious choice of the space-time scales of reference. That is, it can be treated as a scalar (anisotropic) problem rather than a vectorial (isotropic) one. Within the context of the algebra utilised in Chapter 3, the application of Onsager's principle is tantamount to expecting useful free energy flows from system A to B to have a proportional effect upon the useful free energy flows from system B to A—that is, some recycling of energy. This is an assumption that under most circumstances may be considered quite reasonable, given the empirical results of Winberg (1972), Pomeroy (1974), Platt *et al.* (1984), Fath and Patten (1998) and many others that have repeatedly demonstrated the importance of matter and energy cycling (*i.e.*, synergism).

Ignoring the non-linear terms that are customarily removed in linearisation techniques is problematic in highly nonlinear systems as their influence upon the time-evolution of a system can be quite important. However, including such non-linear terms makes intractable the solution and traditional stability analyses (*e.g.*, Liapunov's methods) of the thermodynamic "equations of motion" (*sensu* Denbigh 1951). This is especially the case as current non-linear theory has shown that the "stability" of systems can be quite complex (*e.g.*, see Byers and Hansell 1992, 1996).

However, regardless of the formal (mathematical) assumptions of the approach, the "Least specific dissipation principle" has a wide range of empirical applicability. The range of this applicability can only be determined via empirical studies (*e.g.*, Denbigh 1951, Spanner 1964:234, Katchalsky and Curran 1967). The empirical regularities illustrated for photosynthetic pathways by Spanner (1964); membrane dynamics by Peusner (1970, 1986) and Mikulecky (1977, 1985); developmental patterns by Zotin and Zotina (1967), Lurié and Wagensberg (1979) and Briedis and Seagrave (1984); and population and larger level patterns by Johnson (1994), Gladyshev (1978, 1997:17), all suggest that the linear theory may have some applicability to biological systems and so cannot be rejected without consideration of empirical data.

The perspective adopted in this thesis is to acknowledge the importance of nonlinearity (and pseudo-nonlinearity) but not to assume that it renders every question unanswerable. A case in point is the use of linearisation techniques to characterise a system. The appropriateness of this use varies depending upon the degree of nonlinearity of the region of analysis and the presence of critical points (singularities). This thesis attempts to exploit this varying degree of appropriateness of a linear approximation with deviation from some local quasi-steady state, as an index of the degree of non-linearity manifest in the system (Chapters 2 and 3). This thesis therefore relaxes the constraint of the LSD principle: that systems must be infinitesimally close to thermodynamic equilibrium. By shifting the focus to local (*i.e.*, judiciously chosen space-time scales of reference) quasi-steady ("slowly," time-varying, relative to the space-time scales of reference) states, where the dynamical equations can be arbitrarily linearised (regardless of the intrinsic non-linearity of the systems), it becomes possible to apply these concepts in a scale-free context. Under such a context, the LSD simply implies a slowing down of flows and the reduction of associated free energy gradients (*i.e.*, "irreversibilities", *sensu* Professor J.J. Kay, personal communication). Such a potential was examined with the aid of empirical data. Every attempt has been made to push this approach to its limits to understand the limits of its application. In no way do we claim that this represents the sole approach to the issues treated in the thesis. However, we do claim that it is a utilitarian approach, whose real potential only further empirical work can illustrate.

OTHER THERMODYNAMIC SCHOOLS OF THOUGHT

There exist innumerable thermodynamic schools of thought (see Patten *et al.* 2002 and references therein, for a sample of the currently active and major ecological schools). Amongst these are: "Emergy" Analysis of Odum (1996), genomic (statistical) "Exergy" Analysis of Jørgensen (Jørgensen 1992), free energy "Exergy Analysis" of Schneider and Kay (1994), "Emergy and Transformity Analysis" (Odum 1996), "Power Analysis" (Odum 1983), "Entropy Analysis" (Aoki 1989, 1993), "Kullback Information Analysis" (by Svirezhev, in Patten *et al.* 2002), "Ascendency Analysis" Ulanowicz (1986), "Network Thermodynamic Analysis" (Peusner 1970, Mikulecky 1977), "Action Analysis" of Johnson (1994) and Vanriel and Johnson (1995) and the more information theoretic interpretations of Wicken (1980), and Brooks and Wiley (1986).

Two schools that are particularly similar to that of the Darwin-Boltzmann-Lotka-Prigogine lineage (described above), are both known as "Network thermodynamics". The first, developed by Peusner (1970, 1983, 1986) and Mikulecky (1977, 1984, 1985) uses an analogical scalar representation of systems using the language of electrical circuits (especially those of Kirchhoff's current and voltage laws) and so parallels the work of H. Odum (1983). Due to its scalar nature, the linearity assumptions are less constraining and a full non-linear theory has also been developed (Mikulecky 1977). The second approach is superficially very similar, but more explicitly topological in nature (using "bond graphs") and is due to the work of Oster, Perelson and Katchalsky (1971). In both approaches, more general (widely applicable) equivalents to Onsager's relations and Prigogine' least specific dissipation principles have been demonstrated (*i.e.*, Tellegen's quasi-power theorem).

The work of Ulanowicz (1972, 1980, 1983), Ulanowicz and Hannon (1987) represents a third parallel development, where the network through flows and cycling topologies are dissected and information-theoretic measures of the network topology are used to describe the structure and development of ecological systems. The developmental patterns are summarised through the notion of the "ascendency" which is a combined information-theoretic measure of the network topology and energy through-flow. Patten's (1978, 1985) linear environ theory also converges upon similar approaches although the thermodynamic and information-theoretic concepts are less directly treated but with greater focus upon the unravelling of the cycles and the use of an index of cycling (synergism). All these approaches (and there are many others[2]) rely upon a linear thermodynamic formalism to the analysis of open systems. Each has a nominal "goal function" (*e.g.*, Jørgensen *et al.* 1995) that is phenomenologically derived in some fashion.

Schneider and Kay (1994) have been proponents for the re-statement of the Second law solely in terms of the <u>degradation of exergy gradients</u>. The advantage of such a qualitative formulation avoids the problems inherent in the treatment of nonlinearities (*e.g.*, nonlinearity, the definition of entropy in a nonequilibrium state—but see also the

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[2] *Each of which are more or less variants along a continuum of varying degrees of generality and approaches: e.g., de Groot and Mazur 1962, Brooks and Wiley 1988, Gladyshev 1978, 1997, Meixner 1969, Margalef 1963, Wicken 1980.*

next Section, and Meixner 1969, and Aoki 1989 for contrasting opinions on the immeasurability of exergy).

SECOND LAW ANALYSIS[3]

Second law analysis is the "direct application of the Second Law of Thermodynamics" to the analysis of energy transformations, generally in the context of cost and efficiency optimisations in engineering applications (Gaggioli 1980). The currency that is used in this mode of analysis is exergy (the available or useful free energy). As such, Second law analysis represents a detailed accounting of how processes alter the *quality* of energy. This is in contrast to a "First law analysis" that is a detailed accounting of the *quantity* of energy flows through systems. Thus, for example, the accounting of energy flows for a given food web such as those illustrated by Lindemann (1942) represents a First law analysis (*i.e.*, the conservation of energy). In contrast, Schneider and Kay's (1994) analysis of the change in the quality of high quality incoming solar energy (shortwave) to low quality, outgoing radiation (longwave) as it passes through various ecosystems, represents a Second law analysis.

In the biological sciences, the concept of energy quality has been present from its very beginnings (*e.g.*, notions of food quality; niche exploitation; vitamins and essential amino acids in organismal health; critical stoichiometric elemental ratios such as the Redfield ratios, Smith 1983, Downing and McCauley 1992; relative abundance of

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[3] *Most of the ideas discussed in this section arose due to the very penetrating commentary of Professor J.J. Kay (University of Waterloo) on an earlier version of this thesis.*

different photosynthetic mechanisms such as C3, C4 pathways; pigments using different parts of the light spectra; and switching between detritus/grazing/predation pathways). In fact, it is due to the very large number of currencies of energy qualities, that biologists repeatedly have turned to energy as a common currency. In short, the study of any given biological system's structure and function (*i.e.*, how they are adapted to a particular set of internal-external, structural-functional constraints) fundamentally utilises an implicit form of first and second law analyses.

The myriad ways in which such adaptations are expressed and their plasticity even within those constraints have made the biologists' work that much more delightful to narrate and that much more difficult to assimilate. To conduct an exhaustive (and quite costly) First and Second law analysis with their accompanying thermodynamic systems description would be quite informative and useful, in the narrative sense—particularly at the resolution of ecosystem levels of organisation as they are so lacking. However, exhaustive attempts at accounting flows face the same intrinsic difficulties of circularity and complexity, discussed above. Further, the complete description of all mass, energy and exergy flows *into* and *out* of the relevant systems at relevant space-time scales represents a formidable task that would be difficult to complete within the lifetime of a single researcher. Thirdly, the calculation of the "correct" thermodynamic efficiencies was not the goal of this study, although such information may be useful. Finally, there is no generally accepted way of defining the reference state from which to measure exergy. As such, how one may measure the quantity, let alone the quality of free energy entering and leaving biological systems is not a trivial task (Månsson and McGlade

1993, and Aoki 1993), especially when one accepts that spatial-temporal-organisational variations in these flows generally increase monotonically with the magnitude of these flows. For these reasons, a strict Second Law Analysis was not and could not be undertaken for the thesis.

While Second law analysis was not *explicitly* conducted, the analysis of metabolic rates (waste heat production) represents an *implicit* form of Second law analysis. This is because waste heat production from metabolic activity represents an estimate of the energy converted from high quality, biologically useful free energy to low quality, biologically less useful energy (heat). It is possible for some of this low quality heat energy to be re-used directly or indirectly by the producing system (*e.g.*, organism), however, most of the heat leaving an organism represents a rather permanent loss. This is particularly the case at *synecological* levels of organisation. For this reason, metabolic rates are suggested to be a practical index of the net entropy production (irreversibilities) attributable to the activities of the system (see also, Appendix 2C). Such a focus upon metabolically induced irreversibilities represents a Second Law Analysis in the broadest sense.

As for the material wastes such as urea, faecal matter and other forms of "lost" biomass, these quantities remain part of the ecosystem until their eventual metabolic transformation into waste heat. These mass, energy and exergy flows represent short-term (one-pass) repartitionings of the free energy within the ecosystem. However, in the long-term (iterated, multi-pass) the same mass can and does recycle within the system, until their eventual metabolic passage into waste heat (*i.e.*, entropy production; the "metabolic turnover" of Briedis and Seagrave 1984).

To conclude, the approach of this thesis is fundamentally an attempt to short-circuit the limitations of a reductionistic/holistic approach by starting from a very simple and general premise and drawing from it an equally simple, but hopefully useful expectation of how systems should change. This is done by focusing upon the local irreversibilities (rather than attempting an exhaustive and impossible exergy analysis), estimated as the intensity of waste heat produced due to biological activity (*i.e.*, the R/B ratio). This choice is justified empirically on the grounds that many important biological rates are correlated with each other (ingestion, egestion, excretion, gross primary production, net primary production and total respiration rates; *e.g.*, see Figure 4.3). This is also evidenced in their common allometric basis (*e.g.*, Peters 1983). As such, any one of these flows can also represent useful indices of the irreversibilities attributable to biological activity. The R/B ratio was chosen due to: (1) the relative ease of measurement of respiration rates (relative to production measurements) and (2) its closer relationship to the entropy production term in the linear theory of Prigogine.

PURPOSE AND OVERVIEW

In the spirit of guarded optimism, the purpose of this thesis is two-fold:

1. Explain why the patterns of size and abundance are found in so many diverse environments. More specifically,
    a. Why is the size-abundance relationship log-linear in shape?
    b. Why is the slope of the size-abundance relationship ≈ -1?
2. Illustrate some of the major and fundamental applications and implications that follow from a thermodynamic understanding of this relationship.

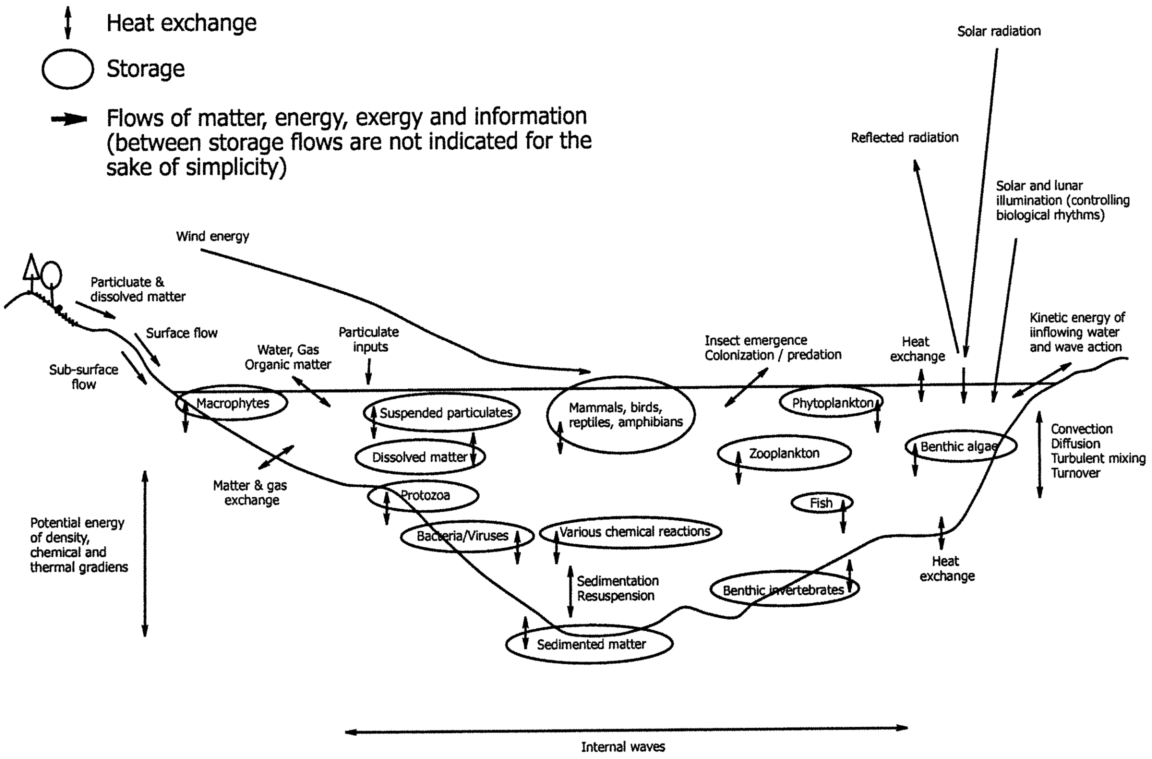
In the previous section, some of the mechanisms that may be involved in creating the size-abundance pattern were outlined. While these and numerous other physiological, ecological and evolutionary interactions are certainly involved in the creation of this pattern, listing and describing them all cannot explain *how* or *why* this pattern comes to be. How does one integrate these ideas and come to a useful understanding of the size-abundance relationship?

The size-abundance relationship may be re-interpreted in a phenomenological context, using the well-established allometric scaling of physiological rates (Chapter 2). In so doing, it is possible to clarify the origins of the size-abundance relationship and suggest a measure of environmental uncertainty, a fundamental concept in biology that has so far eluded any comprehensive or comprehensible expression.

The notion of environmental uncertainty is developed in greater detail by stating explicitly the hierarchical network structure of ecological systems in Chapter 3. The Second Law of Thermodynamics is shown to have a fractal-like scale-dependent asymmetry. This asymmetry is evident as the actions of the Second Law are followed as they descend or ascend hierarchical (holarchical) scale, creating what may be termed local-order and local-disorder, respectively. The balance between these two antagonistic propensities may be interpreted as a balance between processes and constraints *internal* (growth and development) and *external* (interactive and perturbing influences) to a system, respectively. The use of such an index of this balance is demonstrated and is argued to be related to the environmental uncertainty of systems. These issues are explored using the "paradox of enrichment" as a didactic tool. This recontextualisation of the "paradox" to the case of more complex systems is further argued to be convergent with the concept of sustainable development/growth.

To continue in developing and extending the notion of environmental uncertainty emergent from Chapters 2 and 3 (and conversely to test the utility of the concept as well), this approach was applied to the well-known debate on the relationship between biological diversity and the stability of a system (Chapter 4). Some of the confusion surrounding this debate was resolved by using literature data to quantify the notions of perturbation, productivity and stability and demonstrate their relationships. These ideas were synthesised into a more general conceptual model that integrates the "Intermediate disturbance hypothesis", and the "Intermediate productivity hypothesis". We suggested that this simplification be termed the "Greatest adaptability hypothesis", to emphasise its relationship to the evolutionary precursors of the hypothesis, namely the "Red Queen's hypothesis".

Another empirical, albeit simplistic validation (and application) of the ideas stemming from Chapters 2 and 3 was attempted in the context of rapid global climate change as the driving source of environmental uncertainty to ecological systems in Chapter 5. Here the effects of rapid climate change were examined in terms of magnitude and variability effects and explored across a wide range of spatial, temporal and organisational scales (physiological to ecosystem scales). The goal was to determine the expected relationship between biological diversity and rapid climate change. It is shown that this question is but a more global representation of the "paradox of enrichment", where both long-term (magnitude effects) and short-term (variability) effects exist and whose influence must be considered. Its relationship to the recurrent concept of adaptability in the face of environmental uncertainty was again explored.



Other complex interactions:

- genotypic and phenotypic change
- climatic change
- isostatic rebound and infilling of lake
- toxicants and other pollutants
- colonisation and extirpation
- redox, pH and turbidity changes

Figure 1.1. "System's Diagram" depicting the context of the study system and the main driving processes. The focus of this thesis is upon the size-abundance patterns of the planktonic components of the above, namely phytoplankton, zooplankton and bacteria. As is evident, the planktonic system is embedded in a severely complex system that defies exhaustive study. This thesis proposes an approach to the study of such complexly embedded systems that does not require the study and measurement of all interactive components by developing a scale-free, fractal-like approach.

explained in intro?

— Chapter 2 —

MEASURING PERTURBATION IN A COMPLICATED, THERMODYNAMIC WORLD[4]

> *By ecology, we mean the body of knowledge concerning the ECONOMY OF NATURE—the investigation of the total relations of the animal to its inorganic and to its organic environment; including above all, its friendly and inimical relations with those animals and plants with which it comes directly or indirectly into contact—in a word, ecology is the study of all those complex interrelations referred to by Darwin as the conditions for the struggle for existence.*
>
> *Haeckel (1866, translated by McIntosh 1985, p.7)*

ABSTRACT

Our inability to measure perturbation beyond a context- or system-specific manner has been a fundamental bottleneck to the generalisation of a great number of ecological concepts. Here we develop and explore a thermodynamically inspired solution to this problem as developed by Prigogine and colleagues. We empirically and theoretically demonstrate how the ratio of community respiration to community biomass is an index of the distance from a general thermodynamic steady state. Using this approach, we re-examine some very old ecological questions (*e.g.*, the patterns of size and abundance; the spatio-temporal complexity of ecological interactions) and other more recent questions (*e.g.*, the leakiness/efficiency of food webs; the relevance of nonlinear interactions and critical behaviour to ecology). We discuss these implications and

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connections and develop a strong theoretical and physical foundation for the study of ecological change.

INTRODUCTION

The identification and study of biologically important forms of perturbation represents the greater part of the pre-occupation of most ecologists (Thiery 1982; Petraitis *et al.* 1989). However, due to its multi-dimensional nature and the uncertainty of its measurement, it represents one of an ecologist's most difficult tasks. For example, one may ask if a storm event is more important than the effect of ionising radiation near the surface of water bodies, or perhaps the continuous but low-level inputs of heavy metals in a given lake, or the impending extinction of a local gene pool or some mind-boggling combination of these factors; and if so, for which organisms and how? Discerning these causes in a reductionistic approach represents an especially difficult, if not impossible task (*e.g.*, Bertalanffy 1968:66-68; Peters 1991:110).

In the attempt to circumvent this intrinsic difficulty of dealing with such complex, multidimensional, multicausal, scale-dependent and strongly inter-related feedback systems, numerous studies have repeatedly appealed to thermodynamic principles (*e.g.*, Lotka 1922; Odum and Pinkerton 1955; Zotin and Zotina 1967; Eigen and Schuster 1979; Wicken 1980; Johnson 1981, 1994; Bryan *et al.* 1990; Kay 1991; Jørgensen and Padisák 1996, Choi and Patten 2002). While harsh criticisms exist for such attempts (*e.g.*, Månsson and McGlade 1993), the appeal of this approach has been due to two main reasons: first, the special way in which a "system" is treated as a complex whole rather than a mechanical assemblage of atomistic parts (*e.g.*, Spanner 1964); and secondly, the implicit incorporation of the arrow of time that details how a system will change or evolve with time (due to the Second Law of Thermodynamics).

Unfortunately, the application of these thermodynamic principles have been hampered due to their relevance to systems that are "closed" to material or energetic exchanges with their surrounding environment. However, the extension of these principles to systems more "open", non-equilibrium systems has progressed, due in the main to the work of Onsager (1931a,b) and Prigogine (1955) and colleagues (Glansdorff and Prigogine 1971; Nicolis and Prigogine 1977) and in an complementary direction by Hatsopoulos and Keenan (1965), Kestin (1966), Kay (1991) and Schneider and Kay (1994), to the point where today these generalisations have been suggested to be elevated to the level of a new Thermodynamic Law (Jørgensen and Mejer 1977; Morowitz 1992). While there is still some debate as to which specific "goal-functions" are most appropriate/useful: *e.g.*, exergy (free energy; see Jørgensen 1994; Schneider and Kay 1994); emergy (the energy necessary to "build" an organism; Odum 1983); ascendency (Ulanowicz 1986); power (Odum and Pinkerton 1955; Ware 1982; Bryan *et al.* 1990; Loreau 1995); or entropy (Prigogine and Nicolis 1971), their consequences are all similar. The presence of an energy gradient fosters its own degradation via the action of "self-organised dissipative structures" (see below).

In the following, we will take advantage of some of these developments, most notably, the "Order Through Fluctuation" (OTF) principle and the "Least Specific Dissipation" (LSD) principle, made popular by Glansdorff and Prigogine (1971) and Nicolis and Prigogine (1977). Using these two concepts, we delineate a thermodynamically defined local steady state and the distance from this local steady state as the measure of perturbation in ecological systems. We then endeavour to empirically test and utilise these measures using freshwater limnoplankton as a test system and eventually relate our results to the concept of "critical" behaviour of complex systems (*i.e.*, "Self-Organised-Criticality" or "SOC"; Bak *et al.* 1989).

THEORETICAL CONSIDERATIONS: THERMODYNAMICS AND ECOLOGY

Boltzmann (1905), in 1886 borrowed from Darwin's theory of natural selection and with it, the implicit socio-economic views of Malthus, to describe life as a "struggle for free energy" (cited by Lotka 1922). Building upon this, Lotka (1922) proposed that the macroscopic consequence of the microscopic struggle for free energy is to make the energy flux through the system a maximum, subject to the constraints of the system. The thermodynamic mechanism that describes this struggle for free energy is known as the "Order Through Fluctuation" (OTF) principle proposed by Glansdorff and Prigogine (1971). The OTF principle is as follows: small statistical deviations in the flow of energy exist in any thermodynamic system. Such deviations are generally dampened out by dissipative processes. However, as the energy gradient increases, the amplification of these fluctuations becomes increasingly probable. Any fluctuations that can better dissipate the energy gradient become positively selected and amplified over time. These positive feedback structures (*e.g.*, autocatalytic cycles, food webs) are known as "dissipative structures" (Glansdorff and Prigogine 1971; Wicken 1980:17). The result of the combined activity of such dissipative structures is the increase of total energy flux through the system (Johnson 1994; Washida 1995). The OTF principle represents a generalised, phenomenological mechanism by which free energy gradients are broken down.

Internal, mechanical or structural constraints of the system (*e.g.*, limited carrying capacity; or energy transfer efficiency; or availability of key elements for metabolic function) modulate this tendency to increase the energy flow through the biota (Lotka 1922:148-150; Johnson 1994:239). In biological systems, the flow of energy through the system is slowed down by the diversion of free energy to stored energy (chemical potential) in the form of biomass through growth and reproduction. The thermodynamic principle that describes this slowing down of the flow of energy (see Johnson 1994:239) is known as the "Least Specific Dissipation" (or "LSD") principle (Onsager 1931a,b; Prigogine 1955). The LSD principle indicates that any system, in the face of a small but continued energy gradient, will tend towards a local minimum in the rate of entropy production per unit volume or mass (d_is/dt; see Appendices 1, 2C). This specific dissipation rate can be approximated by the ratio of respiration rate to biomass (or the

R/B ratio[5]) when the mass-specific rate of entropy flow (d_es/dt) is assumed to represent the dominant part of biological activity, relative to structural elaboration or anabolic processes (see Zotin and Zotina 1967; Lurié and Wagensberg 1979).

This tendency for imposed gradients to break down via the action of self-organised (auto-catalysed) "dissipative structures" has also been known under the guises of: the "Le Chatelier-Braun Principle" (*e.g.*, Bertalanffy 1950; Schneider and Kay 1994:29); the "Extended Second Law of Thermodynamics" by Schneider and Kay (1994; and according to them, the "Law of Stable Equilibrium" by Hatsopoulos and Keenan (1965); the "Unified Principle of Thermodynamics" by Kestin (1966)); the "Maximum Respiration Hypothesis" by Washida (1995); and even a new Law of Thermodynamics by Morowitz (1992)—all of which deal with the simple tendency of any imposed energy gradient to break down through the action of dissipative structures. For the sake of simplicity, we will continue to refer to this tendency for the intensity of entropy production to decrease as the LSD principle.

Given the above context, the R/B ratio expresses a certain competition for free energy between R (the maintenance of biomass via respiration) and the accumulation of B (via growth and reproduction). The total energy dissipation (R; *i.e.*, the total metabolic activity of a system) is expected to increase via the action of the OTF principle. Concomitantly, a decrease of the R/B ratio is expected by via the action of the LSD

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[5] *Note that R/B (respiration/biomass ratio) is analogous to the well known P/B (production to biomass ratio), made popular by Odum (1953, 1985), Odum (1956a, 1983) and Margalef (1963). Here, the R/B ratio is used because it is easier to measure and more directly related to thermodynamic dissipation.*

principle (*i.e.*, a greater diversion of free energy for the elaboration of biomass relative to maintenance metabolism). Perturbations modify the balance between the two propensities. Large-scale environmental perturbations generally act to reduce the living biomass (B) from a system while increasing the metabolic load upon exposed organisms (R). Consequently, perturbations may generally be expected to increase the R/B ratio, which counteracts the action of the LSD[6] principle's tendency to reduce this ratio. An R/B ratio that is small valued is thus representative of a system that is closer to a local thermodynamic quasi-steady state, while a ratio that is large valued represents one that is further from a local thermodynamic quasi-steady state[7].

EMPIRICAL CONSIDERATIONS: FIELD MEASUREMENT OF PERTURBATION

How then does stress or mortality causing perturbations (Rapport *et al.* 1985) influence this R/B ratio in reality? In biological systems, free energy may be diverted into one of two routes: structural elaboration (B, which is the result of growth and reproduction—the LSD principle; see explanation below), or structural maintenance (R, respiration—the OTF principle). Mortality causing perturbations generally cause an increase in the

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[6] *A difficulty in the application of the LSD principle to biological systems is the assumption of the validity of a linear expansion of the entropy production. Such an expansion is mathematically justifiable only when the energy gradients involved are weak. When the gradients are large, the nonlinear terms cannot be ignored. However, Zotin and Zotina's (1967), and Johnson's (1994) empirical results and Patten's (1983) theoretical results indicate that such a linearised approximation may be quite acceptable for the description of ecological/biological systems. For the purposes of the following, we will assume this validity (see also Appendix 7).*

[7] *As such, the R/B ratio also provides a convenient index of the degree of "nonlinearity" of the energy dissipation in ecological systems. This is because the further a system moves away from a local quasi-steady state, the less valid becomes the linear approximation of the dissipation terms as the non-linear terms become more and more dominant. Consequently, understanding the factors that control the degree of such nonlinearity becomes very important in that they will determine the spatio-temporal-organisational complexity of the ecological system.*

diversion of free energy to structural maintenance while decreasing the biomass directly via mortality factors. As such, the R/B ratio should increase in the face of perturbations.

The empirical demonstration of such an expectation may be attempted by relating the R/B ratio to some dominant form of abiotic perturbation. As argued by MacArthur and Wilson (1963), decreased island size increases the probability of extinction of organisms. That is, the size of a system is a measure of the capacity of a system to absorb or buffer environmental stresses (Schlosser 1990). Similarly, lakes may be considered islands in a continental sea. As such, smaller lakes may also be considered to have a lower capacity to buffer the effects of perturbations: *e.g.*, chemical pollution, eutrophication, acidification, predation, disease, temperature stresses, climatic change, species invasions, relative to larger systems. Smaller lakes should therefore demonstrate elevated R/B ratios.

We use the maximum depth of a lake as a simple and easily obtainable index of lake size. This is because lake morphological characteristics are generally strongly correlated in geomorphologically homogenous areas. For example, maximum depth, surface area, volume, fetch are significantly correlated in the lakes examined ($r>0.7$, $p<0.001$, $n=26$). To ensure that lake size would be the dominant gradient, 14 lakes were studied from the Canadian Shield in a limited spatial range, between latitudes 45°53'29'' to 46°22'05'' N and longitudes 73°19'45'' to 74°22'12'' W. Other sources of variation such as climatic and geochemical sources were consequently minimised. Lake size ranged from 3 to 500 ha (surface area), and 3 to 40 m (maximum depth). Mean summer total phosphorus concentrations ranged from ≈ 10 to 50 mg L^{-1}.

The R/B ratio of the planktonic community in these lakes were determined as follows: limnoplankton were sampled at the point of maximum depth with a conical net (60 um mesh size), a minimum of three times during the growing season (May to September) and the total biovolume measured by an automated particle counting and sizing apparatus (Optical Plankton Counter, Focal Technologies, Inc.). This total biovolume was converted to biomass assuming a density of 1 g mL^{-1}. Planktonic respiration rates were measured over 24 hour incubations at ±1°C of in-situ temperatures with water samples taken from a depth of 2 m near the point of sampling of the limnoplankton. Respiration rates were measured in 300 mL bottles. Changes in the dissolved inorganic carbon levels were measured by a gas-chromatographic method (Stainton 1973; Salonen 1981). This was made possible by the generally low DIC levels found in these lakes situated on the Canadian Shield. Respiration rates are expressed as mol C m^{-2} day^{-1} (Appendices 3, 4, 5).

A significant negative relationship was observed between the R/B ratio and lake size (Figure 2.1), confirming the expectation that the R/B ratio is higher in smaller systems, where perturbing influences are hypothesised to be more dominant.

Examining the data more carefully, much of this increase in the R/B ratio of limnoplankton from smaller lakes is attributable to a decrease in the size of limnoplankton (B) rather than an increase in respiration rates (R; Figure 2.2). This latter result represents a ≈ 60% decrease in the mean body length of plankton in the lakes that were studied. What causes the decrease in the size structure of the plankton across the lake size gradient cannot be stated definitively using a standard ecological (*i.e.*, reductionistic) approach.

The most frequently encountered explanation for this pattern is the influence of size-selective predation by planktivorous fish (*e.g.*, Brooks and Dodson 1965). For example, it has been shown that 16 to 62 % decreases in the mean length of zooplankton are possible in the presence of very strong fish predation (Moore and Folt 1993). Presumably, the importance of such predation effects becomes weaker as lake size increases. This reduction in predation pressure may occur in larger systems because these systems also harbour larger, piscivorous fish that are thought to control the abundance of planktivorous fish. Larger piscivorous fish of course generally have quite stringent habitat requirements that limit them to larger lakes (see below).

There are, however, alternate mechanisms that can explain just as well the observed variations of body size distributions. Moore and Folt (1993) focussed upon the influence of temperature on the growth of zooplankton. Increased temperatures are thought to cause differential responses in zooplankton metabolism causing elevated energetic costs. This simple temperature effect has been demonstrated to decrease the mean size of zooplankton from 10 to 80 % in the mean length of zooplankton, with 5 to 10°C increases in ambient temperature (Moore and Folt 1993). Similar but more complex changes were described with the effects of toxicants as perturbing factors (*i.e.*, metabolic poisons; Moore and Folt 1993).

The magnitude of the above two effects are sufficiently large to account for the observed decreases in limnoplankton body size in the lakes studied in Figure 2.2. However, many other mechanisms exist that can have equally important influences upon size structure for which there exist no comparable data: *e.g.*, the effects of life history evolution, food availability, crowding effects, disease and parasitism and all their numerous interactions. Due to the complexity of the interactions of these mechanisms, identifying THE mechanism that is responsible for the changes in size structure represents another very difficult task. However, the power of the thermodynamic approach can now be exploited: regardless of the specific perturbations that may be involved (predation, toxicant mortality factors, energetic costs, disease, *etc.*), the R/B ratio *integrates* the effects of these biologically relevant perturbations into a conveniently measurable index.

The composition of fish species in lakes represents another ecological pattern that corroborates the above conclusion. Fish communities in smaller, shallower lakes are generally dominated by small body-sized fish (Figure 2.3). As in the case of the limnoplankton, predation and temperature effects are most frequently alluded to in the aquatic literature to explain this pattern (Harvey 1981; Rapport *et al.* 1985). Other perturbing factors that have been identified include: low dissolved oxygen concentrations in winter and summer, turbidity, pH, heavy metals, spawning habitat and habitat complexity (Harvey 1978; Hughes and Gammon 1987; Resh *et al.* 1988; Couillard *et al.* 1995; Yoder and Rankin 1995). However, regardless of the specific factor(s) involved, the effects of such perturbations become much more influential in smaller systems than in larger systems (see Schlosser 1990 for similar observations for fish communities in riverine systems) and is quantifiable with a correlate of R/B, the mean of the ranked adult size of fish species (Figure 2.3).

AN EXTENSION: THERMODYNAMICS, SELF-ORGANISED CRITICALITY AND ECOSYSTEMS

An independent test of the utility of this R/B ratio as a measure of perturbation was attempted. The crux of the argument lies in accepting that the well-known patterns of size and abundance (Sheldon *et al.* 1972; Figure 2.4; Table 2.1) represent an example of "self-organised criticality" (Bak *et al.* 1989; Bak 1996; Jørgensen *et al.* 1998). A brief review of the size-abundance relationship is given in Appendix 6. "Critical" behaviour indicates that small-scaled, local interactions become amplified and have large-scale effects that resonate throughout the system (*i.e.*, non-locality of interactions; Schroeder 1991).

The concept of self-organised criticality is best illustrated with Bak *et al.*'s (1989) original model: the size of avalanches in a pile of sand. When sand is continually poured onto a plate, the pile of sand eventually reaches a state where the rate of sand flowing over the plate equals the rate of sand input into the system. At this steady state, the frequency of avalanches (sand falling over the plate) is a power function of the size of the avalanches (magnitude). This fractal-like (Mandelbrot 1967) power relationship is quite important in that it represents a critical state where the local interaction of the neighbouring grains of sand have effects that are not limited to the local environment but can extend throughout the whole system. Technically, this critical state is identified as the point where the integral correlation length of the spatio-temporal autocorrelation function becomes infinite (Bak *et al.* 1989; Solé et al. 1997) and is attributable to the sensitivity to initial conditions of complexly interacting, many-bodied systems (Poincaré 1892; Kolmogorov 1954; Nicolis and Nicolis 1984), also known as the "butterfly effect" (Lorentz 1963) in catastrophe theory.

Since this initial study, the relationship between SOC and many other phenomena have been noted: the magnitude of earthquakes (Guttenburg-Richter relation; *e.g.*, Scholz 1991), patterns of drainage networks, lake sizes (Turcotte 1995), the size of clusters in the game of life (Bak *et al.* 1989); the gap sizes in a tropical forest (Solé and Manrubia 1995); size of changes in primary production in lakes (Jørgensen *et al.* 1998); and the patterns of extinction (Bak and Sneppen 1993; Newman 1996; Solé *et al.* 1997). This fractal-like marginal steady state is characterised by having continual inputs of energy (*i.e.*, an open thermodynamical system) but with dissipative outputs that are discontinuous and following a power-law distribution:

(1) $F \alpha q^{u}$

where F represents the frequency of energy dissipating events and q the magnitude of the energy-dissipating event.

Ecological systems have continual energy inputs from the sun, which are dissipated in a fractal-like fashion. This fractal-like (*i.e.*, power-law distribution) pattern may be identified in the size-abundance relationship, which due to the strong relationship between the size of an organism and its respiration rate (Hemmingsen 1960; Klieber 1961) may be transposed as a frequency-magnitude distribution of energy dissipation:

$$(2) \qquad F \alpha r^{v}$$

where F is the frequency of energy dissipating events (*i.e.*, the number of organisms); r represents the magnitude of energy dissipating events (*i.e.*, the magnitude of respiration rates for an organism of mass, m; $r \alpha m^{w}$); and $v = x/w$. The exponent w from the size-respiration relationship has been empirically determined to be $\approx$ 0.75, while the exponent x from the size-abundance relationship has been empirically determined to be ≈ -1 (see Appendix 6; Table 2.1).

This connection between SOC and the size-abundance relationship is very important as such systems have a very particular stability characteristic. SOC systems are known to be robustly stable to perturbations at all length scales. In an ecological context, this means that perturbations of any given size, from large-scale disturbances such as climatic cycles or catastrophes to small-scale disturbances such as a tree fall, may act as destabilising factors that move the system away from this fractal-like steady state. However, the system will return to this steady state as long as there is a continual input of free energy (note the correspondence of this statement with that of the LSD principle). This is essentially the concept of ecological succession and climax formulated in energetic terms and argues for the presence of a size-dependent carrying capacity.

If this relationship between SOC and the size-abundance relationship is valid, the following hypothesis may be proposed: the relative deviation of the size-abundance relationship from the power function is a measure of the relative distance from the steady state. That is, the coefficient of determination (R^2) of the size-abundance relationship is another integrated measure of the perturbation regime in a given system, with low values expected in systems that are strongly perturbed (far from the steady state) and high values expected in systems closer to the steady state (see also Sprules and Munawar 1986). Thus, the coefficient of determination should be positively correlated with the R/B ratio and inversely correlated with the geometric mean size of organisms.

When we return to the data set reported above and examine the relationship between the coefficient of determination (R^2) of the log(size) vs. log(abundance) relationship to the R/B ratio, we find a statistically significant negative relationship (Figure 2.5). That is, systems that demonstrate size-abundance relationships that deviate from the power-function relationship (low R^2) are found to demonstrate high R/B ratios, a state that is, thermodynamically, more "perturbed" state. This independently suggests that the R/B ratio represents a practical thermodynamic measure of perturbation from a local steady state. Conversely, this result also suggests that ecological systems may also be considered *Self-Organised Critical systems.*

Perhaps the most interesting and controversial implication of this relationship between SOC and ecological systems is that the statistically robust stable steady state of SOC systems is subject to an indeterminacy between the magnitude of a cause (*i.e.*, a perturbation or random "fluctuation") and its effect (*i.e.*, response). That is, even the smallest of fluctuations can create an "avalanche" of cascading effects at all scales (critical behaviour). This indeterminacy between the magnitude of a cause and its effect is due to the sensitivity to initial conditions found in nonlinear dissipative systems and the increasing importance of nonlinear effects when perturbations move the system further away from the local quasi-steady state (Kolmogorov 1954; Lorentz 1963). Some simple biological examples of this indeterminacy include: the uncertain effect of invading species; the lag period before a massive population explosion of invading species; or the unpredictable occurrence of pest and disease outbreaks (*e.g.*, spruce budworm, influenza, measles, the plague; Sugihara and May 1990).

GENERAL DISCUSSION AND CONCLUSIONS

While SOC may explain the structure of the power-function relationship between size and abundance in a statistical-mechanical context, it does not address why the magnitudes of the exponent seem to be restricted to the interval (–0.7, –1.2). Interestingly, Figure 2.6 demonstrates how the R/B ratio varies with the exponent of the size-abundance relationship. An ever-increasing exponent (to the right of Figure 2.6) represents a thermodynamically more stable configuration (the principle of Least Specific Dissipation). That is, solely from thermodynamic considerations, change in the direction of ever increasing numbers of large-sized organisms is more probable. Immediately, this principle may be recognised in the increase in animal size over evolutionary time, a pattern known as Cope's Law (Stanley 1973), and also along a successional gradient over ecological time. Presumably, what keeps the exponent from continually increasing is the influence of disturbance, maintaining these systems in a dynamic steady state with the exponent near –1.

Another striking pattern that must be noted is that the first derivative of the relationship represented in Figure 2.6 (*i.e.*, the rate of change of the specific dissipation rate with respect to the magnitude of the size-abundance relationship) is maximal when the exponent is near –1. That is, the specific dissipation rate can change rapidly with only minor changes to the size structure of a community when the exponent is near –1. This characteristic relates to another often discussed and rather controversial characteristic of SOC systems: their capacity to "adapt" rapidly to novel conditions. In the case of the patterns of size and abundance, this "adaptability" seems to manifest itself by this potential to accommodate variations in energy inflow and outflow with only minimal changes to the size-abundance relationship. Thus, the limited nature of the exponents of the size-abundance relationship indicates that these ecological systems exist in a state where fluctuations in energy influxes or deficits are rapidly "relaxed", allowing for the homeostatic maintenance of a thermodynamic steady state.

Complementary findings have also been reported by Jørgensen (1995) and Jørgensen *et al.* (1998) in an information-theoretic interpretation of the Second Law of Thermodynamics. He found that systems with the greatest amount of thermodynamic information (*i.e.*, the most probable state of an open thermodynamic system) are in a state that he calls, "on the edge of chaos" (*i.e.*, verging upon chaotic dynamics; see also Kauffman 1991). This state is that which is thought to be most "adaptable" in that such systems can be structurally complex and developed yet they can very rapidly change their state to match fluctuating environmental conditions.

As previously mentioned, the R/B ratio can be more generally considered an index of the degree of nonlinearity of energetic interactions in the system. When a system is near the thermodynamic steady state (low R/B ratios), the assumption of linearity discussed in the Introduction is more valid (see also Appendix 1). When the energy gradient becomes larger (higher R/B ratios), the nonlinear terms become more important. This is quite important because the more nonlinear the energetic interactions are in a system, the more complex will be the spatio-temporal patterns of these interaction. This sense of spatio-temporal complexity has been another very important concept with which ecologists have been grappling for a very long time. Its implications are especially important from a population-dynamic point of view as well as the management-conservation perspective (Hassell *et al.* 1976; Berryman and Millstein 1989; Scheffer 1991).

This relationship between the R/B ratio and the spatio-temporal complexity of energetic interactions may be conceptualised with what is known as a bifurcation sequence (Figure 2.7). Focussing upon the time-domain, temporal variations of population number may be expressed in terms of their domains of attraction, as a function of the R/B ratio (*e.g.*, see May and Oster 1976; Nicolis and Nicolis 1984). When the R/B ratio increases (*e.g.*, from system a to b in Figure 2.7), more complex, variable and unpredictable patterns of population dynamics may be expected. This was in fact experimentally shown by Halbach (1973) where he noted increased oscillations of rotifer abundance when their average body size was forced to decrease through temperature stresses—a pattern strongly suggestive of a bifurcation sequence. Such changes were also accompanied with an extended de-synchrony in the reproductive cycle of the rotifers and a reduced size at maturity.

To conclude, the R/B ratio seems to be a functional index of the degree of perturbation from a local quasi-steady thermodynamic state. The utility of this measure was confirmed empirically in a limited set of lakes and independently validated by using the concept of self-organised criticality. These results demonstrate that the thermodynamic principles of least specific dissipation and order through fluctuation are useful ecological concepts that aid in the development of some very simple approaches to seemingly very difficult questions.

A greater spatio-temporal variation in population numbers may be predicted with systems that exhibit higher R/B ratios (*e.g.*, system b in Figure 2.7). This is graphically represented by the greater number of potential states (the dynamical attractor is more complex) and represents a prediction that is quite reasonable in that such systems are more perturbed from the thermodynamic steady state. How the above spatio-temporal complexity of the system is related to the structural (*i.e.*, organisational) complexity of the system represents an old ecological question better known as the "stability-diversity" or "stability-complexity" relationship. Whether a thermodynamic approach can shed any more light onto this rather complex issue is not known but is examined in Chapter 4.

Furthermore, the relationship between the R/B ratio as a measure of perturbation and dynamical variability to the "paradox of enrichment" (the destabilisation of a system through nutrient enrichment; Rosenzweig 1971; Chapter 3) and the "paradox of the plankton" (the maintenance of a high species diversity through the action of continued disturbance; Hutchinson 1961; Sommer 1984; Jørgensen and Padisák 1996; Chapter 4) are quite intriguing and represent fruitful avenues for future research. Coincident with higher R/B ratios are also energetically more "leaky" ecological interactions (*i.e.*, thermodynamically inefficient). This can be said because there is a greater energetic cost for the maintenance of structural integrity (*i.e.*, biomass; see Wicken 1980:14). The development and clarification of these numerous relationships represent promising work for the future. It is hoped that this study will serve as a foundation for such a synthesis.

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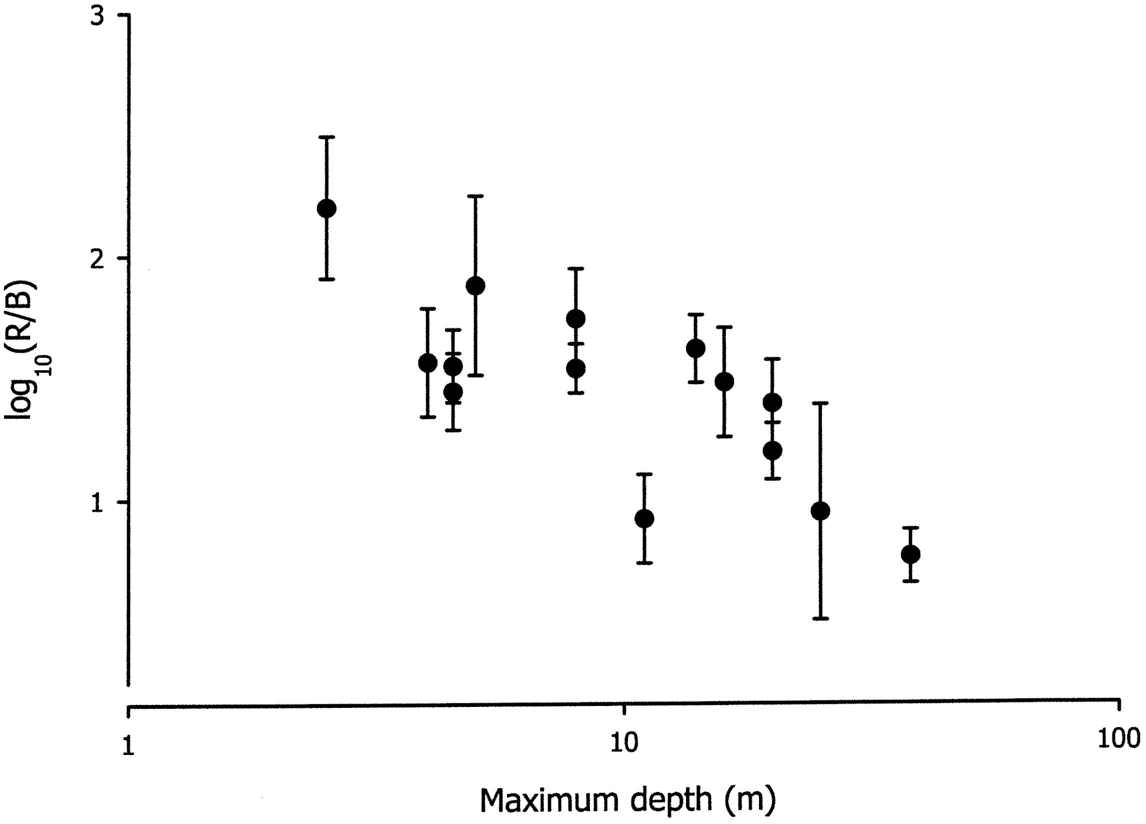

Figure 2.1. The relationship between the R/B ratio (mol C g^{-1} wet weight day^{-1}) and the maximum depth of 14 lakes (m). The standard errors represent the seasonal variation found between May to September. The relationship is a statistically significant correlation: $R^2_{Pearson} = 0.604$, n=14, p=0.001.

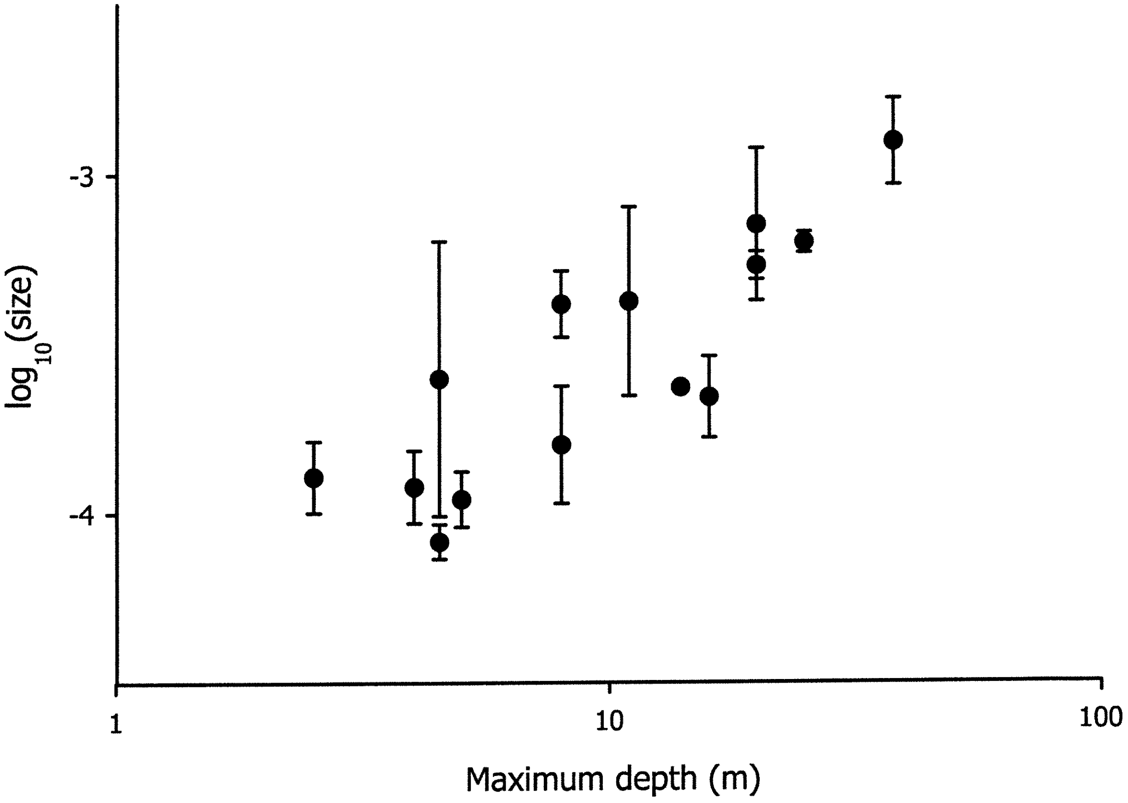

Figure 2.2. The relationship between the geometric mean size of plankton (g) and lake depth (m). The standard errors demonstrate the seasonal variation found between May to September. The relationship is a statistically significant correlation: $R^2_{\text{Pearson}} = 0.727$, n=14, p=0.0001.

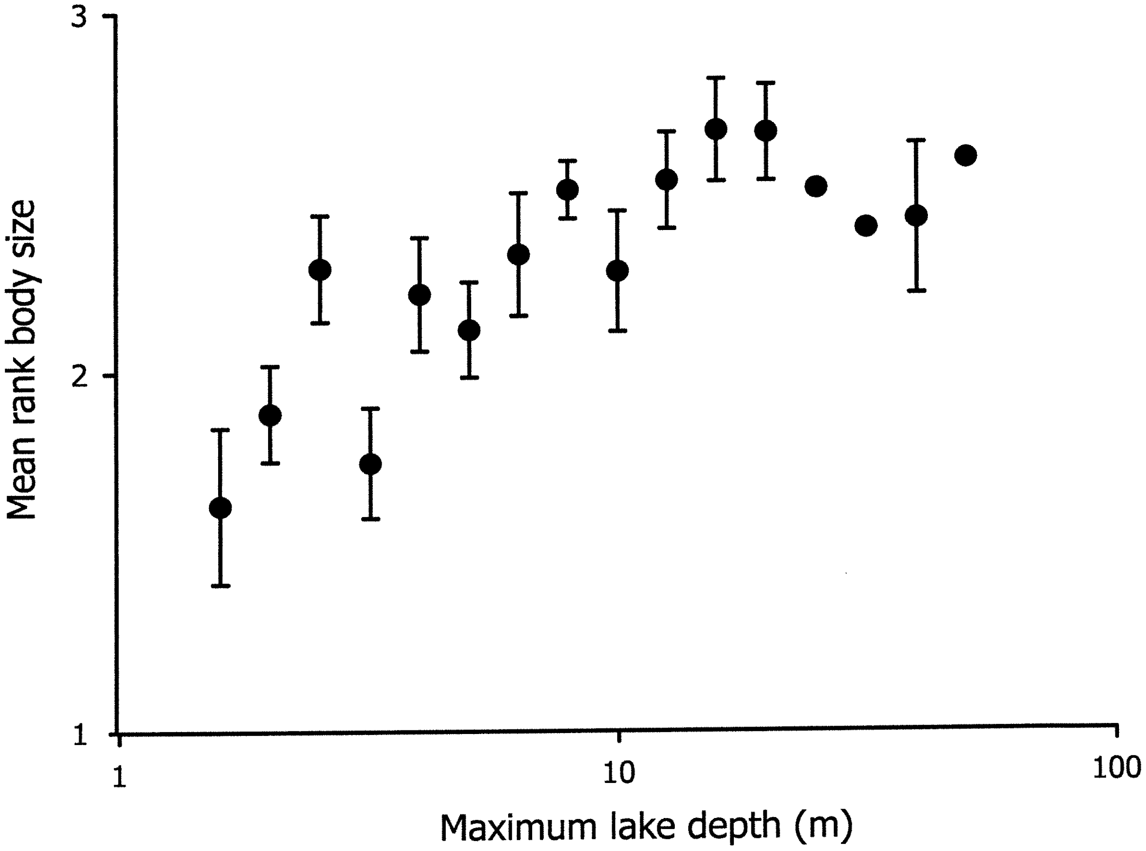

Figure 2.3. The relationship between the mean rank body size fish and lake depth. Data sources: Harvey 1978, 1981, Harvey and Coombs 1971. Fish sizes were ranked based upon the average size of adult fish found in the region (Scott and Crossman 1973). Lakes were categorised into a logarithmic sequence of increasing lake depth. Standard errors represent variations found within each size category of lake ($R^2_{\text{Pearson}} = 0.632$, n=16, p=0.0002). Modified from Choi (1994, 1998).

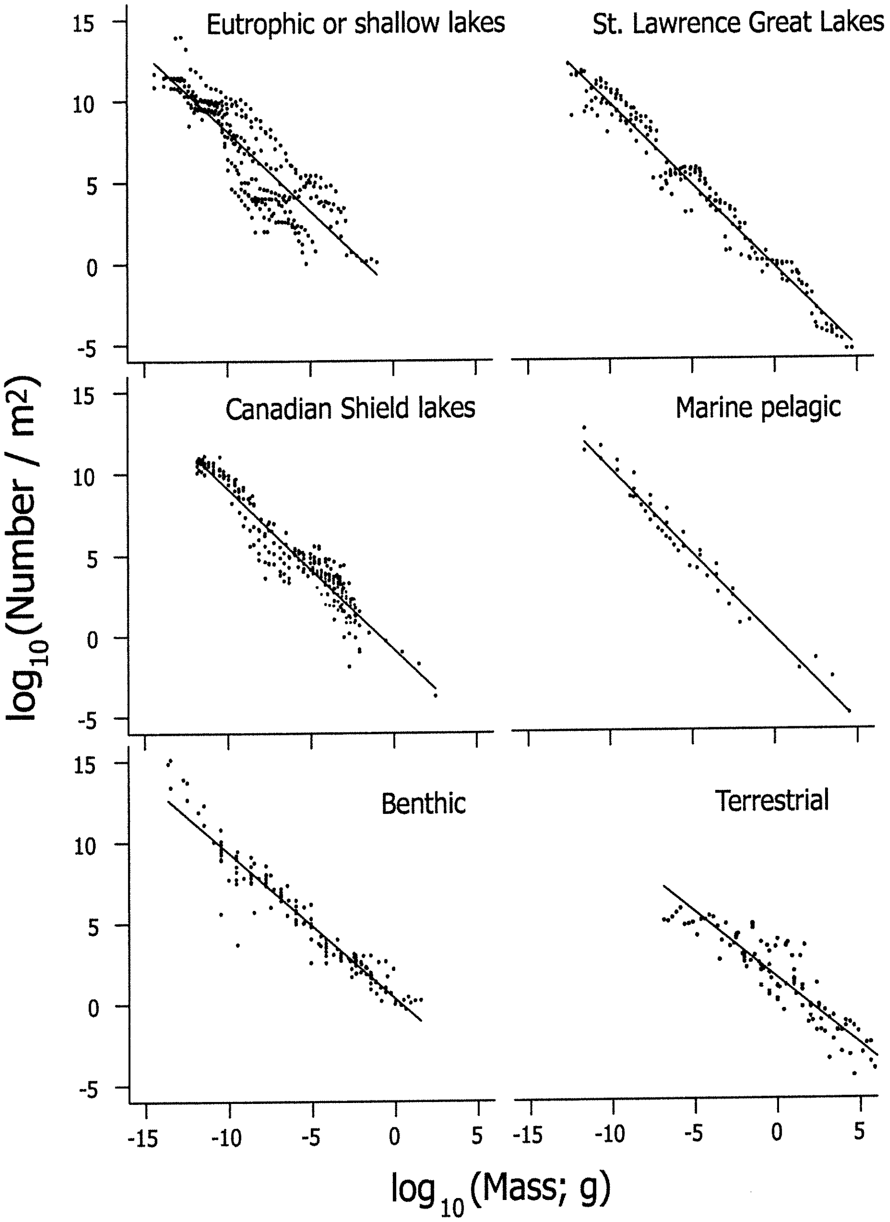

Figure 2.4. The relationship between numerical density (m^{-2}) and organism size (g), compiled from the literature. Note the greater scatter in shallow lakes and Shield lakes relative to that of the larger Great Lakes and the marine pelagic systems. Conversion factors as in Boudreau and Dickie 1992. Sources: Gaedke 1992, Garcia *et al.* 1995, Gasol *et al.* 1991, Rodríguez and Mullin 1986, Echevarría *et al.* 1990, Echevarría and Rodríguez 1994, Schwinghamer 1981, Hanson *et al.* 1989, Cattaneo 1993, Rodriguez and Magnan 1993, Sprules *et al.* 1991, Sprules and Knoechel 1983, Sprules and Stockwell 1995, Sprules and Munawar 1986, Sprules and Goyke 1994, Peters 1983.

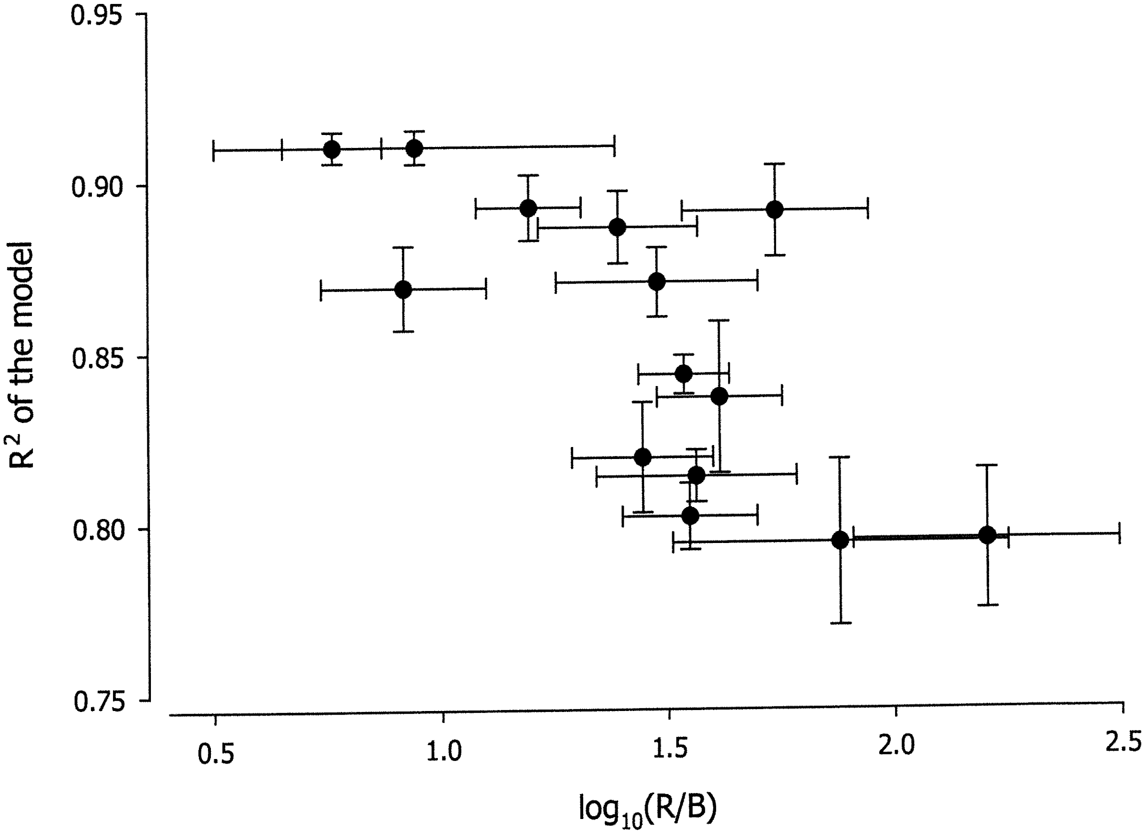

Figure 2.5. The coefficient of determination (R^2) of the size-abundance relationship as a function of the R/B ratio. The statistically significant negative correlation (R^2_{Pearson} = 0.541, n=14, p=0.002) independently confirms that the R/B ratio may be considered a measure of perturbation. The mean and standard error over the growing season is presented for each lake.

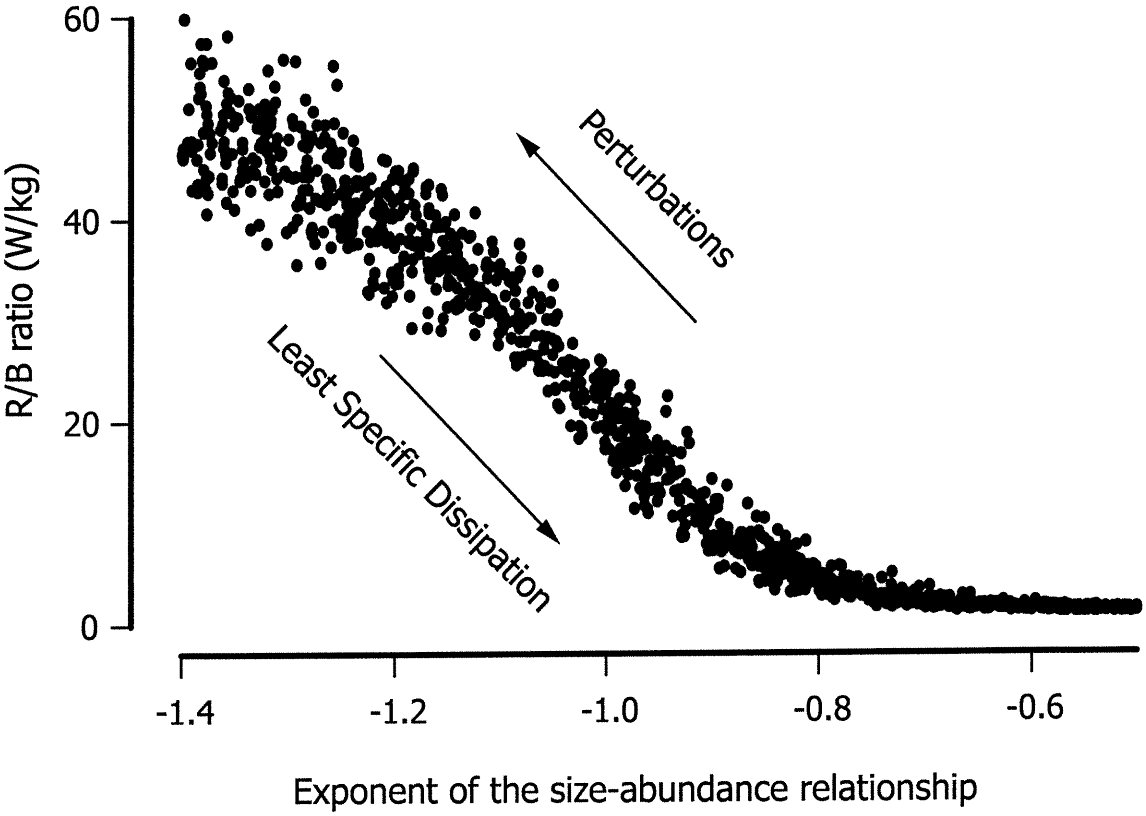

Figure 2.6. The predicted relationship between the R/B ratio and the exponent of the size-abundance relationship. Note the decrease in the R/B ratio with an increase in the exponent of the size-abundance relationship—the direction of change that is thermodynamically most probable according to the least specific dissipation principle. Perturbations are suggested to counter-act this thermodynamic principle and maintain systems in the empirically observed range of exponents. The R/B ratio is calculated from allometric relationships (Hemmingsen 1960, Peters 1983) and based upon the natural range in variation of the size-abundance relationship published in the aquatic literature.

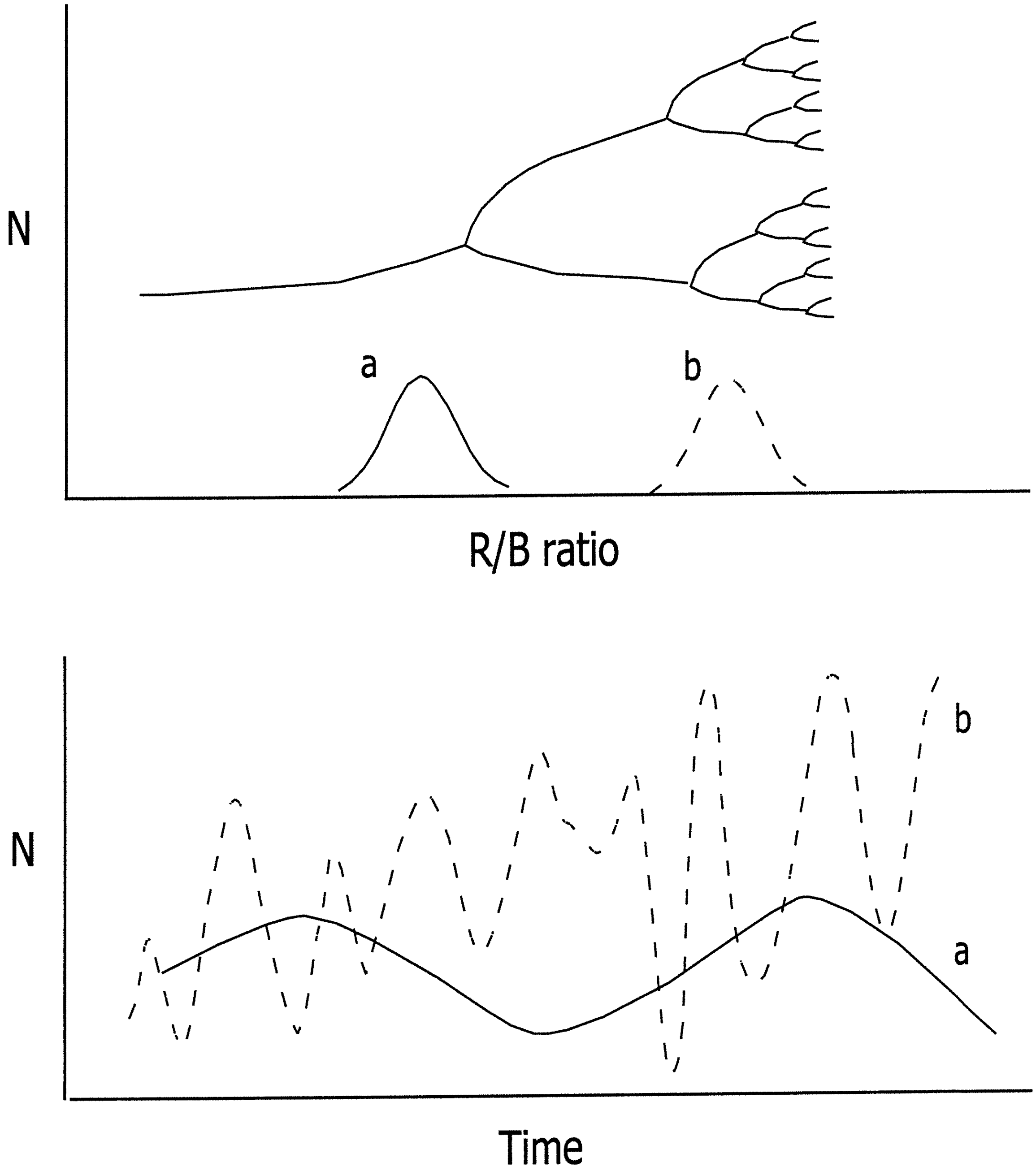

Figure 2.7. A bifurcation sequence (top) that conceptually depicts the increased dynamic complexity of population number (N) with increased nonlinear interactions (high R/B ratios). Below are depicted the idealised dynamics in the time domain. System (b) represents a more perturbed system relative to system (a).

Table 2.1. Range of variation of the exponent of the size-abundance relationship in various environments.

EXPONENT	ORGANISMS	LOCATION	SOURCES
-1.34 to -1.07	marine plankton (10 um to 8000 um)	North Pacific Central Gyre	Rodriguez and Mullin 1986
-1.24 to -0.62	freshwater phytoplankton and zooplankton	Canadian Great Lakes and some smaller inland lakes	Sprules and Munawar 1986, Sprules *et al.* 1991, Sprules and Goyke 1994
-1.01 to -0.75	bacteria to zooplankton (0.2 to 1600 um)	Canadian freshwater lakes	Ahrens 1989 Ahrens and Peters 1991a,b
-1.3 to -0.9	freshwater bacteria to fish	Lake Constance	Gaedke 1992
-0.9 to -1	cohorts of Atlantic salmon, brown trout and sea trout	Swedish rivers	Bohlin *et al.* 1994
-1.06	plankton (2 to 4000 um)	shallow saline lake	Garcia *et al.* 1995
-0.97 to -0.81	benthic organisms	Marine sediments, freshwater lakes and rivers	Schwinghamer 1981 Cattaneo 1993
-0.75	terrestrial organisms	Terrestrial systems	Damuth 1991
-0.67	plant monocultures	Terrestrial systems	Yoda *et al.* 1963

— Chapter 3 —

SUSTAINABLE DEVELOPMENT FROM A NETWORK THERMODYNAMIC PERSPECTIVE: LESSONS FROM THE PARADOX OF ENRICHMENT[8]

> *The lake is an old and relatively primitive system, isolated from its surroundings. Within it matter circulates, and controls operate to produce an equilibrium comparable with that in a similar area of land. In this microcosm nothing can be fully understood until its relationship to the whole is clearly seen.*
>
> *Forbes 1880*

ABSTRACT

With the current struggle to "sustainably" exploit our biosphere, the "paradox of enrichment" remains an issue that is just as relevant today as it was when it was first formalised by Rosenzweig in 1971. This paradox is relevant because it predicts that attempts to sustain a population by making its food supply more abundant (*e.g.*, by nutrient enrichment) may actually have the reverse (paradoxical) effect of destabilising the network. Originally, this paradox was based upon studies of "reasonable" but quite simple predator-prey models. Here, we attempt a more "realistic" revision of the paradox that explicitly accounts for the embedded nature of the human system in a complexly interwoven set of hierarchical (spatial, temporal and organisational) relations with the rest of the ecosphere—a relationship whose exploitative nature continues to

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grow in intensity and extent. This revision is attempted with the aid of a combined thermodynamic and network approach. The result is that a scale-dependent asymmetry in the action of the Second Law of Thermodynamics is shown—an asymmetry that results in the creation of two antagonistic propensities: local-order and local-disorder. The point of balance between these two propensities is empirically measurable and represents a balance between processes and constraints *internal* (growth and development) and *external* (interactive and perturbing influences) to a system—a balance that may be called the most "adaptive" state (*sensu*, Conrad 1983). The use of such an index of this balance is demonstrated and is used to clarify the relevance of the paradox to more complexly organised systems. As a consequence, we conclude that the concept of "sustainable exploitation and growth" is an oxymoron.

INTRODUCTION

Sustainable Development represents a slippery concept due to its context-specific nature. That is, the degree of success attributable to any implementation of a Sustainable Development initiative is strongly dependent upon the temporal, spatial and organisational frames of reference under which it is examined. The concept of Sustainable Development suffers from this ailment due in the main to the unforgivingly complicated and complex nature of even the simplest of natural systems.

In many ways, the current concept of Sustainable Development represents an attempt to move away from its even more reductionistically slanted precursor, the concept of

Maximum Sustainable Yield. The sole focus of Maximum Sustainable Yield was a binary, predator-prey (exploited-exploiter) system of interactions that ignored all other interactions. However, to move away from such strong reductionistic underpinnings has been an arduous task as it is not at all clear how to even begin integrating such temporally, spatially and organisationally complex and interwoven systems. When the added complexities of interactions other than such "parasitic" modes are also considered (*e.g.*, the "symbiotic" modes, *sensu* Peacock 1999), the situation becomes intractable.

One potential solution to this dilemma is to search for a scale-independent (*i.e.*, fractal-like) phenomenon that can go across scales of time, space and organisational structure, beyond the simplistic reductionistic modes of binary interactions as predation, parasitism or symbiosis. This is the solution that we entertain. We do this by appealing to new and old developments in the study of networks and thermodynamics and using by way of example the concept of the Paradox of Enrichment. We focus upon the Paradox of Enrichment because it represents an alternate and well-known formulation of Sustainable Development that is based upon the stability characteristics of interacting systems, in contrast to the emphasis upon simple yield as in Maximum Sustainable Yield.

Fertilization for the purpose of increasing the yield available for consumption represents a widespread practice amongst humans. To have a plentiful supply of food is accepted by most as being a desirable state as it is thought to alleviate political and economic instability attributable to famine, disease and military conflicts. However, such attempts to stabilise the human population by increasing the food resources available to them were argued to be potentially disastrous, in biological terms by Rosenzweig (1971) and called the "Paradox of Enrichment" (henceforth, "Paradox").

This Paradox represents the loss of local asymptotic steady states in predator-prey relationships that was caused by the switching of the relationship from a negative-feedback control to a positive-feedback explosion (*i.e.*, population explosion and then implosion). Empirical evidence exists that both support (Huffaker 1958) and refute (McAllister *et al.* 1972, McCauley and Murdoch 1990, Murdoch *et al.* 1998) the presence of such Paradox-like behaviour, indicating that in reality, the situation is (as may be expected) more complicated than may be extrapolated from such simple predator-prey models.

In essence, the Paradox asks the following question: Are modifications to the carrying capacity of a system detrimental to the stability of another system that is dependent upon it, and by extension, to the stability of the whole (combined) system as well? As such, this is an important question as it has direct implications to a subset of the current notions of sustainable development/exploitation. However, the Paradox must be extended from a simple, local two-component (binary) system to the more general case of a complex, global multi-component system, before this connection can be made more tangible. That is, the paradox must also address at the very least, the following four, related issues:

1. Bifurcation trajectories—Soon after Rosenzweig's initial paper, the paradox was shown to be due to the bifurcation of asymptotic steady states into globally stable limit cycles (*i.e.*, time-varying equilibria) via a so-called "Hopf bifurcation" (Gilpin 1972, May 1972a). The lesson learned was that loss of local (component-level) asymptotic stability does not necessarily mean that global (system-level) stability is also lost (*e.g.*, Gilpin 1972). However, it is nonetheless quite possible, as pointed out by Rosenzweig himself (1972), that the mere presence of "fluctuating" populations (implying more variable dynamics) may increase the potential for extreme population lows or highs, which in turn may increase the probability of local extinctions. The potential for asymptotic equilibria (henceforth "attractive sets" of points in state space) to follow a cascading sequence of bifurcations due to changes in some driving parameter (*e.g.*, such as nutrient loading, climatic change, carrying capacity) is today well appreciated (*e.g.*, Schaffer 1985, Scheffer 1991, Scheffer *et al.* 1993). However, how the presence of numerous interrelated and time-varying local attractive (and "repelling") sets may influence the dynamics and stability of an entire connected system is far from being understood. Variations in the local structure of attractive sets of component-level systems can make the attractive sets of the corresponding whole system, and therefore also the latter's dynamics, quite incomprehensible.

2. Transient dynamics—Making the situation even more difficult are the rich and complex sets of "transient" (*i.e.*, non-asymptotic or "non-equilibrium") dynamics. This is especially the case for "semi-stable" attractive sets (Byers and Hansell 1992, 1996), where a dynamical system may stay in a seemingly stable configuration for a long time before eventually moving off toward its "true" attractive set, without the action of any other external influences. The concepts of bifurcation and transient dynamics go hand-in-hand as changes in a component-level system's carrying capacity changes its attractive set, and so also the system's transient behaviour. This is especially the case when the driving parameters themselves (*i.e.*, carrying capacity as in the case of the Paradox) are dynamically changing, continuously or discontinuously (Patten 1983). Thus, enormously complicated situations can be anticipated if the carrying capacities of any systems are modified.

3. SPATIAL AND TEMPORAL STRUCTURE—Spatiotemporal constraints upon resource-consumer interactions are able to modify (especially diminish) paradox-like behaviour. This has been demonstrated both empirically (Huffaker 1958) and theoretically (Holt 1984, Ballyk and Wolowicz 1995, Scheffer and De Boer 1995, Abrams and Walters 1996, Jansen 1995, Deroos *et al.* 1998), and popularised as "metapopulation" processes (Levins 1969, Hanski 1982, 1989, 1991). That is, in the presence of refuge or source populations (*e.g.*, prey) protected from strong predation pressures, system-level stability is modified (enhanced; Scheffer and De Boer 1995). However, this stabilising effect of spatiotemporal (and organisational) structure and associated constraints should not be taken for granted. It is well known that such structure can also induce instability, depending upon the specifics of flow rates and gradients of the interacting systems. Such standing-wave-like instabilities are known as "Turing instabilities" (Turing 1952, Bard and Lauder 1974). With such phenomena, the situation becomes ever more complicated when we attempt to extrapolate to larger and more global spatiotemporal scales.

4. NETWORK INDIRECT EFFECTS (ORGANISATIONAL STRUCTURE)—The strongly embedded, hierarchical/holarchical, web-like nature of ecological systems adds another layer of rather unforgiving complexity to our capacity to understand the stability characteristics of real systems (*e.g.*, see schematic in Figure 3.1). This is because "indirect effects", also known as "higher order interactions", can become greatly pronounced when linkages are many (*i.e.*, the "n-body problem"; Poincaré 1892), as in high-dimensional, hierarchically-ordered systems (Higashi and Patten 1989). This results in nonlinear or nonlinear-like (*i.e.*, "pseudo-nonlinear"; *sensu* Patten 1983) dynamics being observed at the whole-system level—even if the components' interactions are completely linear. (Pseudo-nonlinearity, if not true nonlinearity itself, must therefore be the universally observed situation because for complex systems it is impossible to determine all the inputs that influence a given output. In fact, for this reason, the general assumption that most systems are nonlinear because their observed dynamics appear nonlinear may not be entirely true if complexity is involved in determining their behaviour.) In this, we have another factor that drastically increases the uncertainty of our capacity to understand the effects of modifications to the structure of a network (*e.g.*, changes in carrying capacity).

How can we integrate the natural complexity of these densely interwoven processes to arrive at some semblance of understanding of the relevance of the paradox? One possibility is to couple the concepts and perspectives that arise from linear thermodynamics and linear network formulations of systems (environ theory—Patten 1978, 1982, 1985. The latter expresses in a very general way, the flow-storage networks of systems and so provides a useful context for the expression of the former thermodynamic (evolutive) principles with its focus upon gradients and their breakdown. Both environ theory and thermodynamic theory build from the same dynamical equations that describe general systems. This point of conceptual commonality (reviewed in Appendix 2) is used in what follows to develop a fractal-like (scale-free) understanding of stability and its inverse concept of dynamical uncertainty. In no way do we suggest to develop a general theory that merges these two distinct theories. Rather, it is the juxtaposition of a subset of perspectives and concepts foundational to the two theories that is attempted in what follows.

GRADIENTS AND THEIR BREAKDOWN IN HOLARCHICAL NETWORKS

The focus of the Paradox is upon the influence of variations of carrying capacity upon a system. However, the focus of a thermodynamic analysis is slightly different: the influence of variations in gradients and flows. We will discuss this latter emphasis upon flows and gradients in this section and then return to the case of variations in carrying capacity in the next section.

The presence of energy or matter gradients represents an instability, in the most general sense. Such gradients cause[9] increased intensities of energy and matter flows (fluxes). In turn, these flows degrade the very gradients that cause their existence. "Living" systems are able to harness such gradients and flows to do work that increase their structural/functional integrity and complexity ("local-order").

As such, gradients represent increases in the capacity to do work, which in an ecological sense represents a resource of the most general kind (*e.g.*, highest biological productivities are associated with the steepest gradients: vertically (altitudinal zonation, *e.g.*, Merriam's life zones), horizontally (edges, hedgerows, corridors, ecotones, riparian and coastal zones and ergoclines) and latitudinally). The local flows of matter and energy associated/caused by these gradients represent the mechanisms by which these same gradients are eroded/destroyed. As the magnitude of the gradients is eroded with time, the magnitude of matter flows associated with the gradients also decreases with time. This tendency for the *intensity* of flows to *slow down* with time is described by the *Least specific dissipation principle* (Prigogine 1947; see Appendices 1 and 2C for more details), for energetically "open" systems (*i.e.*, where flows of energy into and out of a system exist) that are near some *local quasi-steady-state* of inputs and outputs of energy.

The general (theoretical) applicability of this principle is limited due to some simplifying assumptions in its derivation, in particular, that of a *local quasi-steady state*

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[9] *"Cause" in the thermodynamic sense (phenomenologically and probabilistically).*

(Appendix 2C). However, it is here assumed that the description of a system may be made at any arbitrary spatial-temporal-organisational scale such that this latter assumption can be appropriate. In other words, the dynamical equations of "motion" (*sensu* Denbigh 1951) of any non-linear system (including those that are "far-from-thermodynamic equilibrium") can be linearised (via the application of a Taylor Series Expansion), and while the range of validity of such linearisations may be limited, they can still represent qualitatively useful indications of the state of the system when an appropriate spatial-temporal-organisation scale is used. In empirical practice, the range of applicability is known to be large in many systems and it is widely appreciated that this range can only be determined empirically (*e.g.*, see Denbigh 1951, Spanner 1964, Katchalsky and Curran 1967, Mikulecky 1985). For the sake of simplicity, this validity for ecological systems will be assumed due to the empirical evidence provided in Choi *et al.* (1999; the reader is also directed to Appendix 2C and Fath *et al.* 2001), although what follows is not entirely dependent upon this assumption.

It must be emphasised that the creation of local-order represents a gradient that is itself also subject to degradation, which in turn creates subgradients, in a hierarchically recursive manner. That is, degradation of gradients at level $x^{(0)}$ creates local gradients (local-order) in subsystem $x^{(-1)}$, which in turn creates local gradients (local-order) in sub-subsystem $x^{(-2)}$, and so on, ..., in a cascading, fractal-like sequence, as one descends the organisational holarchy/hierarchy. Simultaneously, as one ascends the holarchy/hierarchy, the flows associated with subsystem $x^{(-1)}$ act to degrade the gradients (local-disorder) that are associated with its encompassing system level $x^{(0)}$, and so on, …, in a fractal-like manner. There is therefore, a fundamental fractal-like asymmetry in the action of the Second Law as one descends or ascends the holarchical/hierarchical scales of embedded structures (Figure 3.2). (This asymmetry was implied by Lotka 1922 and noted more explicitly by Schrödinger 1945, Prigogine 1947, Bertalanffy 1950, Odum and Pinkerton 1955, and many others. Here we have only formalised this concept in the current context to simplify the arguments that follow).

Any given system exists in a balance between these two asymmetric propensities that derive from the very same Second Law. The order-creating propensity becomes manifest as one descends organisational structure while the order-destroying propensity becomes manifest as one ascends organisational structure. The complex suite of interacting gradients and flows across numerous organisational scales that influence any given system can therefore be attributed to a quasi-local balance of local-order creating processes and local-disorder creating processes. The relative dominance of one or the other principle may be indexed by the local specific dissipation rate (*i.e.*, the ratio between boundary system free energy loss (y) and system storage (x), also known as the Respiration/Biomass ratio (or R/B) in ecological circles, dimensioned [T^{-1}]; Choi *et al.* 1999, Fath *et al.* 2001). By biomass, we refer to the mass of the living matter in question. By respiration, we refer to the biochemical oxidation (*i.e.*, "catabolism") of organic molecules in plants and animals that provides biochemically useful free energy (generally in the form of high energy phosphate groups—ATP). There are many ways of estimating respiration rates, depending upon the specifics of the biochemical pathways involved. However, all methods attempt to quantify the rates of energy transformation of useful free energy to "boundary outflows" that do not return to the originating system. As such, respiration rates represent the rate of free energy lost permanently to the originating system, and the R/B ratio represents the intensity of these losses attributable to the structure (the biomass of the originating system).

Depending upon the details of the gradients and flows and their corresponding interactions propagated through the systems, a characteristic range of the specific dissipation rate (its "realised" attractive set) can be expected which indicates the relative balance between propensities for "local-order" vs. "local-disorder" for a particular system, at a particular spatial/temporal/organisational level of resolution. For example, any changes (perturbations) to a system $x^{(0)}$ via enrichment, exploitation, genetic manipulation, climatic change, *etc.*, interact to create a local alteration of flows, gradients and interactions associated with that system. The system within which $x^{(0)}$ is nested, $x^{(1)}$, as well as the system $x^{(2)}$ encompassing this, are also potentially affected. The relative influence of such changes (perturbations) upon system $x^{(0)}$ may be indexed by monitoring their effects upon the local boundary outflow (dissipation)-to-storage ratio, y/x (or R/B ratio) of the system. When there is greater environmental uncertainty, local-disorder dominates a system and R/B ratios are reduced. This means simply that when local-disorder dominates, useful free energy is lost from the system at higher intensities.

There is a second aspect of the dissipation/storage (or R/B) ratio that must be emphasised. This magnitude of the storage specific dissipation rate provides a measure of the system's deviation from thermodynamic equilibrium. That is, y/x (or R/B) measures the “effective” gradient to which the system is exposed. When modifications increase the effective gradient, this is indicative of increased deviation from the quasi-steady-state. Conversely, modifications that decrease the ratio indicate increased proximity to the quasi-steady-state (see Appendix 2C). That is, when the magnitude of R/B (the intensity of energy dissipation) is large, the assumed linear relationship between gradients and flows becomes less tenable and intrinsic nonlinearities and pseudo-nonlinearities of intersystem dynamics may be expected to become more dominant. In terms of the attractive sets of these dynamical systems, a bifurcation sequence of the attractive states a system $x_k^{(-1)}$, becomes increasingly probable as the R/B ratio increases (*i.e.*, the nonlinear terms of the “equations of motion” become more dominant; see Appendix 2C). Figure 3.3 schematically shows how the dynamical and structural uncertainty of a system increases when local-disorder dominates over local-order.

Using R/B as a universal "measuring stick", it becomes possible to study paradox-like behaviour in network-relevant thermodynamic terms. As an example, the empirical form of the relationship between specific dissipation (R/B) and the dynamic/structural variability of limnoplankton is presented in Figure 3.4. Dynamic/structural variability is expressed, after log-log transformation, as: 1 minus the coefficient of determination of the body size-abundance relationship. This has elsewhere been shown to be a practical index of dynamical/structural variability (Choi *et al.* 1999; see also Table 3.1). As Figure 3.4 depicts, the dynamical/structural variability of limnoplankton increases as storage-specific dissipation increases.

The biological implications of this observation become clearer when it is realised that near steady states, a system's turnover rate, τ_k^{-1}, approximates its specific dissipation rate:

$$\tau_k^{-1} = y_k/x_k$$

The reciprocal of this turnover rate is turnover or residence time, τ_k, with time [T] dimensions. Thus, at or near steady state, elevated dissipation rates can be expected to correspond to faster turnover rates and, reciprocally, shorter residence times. The approximation of turnover by specific dissipation (or vice versa), though less appropriate when a system deviates from steady state, remains a useful index for empirical applications. When turnover rates are larger, the rate of return of a system to a steady state from which it has been perturbed is faster and the duration of deviation is shorter. This reflects increased "resilience", the ability to return to a steady state after deflection (Webster, et al. 1975). Such faster return rates, however, mean greater dynamic uncertainty. Within ecological circles, this is commonly referred to as an "r-adapted" system. This is because, when turnover (or specific dissipation) rates are elevated, systems are further from the quasi-steady-state which implies the existence of strong thermodynamic gradients. Matter and energy flows and gradient strength go together, the latter driving the former—the stronger the gradients the more important become the influence of true- and pseudo-nonlinearities (*e.g.*, see Figure 3.3).

With this background, the paradox of enrichment can now be interpreted in near-linear thermodynamic and environ-theoretic network terms. In particular, we can now focus upon the influence of variations in the carrying capacity of systems embedded in complex networks.

UNDERSTANDING THE PARADOX

ECOLOGICAL AND EVOLUTIONARY TIME

To see how the paradox of enrichment works in ecological networks, it is necessary to understand the manner in which specific dissipation is modified by changes in the carrying capacity of a system. As mentioned in the Introduction, a change (*e.g.*, increase) in the carrying capacity of a system represents a displacement from the attractive set prior to the change. This means that at the very least, the influence of (1) transient behaviour and (2) the form of the attractive set as a function of carrying capacity must be addressed. That is, there will exist consequences in both the short-term (*i.e.*, ecological scales) and long-term (*i.e.*, evolutionary scales).

The long-term effects are readily addressed. Let $K_k^{(-1)}$ be the carrying capacity of system $x_k^{(-1)}$ (*i.e.*, when $J_k=0$ in Appendix 2C). If the expected value of storage, $E[x_k^{(-}$

${}^{1)}$], can be taken as proportional to or an approximation of carrying capacity, $E[x_k^{(-1)}] \propto K_k^{(-1)}$, then it follows from the dimensionality of specific dissipation ($y_k^{(-1)}/x_k^{(-1)}$) and carrying capacity ($\approx E[x_k^{(-1)}]$) that these two quantities are inversely related. Any increase in carrying capacity, by enhancing storage, should reduce specific dissipation and turnover rates (Figure 3.5). This in turn would, because of the lowered intensity of activity implied by storage be associated with decreased dynamic variability (Figure 3.4). Thus, if transient effects are not important, the paradox of enrichment may actually be erroneous in that enrichment may result in a generally more stable, less variable system $x_k^{(-1)}$, over the long term (enhanced local-order). Of course, the cost of this local-order is a quadratically increasing local-disorder (Appendix 2C) to it's encompassing system $x^{(0)}$, with associated increases to the uncertainty of the system $x^{(0)}$. If the changes in $x_k^{(-1)}$ are large (dominant), the probability of such increases in environmental uncertainty percolating back to the focal system $x_k^{(-1)}$ and all other systems of the same and lower hierarchical level increases, possibly negating or even over-powering any local gains in stability and order.

The above is relevant for the ideal case where transient behaviour is unimportant. When a system is in constant interaction with other systems, subsystems and supersystems, each itself being in somewhat of a perturbed state, transient effects and semi-stability cannot be ignored. In the short term, perturbations of any kind upon a system $x_k^{(-1)}$, including nutrient enrichment, will elevate the specific dissipation rate, $y_k^{(-1)}/x_k^{(-1)}$, and therefore also the system's dynamic and structural uncertainty, as reflected in increased turnover. Such perturbations may have cascading effects upon other systems at the same hierarchical level $x_j^{(-1)}$, which in turn would be expected to increase their specific dissipation rates and dynamic variability. Some of the interior subsystems, $x_j^{(-1)}$, $j \neq k$, may also demonstrate the realisation of greater local-order (as lowered specific dissipation). In this case, this would have come about via local-disordering of a companion system, $x_k^{(-1)}$, at the same level of organization (see Appendix 2C). Regardless, if the gains in local-order for system $x_k^{(-1)}$ are large and increasingly dominate the flow network, the probability of destabilising the whole network $x_i^{(0)}$, increases quadratically (as mentioned above; see Appendix 2C).

Thus, the immediate effects of nutrient enrichment of a system $x_k^{(-1)}$ within a larger system $x_i^{(0)}$ may indeed be, in accordance with the paradox of enrichment, to destabilise the system and some or all of its interacting systems at the same level, and in so doing perturb the overall system as well. If the enrichment is sustained (and gradual such as on evolutionary time scales, to prevent the over-dominance of transient behaviour) and does not dominate the flow network, the long-term effects may be for the subsystems and supersystem both to return to more thermodynamically quasi-steady-states, marked by lower dynamical and structural uncertainty.

To summarise, there is indeed a paradox of enrichment that can be restated from network and thermodynamic perspectives: In the short term (ecological time scales), a sustained increase in carrying capacity at some level of organization will tend initially to increase the dynamic uncertainty of all systems, at all levels, that interact with the subject system. In the long run (evolutionary time scales), however, after an indeterminate period of uncertainty, the perturbed system and all its interrelated systems may settle back into attractive sets of greater dynamic certainty, so long as the local-ordering does not dominate the flows of the whole network.

THE PARADOX OF HUMAN SYSTEMS: THE PARADOX OF SUSTAINABLE DEVELOPMENT

The human system, x_h, more effectively than most, it seems, manipulates its environment to increase its local-order (manifested as reduced local fluctuations and uncertainty, and increased carrying capacity, $E[x_h]$). Interventions initially increase the local-disorder of other systems, x_k, $k \neq h$, sometimes driving them to avalanche-like behaviour, via cross-scale cascading effects of perturbations percolating through the complex interactive network and so also the human agent (at the $^{(+1)}$ environmental level) originally responsible for the enrichment (Bak *et al.* 1989; Choi *et al.* 1999). For example, the planetary supersystem is also currently affected, as seen in the potential global bifurcation of stable states in ambient temperatures and climate due to the influence of rapid global climate change and other large-scale perturbational phenomena.

What is somewhat unique in the human case is their attempts at an extremely active maintenance of local-order in a small subset, x_r, of companion systems which serve as “resources”. These include agriculture, silviculture, fisheries management, *etc.*, managed and manipulated by practices that include ecological engineering, biological control, nutrient enrichment, ecosystem management, ecological economics and sustainable development/exploitation. The invariably unintegrated, piecemeal, punctual and increasingly dominating nature of human interventions creates spiralling increases in local-disordering of other systems and the supersystem which are eventually received as disordering repercussions that propagates to our cultural sphere, taking various forms as human instability and strife. This is the Paradox manifested as a paradox in the most general sense: a Paradox of manipulation.

Natural selection and ecological succession have it that if one species is unable to sustain its current practices, the changes it induces will lead to its eventual replacement by other, better-adapted species. Such change takes place on evolutionary time scales, and in the interim, the maladaptive practices can cause destabilisation and uncertainty in the whole system. The only certainty is that each system will "adaptively" tend towards a state of greatest local-order (least possible specific dissipation). If, however, mechanisms that maintain perturbational dynamics are suddenly relaxed, altered, or stopped, the change of direction necessitated by this can itself appear as a secondary perturbation. Problem-solution sequences, the essence of adaptation, can therefore in themselves cause escalating chain reactions of increasing uncertainty, marked by elevated specific dissipation and turnover rates. These kinds of adaptation-related perturbations are especially likely to be expressed when human value systems (economic, social, political, religious, ethical, aesthetic) interact in their own complex ways. This is the great danger, for when uncertainty becomes elevated, fear and irrationality take over and death, disaster and extinction become all the more probable.

This is not to say that humanity should abandon its attempts to modify or enrich its resource base and through this, itself. To do this would also be a dangerous alteration of the current network of balances. But such use should be carried out with the acute awareness that any kind of intervention to alter an established state, including attempts at sustainable development, is fraught with uncertainty. This is especially true when many interventions are attempted independently at large scales. The whole network of interacting systems must be given time to adapt. Slow, carefully monitored, graduated change can be recommended as the best policy for long-term resource management. Deforestation, overfishing and population growth at current rates represent dangerously rapid alterations to the relative balance of local and global order that can only have deleterious outcomes.

Another solution element suggested by network-thermodynamic considerations is to decrease system leakiness. When a system gets closer to a local steady state, internal cycling of energy and matter becomes an increasingly important property. Cycling increases the efficiency of energetic transactions (as specific dissipation decreases) and also the contribution of indirect flows to throughflows and storages (*i.e.*, to organization). Cycling itself is organization. Closing cycles means containing the substance and energy of a system within the system, not letting it escape to the outside (that is, dissipate). While the order represented by cycling is not completely free, increased transfer efficiencies can go a long way toward abating environmental uncertainty and achieving greatest local-order, convergent with Peacock's (1999) symbiotic mode.

Recent attempts to put economic values upon ecological structures and functions have been made in the hope that such mappings would facilitate a better accounting and management of natural resources. While laudable in focusing the attention of policy and decision-makers on their lack of consideration of ecological structures and functions, and on the notion of a sustainably integrated human society, such attempts represent quite a dangerous form of hubris when used as a mechanism for ecological management. This is because the "logic" of neoclassical economics, oriented to profit- and growth-maximising systems, does not match the "logic" of natural systems, which are oriented to adaptability-maximising systems in the face of an always-uncertain future (Conrad 1983). Such "logical" inconsistencies would introduce too many non-linearities into the management process, and so potentially greatly amplify the effects of any errors to an already uncertain science.

To summarise, human interventions of any kind may also be considered uncertainty-elevating factors, such interventions include the implementation of Sustainable Development practices. That is, Sustainable Development is an oxymoron in the deepest sense as ultimately, it is impossible to sustain that which is being altered. Peacock (1999), following upon the earlier writings of Lotka (1922) and Odum and Pinkerton (1955), has suggested that such sustainable practices may be possible if more coherent mutualistic or synergistic modes are encouraged, rather than the exploitative, "parasitic" mode that is currently dominant. This may indeed be a useful solution to a more Sustainable Development. However, what the above analysis indicates is something quite simple and perhaps obvious in retrospect: Interventions of any kind, including parasitic or coherent synergistic modes (*sensu* Peacock 1999) are dangerous because they modify the previously negotiated balances (quasi-local steady states) of a complex network. If interventions are made, be they for reasons of management or development, they must be done so carefully and gradually to allow adaptation of the whole network and prevent the over-dominance of uncertainty enhancing transient effects. The key idea is that the rate of change of these balances caused by interventions must not exceed the adaptive capabilities of the network.

UNCERTAINTY AND ECOLOGICAL HEALTH

In the above, a scale-free, fractal-like approach to the quantification/qualification of the dynamical uncertainty of realistically complex systems was developed and used to study the concept of sustainability, using the Paradox of enrichment as a pedagogical tool. We now turn to the question of Ecosystem Health (*e.g.*, Rapport *et al.* 1999), to which we extend this perspective. For this purpose, we focus upon the intimately related concept of the adaptive capacity of complex holarchically organised systems because this latter concept is directly related to the above notion of dynamical uncertainty. It is assumed for the sake of argument, that adaptive capacity is an important indicator of Ecosystem Health.

In the face of a constantly shifting and varying network of interactions, "one must keep running to stay still" (in the game of life). Such was the wisdom of the Red Queen in the Adventures of Alice in Wonderland—the necessity of continuously adapting in the face of an ever-changing context (The Red Queen's Hypothesis of Van Valen 1976; see also Holling 1973). There exist two main strategies in the face of such contextual heterogeneity (*e.g.*, Rosen 1967:166-169; Holling 1973). One is to respond rapidly to the various manifestations of uncertainty. The other is to resist the various manifestations of uncertainty. In the evolutionary biology literature, these are known respectively as, the "Scramble" strategy—to take advantage of available resources as much as possible because you will never see them again (*e.g.*, the dominant human mode), and the "Hedge-betting" strategy—to tide over or adsorb environmental fluctuations, waiting for a better day (*e.g.*, turtles). (Parenthetically, in the ecological literature, the former strategy has dominated over the latter as to a mechanism for the reduction of uncertainty and has even become almost synonymous with the concept of stability; DeAngelis 1980, 1992).

The first strategy ("scramble") is embodied in the concept of "resilience", the rate of return to some local quasi-steady state. In the previous section, we suggested that resilience may be simply and usefully measured by the R/B ratio. This was because high R/B ratios are indicative of high intensities of biological activity and faster turnover times. That is, systems of diminished local-order (*i.e.*, greater dynamical uncertainty) represent more "resilient" systems. In ecological circles, this is commonly referred to as "r-adapted" systems.

The second strategy ("hedge-betting") is embodied in the capacity of a system to "resist" or "absorb" perturbations to state variables and driving variables and so persist in space-time-organisation (*i.e.*, an inertial characteristic) has unfortunately also been called "resilience" by some authors (*e.g.*, Holling 1973). To avoid confusion, we will refer to this concept as "resistance". This biological inertia of a system may be quantified as the amount of biomass simply because larger systems have a greater capacity to buffer the effects of short-term perturbations/fluctuations in energy deficits or surpluses (*e.g.*, see Choi *et al.* 1999). That is, systems of enhanced local-order represent more "resistant" systems. In ecological circles, this is commonly referred to as "K-adapted" systems.

What is immediately striking is that dimensionally, resilience and resistance are inversely related quantities/qualities (Figures 3.6a and 3.6b; similar relationships are well known at the organism level and known as allometric relationships; reviewed by Peters 1983). That is, when resilience is high, resistance is low, and vice-versa. In the face of environmental ($x^{(0)}$) uncertainty, extreme resilience is just as detrimental as extreme resistance: When resilience is too great, a system is more prone to rapid environmental fluctuations (*i.e.*, there is not enough "resistance" to environmental fluctuations), resulting in dynamical uncertainty of such systems (*e.g.*, leading to elevated rates of local extinctions and invasions). When resistance is too great, the capacity to track/follow environmental fluctuations is decreased (*i.e.*, not enough "resilience" to respond to environmental fluctuations), resulting in inadequate responsiveness to perturbations to maintain the system's integrity (too slow, too rigid).

The above dimensional relationship leads directly to the following observation: only at some intermediate level of resilience and resistance can a system be said to be optimally adapted to the predominant environmental fluctuations to which it is subject. There is no way to determine, *apriori*, the exact nature of this optimally adapted state—it can only be known empirically. The significance of this optimally adapted (or "adjusted") state cannot be emphasised enough as its relationship to the current concepts of ecological integrity and health are striking. What is extremely clear is that the dynamical uncertainty (the balance between local-order and local-disorder) at the environmental ($x^{(0)}$) level has a direct effect upon the dynamical uncertainty of the focal system $x_k^{(-1)}$. Any activities of $x_k^{(-1)}$ that alters the local-balance of the containing system $x^{(0)}$ has a direct influence upon the short- and long-term adaptive capacity (and ecological health) of the focal system $x_k^{(-1)}$. In other words, human interventions of any kind are uncertainty elevating factors that not only modify the short- and long-term sustainability of a system but also the short- and long-term health or adaptability of the system.

A probability level may be assigned to a specific location in the attractive region as a function of the distance from the expected state of system (Figure 3.6a). Those systems that exist in an increasingly more improbable state relative to such a system-specific attractive regions may thus be expected to be more prone to strong/rapid ecological change (*e.g.*, invasions, cataclysmic extinctions, variable population dynamics, strong/rapid evolutionary change—*i.e.*, an "unstable" system; Figure 3.6a: systems 2a and 2b).

Attempts to maintain a system in a precarious, unadapted (unadjusted) situation (*e.g.*, the practice of monocultures) would require enormous expenditures of energy. Such a situation may appropriately be labelled an "unsustainable" system or a system that has lost its global “integrity” or “health”. For example, the current human system modifies enormously its environment to increase material and energy flows available for its use via fertilisation, genetic modification, monocultures, pesticides, and other forms of environmental and biological manipulations. As the yield of plants and animals matter is being aggressively increased, the total metabolic flows (*i.e.*, respiration rates) are also being elevated while the total system storage (standing biomass) of all organisms is being depleted. The creation of such a persistently diminished local-order system (high R/B system), will lead to less resistant, more resilient ecosystems.

There exists one final layer of complexity in these matters that must be here addressed: the interaction between local and global stability (Figure 3.6a). Influences that are locally stabilising can be globally destabilising. This is because the unique historical and compositional nature of an isolated system may exist in a locally stable or semi-stable state (*sensu* Byers and Hansell 1992) but simultaneously in a globally unstable state. There is a decoupling between how variations in the state variables influence the global and local stability of systems. The potential for locally stabilising influences to be antagonistic to global stability (*e.g.*, consider the attempt to maintain boreal forests even though climate changes to another climatic regime) and vice versa (*e.g.*, see Figures 3.6a, 3.6b) represents a particularly important issue in the management context and as such great care must be taken in any attempts at remediation.

The determination of these relationships and breakpoints at both local (ecological) and global (evolutionary) scales would be the critical task that needs to be addressed. Any attempts to ameliorate the sustainability or integrity of systems must make explicit reference to the locally and globally "expected" state of such systems. We must therefore focus our efforts at delineating acceptable distances from, or ranges in the locally and globally expected states, such that the adaptive capacity of the system is compatible with our own tolerances for environmental uncertainty. We must be critically aware of the biota and environment that can catalytically modulate these state variables (*i.e.*, "keystone" species) and appreciate the delicate nature of any tenuous balance within which we exist, as we continue to grapple with the health of our environment and our selves.

ACKNOWLEDGEMENTS

The many insightful thoughts of Nathalie Saint-Jacques Roger I.C. Hansell, Henry Regier, James J. Kay, Pierre Legendre, L. Van Valen, Brian Fath and an anonymous reviewer were sincerely appreciated. This work is dedicated to three special children whose lives were lost all too early, but whose loving memory will continue to inspire.

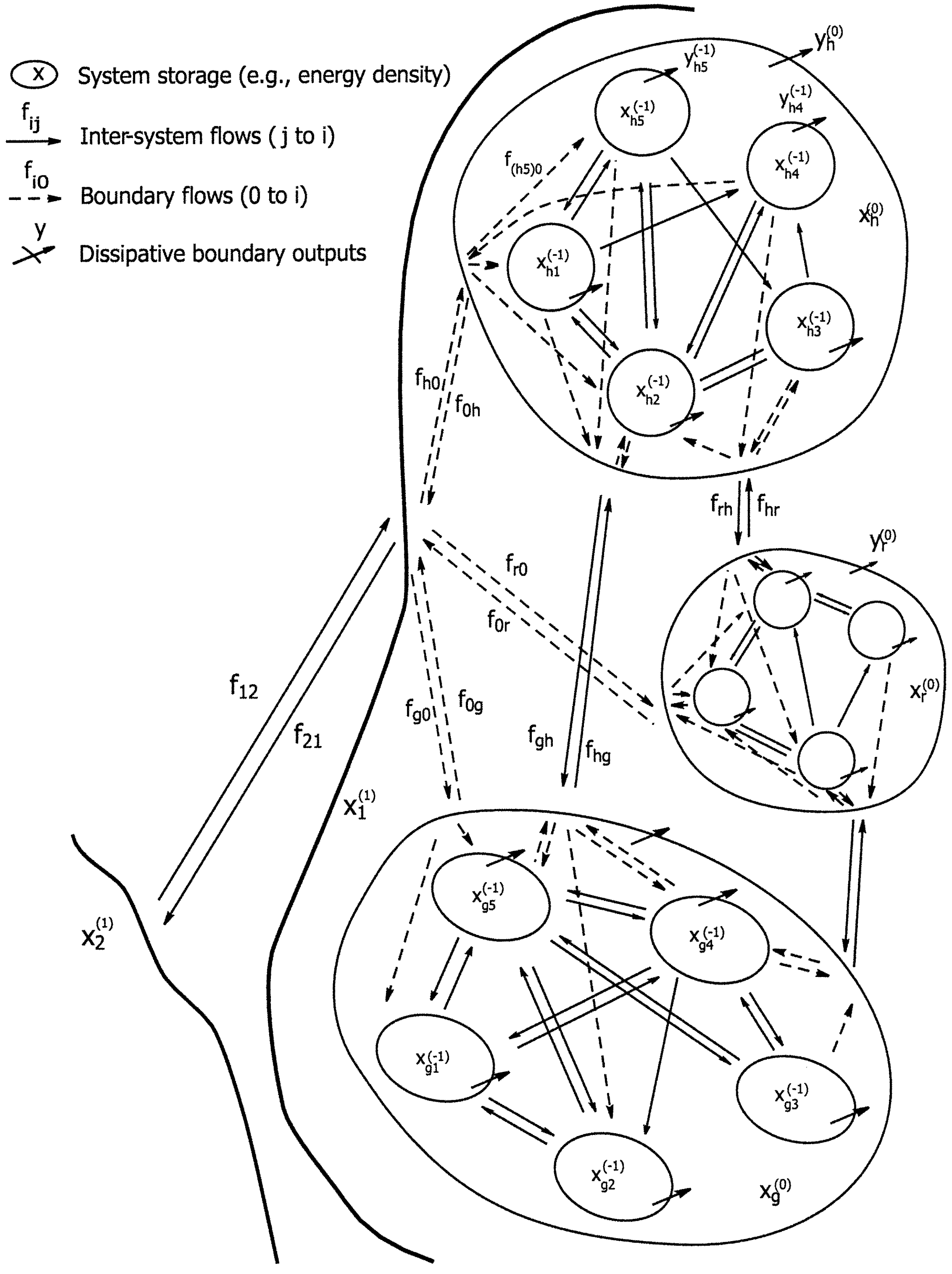

Figure 3.1. Conceptual schematic depicting the storage and flows between systems of various hierarchical levels. Subscripts identify systems and superscripts identify hierarchical level. Boundary outputs are represented by, y; system storage by, x.

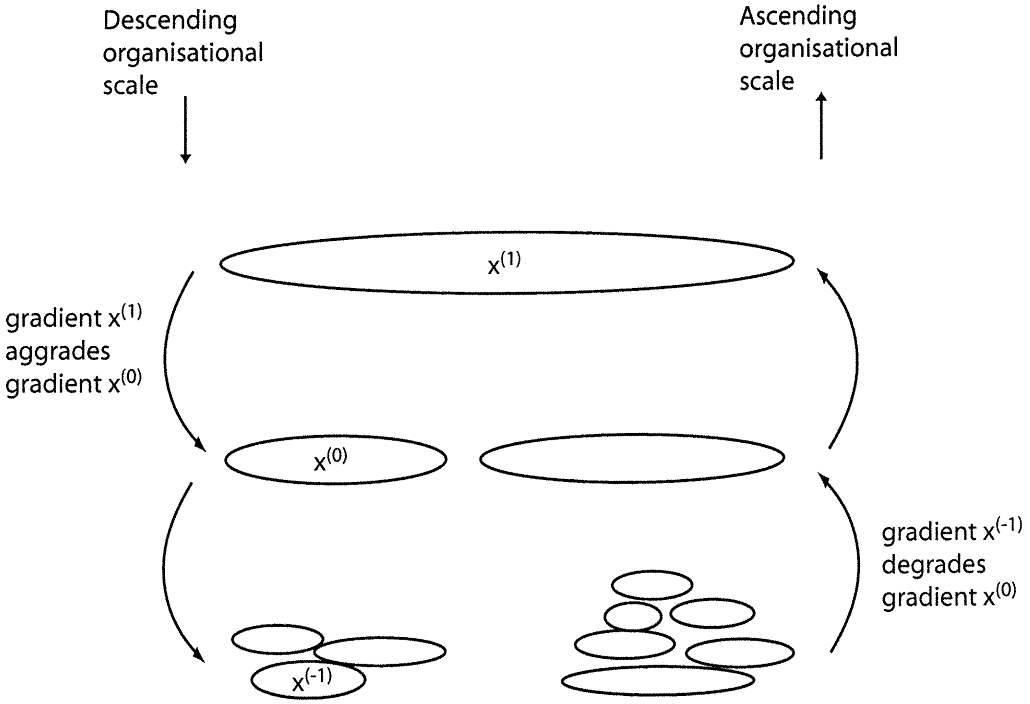

Figure 3.2. A schematic showing the fractal-like, asymmetrical influence of the Second Law of Thermodynamics as one ascends or descends spatial-temporal-organisational scales. The existence of a gradient at the super-system level $x^{(1)}$ creates and aggrades the gradients of system $x^{(0)}$ which in turn creates and aggrades gradients of its sub-system $x^{(-1)}$. This cascading sequence as one descends the holarchical/hierarchical scale may be termed the propensity for "local-order"—that gradients from the nesting system $x^{(1)}$ help to increase the structure (storage) and function (flows) of the focal system $x^{(0)}$. As one ascends spatial-temporal-organisational scales, the gradients and associated flows of sub-system $x^{(-1)}$ act to degrade the gradients $x^{(0)}$ that cause them which in turn act to degrade the gradient $x^{(1)}$. This process of gradient degradation may be termed the propensity for "local-disorder". Any system $x^{(0)}$ exists in a dynamic interplay between local-ordering and local-disordering processes. This characteristic balance is quantifiable and related to other structural and dynamical properties of the system. See text for more details. Lateral and cross-holarchical interactions are ignored for simplicity but similarly influence the balance between local-order and local-disorder.

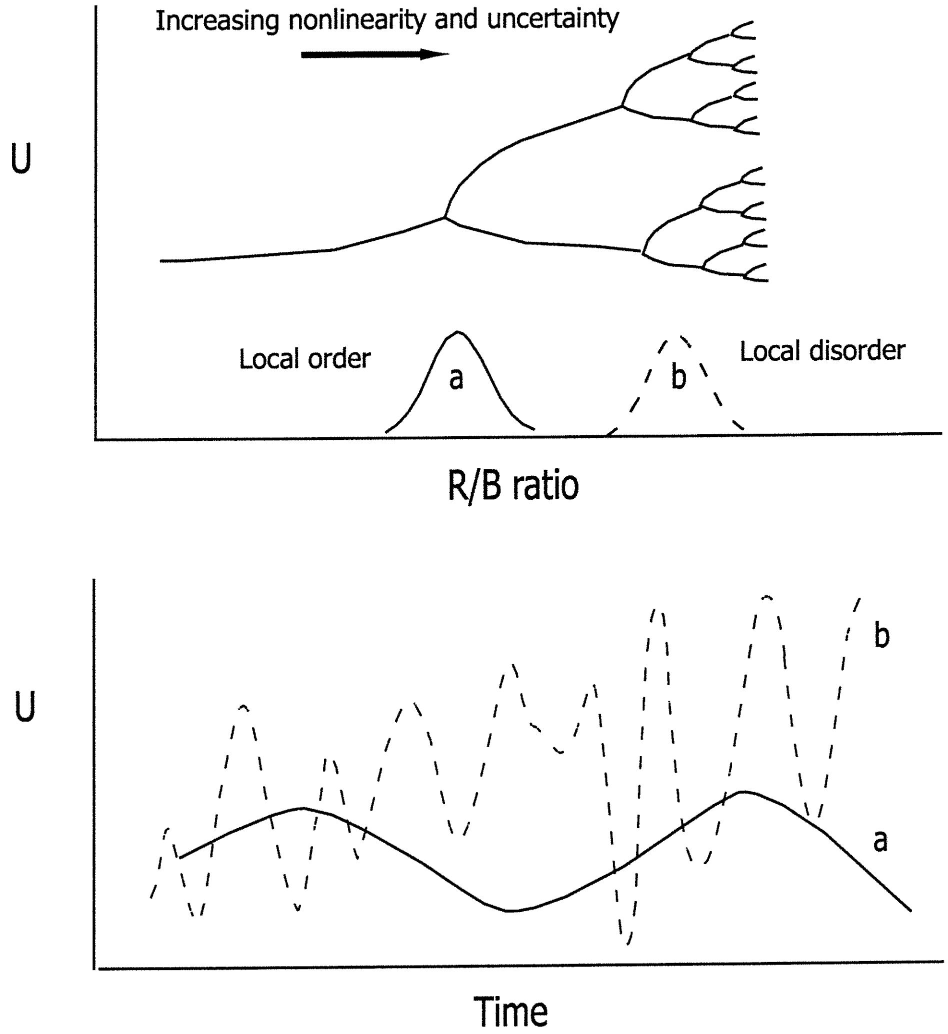

Figure 3.3. A bifurcation sequence is shown in the top panel. The state variable "U" (*e.g.*, biomass or storage, respiration rate, numerical abundance) of a given system as a function of the R/B ratio. As the magnitude of the intensity of energy dissipation (R/B) increases, the linear approximation of the gradients and flows breaks down and nonlinear dynamics become important. Increasing complexity of the attractive region is heuristically represented as this classical bifurcation sequence. Increased R/B ratios (*e.g.*, system b, reflecting increased local-disorder due to perturbing interactions with other systems of all hierarchical levels) increases system uncertainty (the attractive set is more complex—the Boltzmann entropy increases). Such a sequence is diagrammed in the time domain in the bottom panel. Modified from Choi *et al.* (1999).

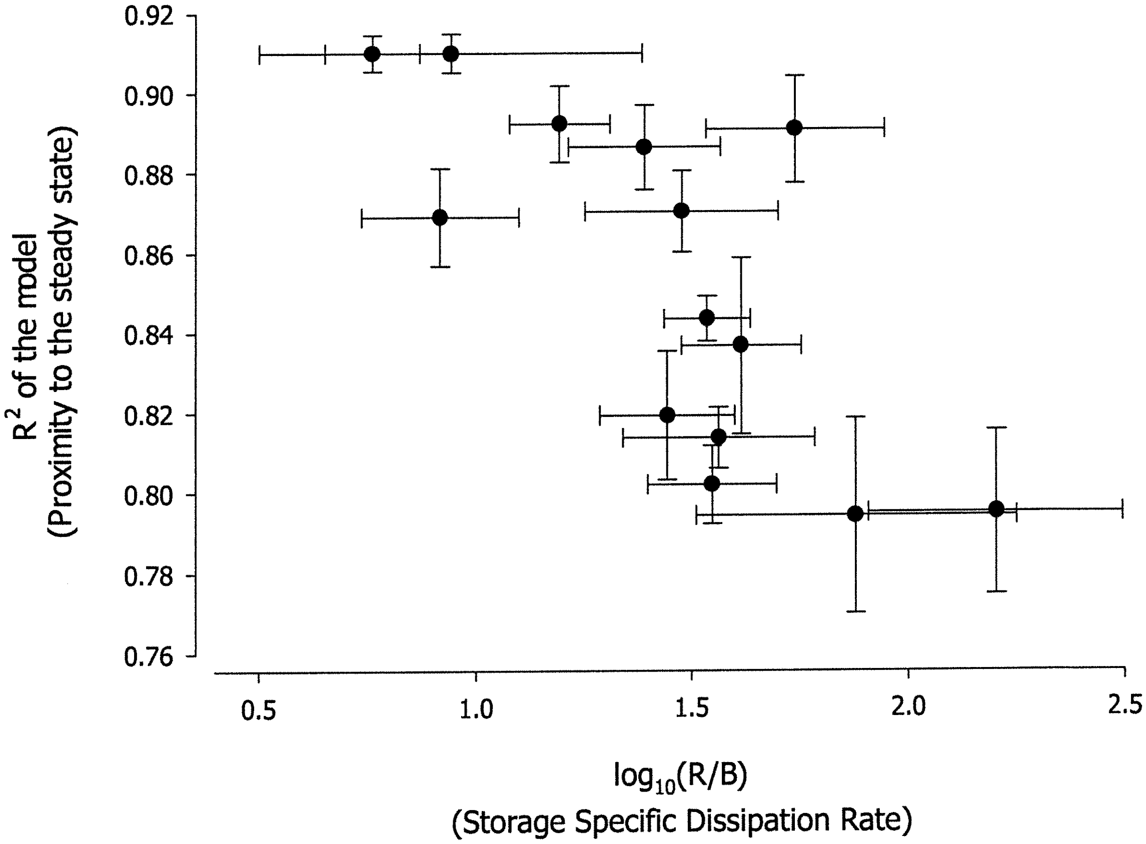

Figure 3.4. Dynamical/structural determination of a system (the R^2 of the size-abundance relationship, after log-log transformation) as a function of the specific dissipation rate of limnoplankton (units of yr^{-1}). $(1-R^2)$ thus represents the degree of non-determination (variability), or more simply the degree of perturbation of the size-abundance relationship. Note the statistically significant negative correlation ($R^2_{Pearson} = 0.541$, n=14, p=0.002). Modified from Choi *et al.* (1999).

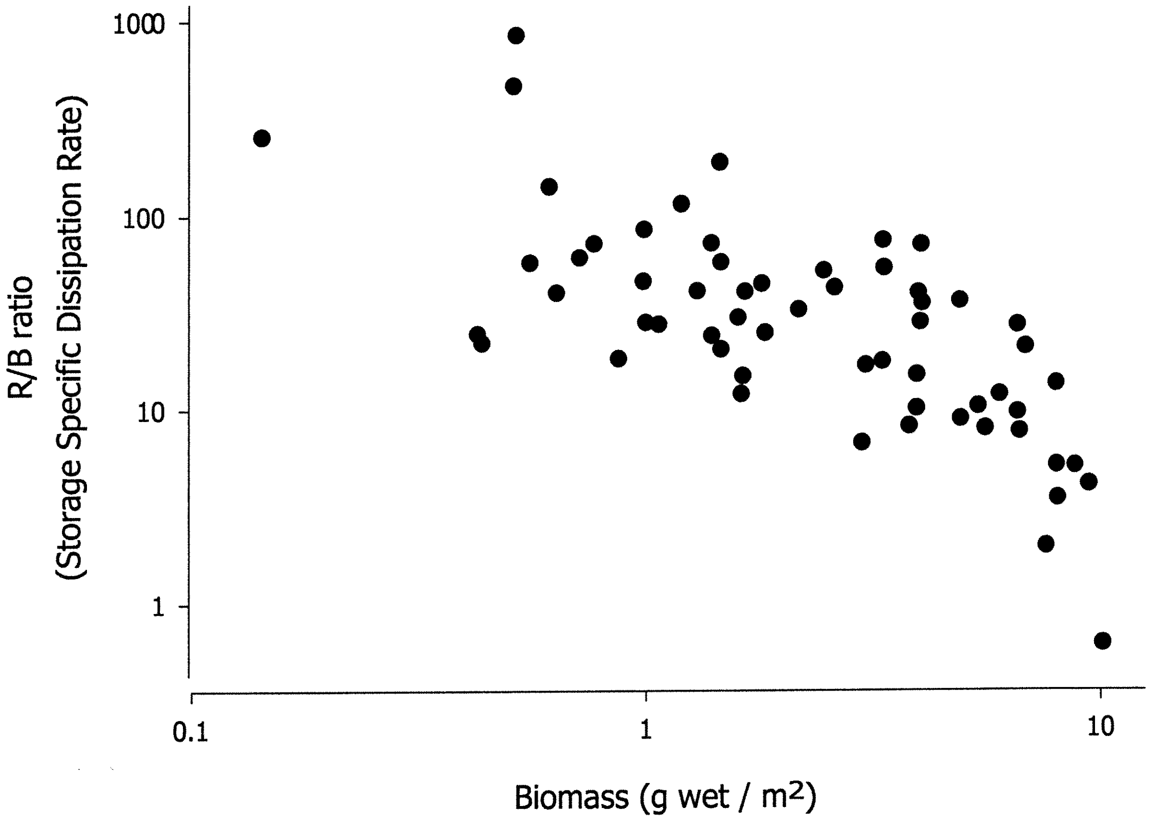

Figure 3.5. Respiration to biomass ratio (R/B; units of yr^{-1}) as a function of the standing biomass (~ carrying capacity) of limnoplankton. Increases in the carrying capacity should dimensionally reduce the storage-specific dissipation, which in turn indicates a decrease in long-term dynamical variability of the system. Data from a subset of Canadian Shield lakes, modified from Choi *et al.* (1999).

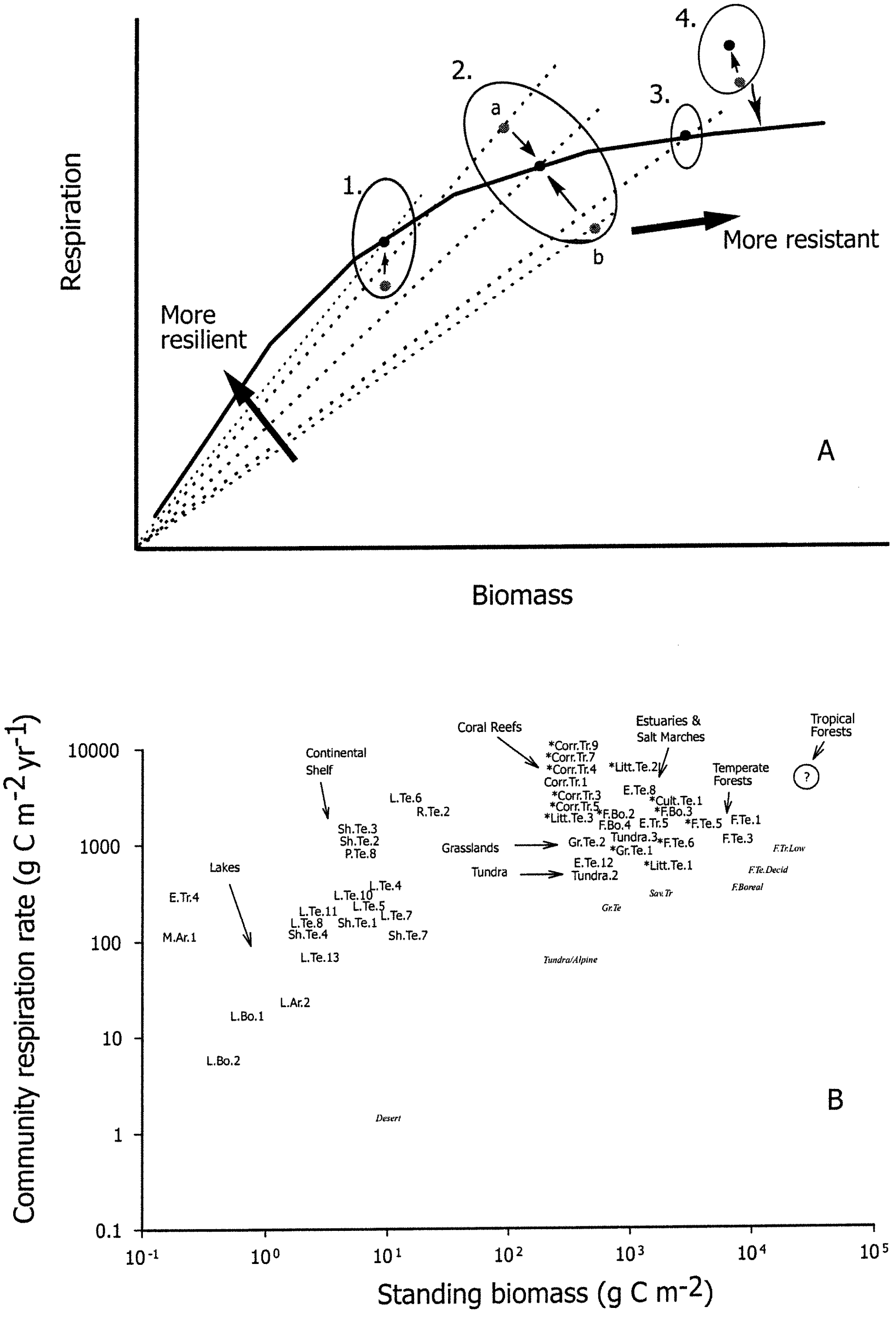

Figure 3.6. … caption on following page

Figure 3.6. The relationship between Respiration rate (R) and biomass (B) in theory (A—Top panel) and in practice (B—Bottom panel; data obtained from the literature; see Choi 2002 for details). The form of this relationship is constrained by allometric relationships between size and metabolic rates (Peters 1983). Due to this constraint, high resilience systems (*e.g.*, system 1—with a high R/B ratio) are also low resistance systems (low biomass); and low resilience systems (*e.g.*, system 3—with a low R/B ratio) are also more resistant systems (high biomass). Any local deviations from this pattern (*e.g.*, system 4) represents a globally unstable situation and a return towards the global pattern becomes more probable. Within each system, local deviations from the system-specific expected behaviour represents a more ecologically unstable situation. As can be seen, ecologically (local) and evolutionarily (global) favoured directions for change can be antagonistic or mutualistic, depending upon the specific configuration of the system concerned. In the Bottom panel, systems marked with an asterisk (*) represent order of magnitude estimates; italicised systems indicate the relative magnitude of the net primary production (NPP) of representative systems and so serves to approximately delineate the lower bound of community respiration rates for each representative system. The codes are structured as follows: [ecological type].[climatic region].[ID number]. Climatic regions: Te=temperate; Tr=tropical; Ar=arctic; Bo=boreal. Ecological types: E=estuary/brackish water; L=whole lake; P=freshwater pelagic; Lit=littoral; M=marine pelagic; Sh=continental shelf; CR=coral reef; R=river; Tu=tundra; Gr=grassland; Cul=culture; and F=forest.

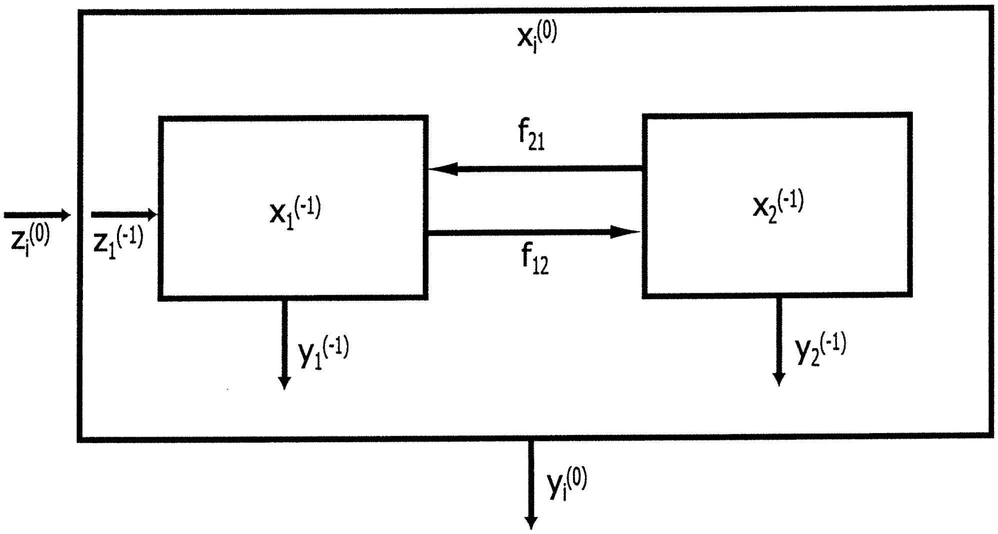

Figure 3.7. A simple system with two subsystems. See Appendix 2 for discussion.

Table 3.1. Linear regression parameters of the relationship between $\log_{10}$(numerical abundance) vs. $\log_{10}$(organism size). Data were obtained from the literature (details in Choi *et al.* 1999), and ranked in order of R^2, the coefficient of determination of the relationship. Deviations from the log-linear state have been shown to be representative of systems that are perturbed (Choi *et al.* 1999). When the deviations are large, this is generally due to large fluctuations in the abundance of organisms, which indicates a system that is dynamically and structurally more variable. Thus, the relative placement of each ecosystem type along the sequence is an index of the relative degree of perturbation of that system. All relationships are statistically significant ($p << 0.0001$).

	INTERCEPT	SLOPE	R^2	N
MARINE PELAGIC	–0.278	–1.053	0.971	44
GREAT LAKES	–0.289	–1.006	0.965	182
BENTHIC SYSTEMS	0.339	–0.899	0.930	159
CANADIAN SHIELD LAKES	–0.832	–0.991	0.898	288
EUTROPHIC/SHALLOW LAKES	–1.621	–0.975	0.755	308
INTERTIDAL	1.831	–0.782	0.520	50

— *Chapter 4* —

THE DIVERSITY-STABILITY DEBATE: WHAT IS THE QUESTION?[10]

> *In order to survive and reproduce biological systems must be adapted to the specific features of their environment. They must also be adaptable, or capable of functioning in an uncertain environment. The adaptability of biological matter is one of its most striking properties.*
>
> *Conrad 1983*

ABSTRACT

Does an alteration of biological diversity (*i.e.*, species richness) modify the stability of an ecological system? An enormous number of studies have addressed this seemingly simple question with only a great deal of disagreement and misunderstanding to show for all the effort—so much so that today, the question is almost completely ignored, and relegated as an embarrassing fad. This ambiguous state cannot be allowed to continue. The accelerating rates of environmental degradation and species extinction demand a concerted human response. In the following, we attempt a resolution of the stability-diversity debate to aid in this endeavour. This is done by providing a coherent context from which to examine this debate and bringing to light a critical flaw that has been propagated in the diversity-stability debate: a disregard of those factors that can influence the *expected* species richness of a system. We argue that ignoring this rather

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[10] *Co-written with Roger I. C. Hansell (Department of Zoology, University of Toronto, Toronto, Ontario, Canada, M5S 1A1) and Pierre Legendre (Département de sciences biologiques, Université de Montréal, Montréal, Québec, Canada, H3C 3J7). Work in progress.*

basic consideration has generated a great deal of needless controversy. We remedy this omission by developing this new context and suggesting a more useful and answerable question: Under what conditions do changes in diversity modify the stability of an ecological system?

INTRODUCTION

The traditionally accepted wisdom is that simpler biological communities are more unstable. (For the sake of simplicity, we will refer to this as the "holist's" position). The primary rationale behind this truism was that food webs that are more diverse provide a greater number of alternative feeding paths for a given organism (*e.g.*, MacArthur 1955, Elton 1958, Pimentel 1961, Leigh 1965). Having access to alternate resources was assumed to decrease the probability of extirpation/extinction of species and consequently increase the stability of the food web as a whole (*i.e.*, a "global" capacity to *persist* in the face of perturbations). Implicit in the argument was that access to a greater variety of resources *buffers* disruptive abiotic and biotic influences. At the opposite extreme, less complex food webs (*e.g.*, those found on islands) were commonly thought to be more susceptible to invasion/immigration (and extinction/extirpation) relative to more complex food webs (*e.g.*, mainland) and as a consequence, less "stable" as a whole (*e.g.*, Hutchinson 1959, Pimentel 1961, Tilman 1997).

In contrast, the currently more dominant perspective adopts a more "reductionist" stance which finds the above arguments to be too naïve (*e.g.*, Holdgate 1996, May 1972a, Nee 1990, Pimm 1984, Seitz 1994). The most influential of such works may be attributed to May (1972a,b), which set off a frenzy of activity studying the properties of model food webs. May elaborated upon the more general work of Gardner and Ashby (1970) that examined how the connectivity of systems influenced the local stability of generalised systems. His finding was that increasing the strength of interactions and the number of connections in a food web can in fact locally "destabilise" the system. This rather strong and *seemingly* contradictory conclusion stemmed from analytical and simulation studies using community matrix models (*e.g.*, of the Lotka-Volterra type) and the local stability formalism of *Liapunov* (*i.e.*, Will a system return to its initial local equilibrium after a small perturbation from it, as time approaches infinity.)

The results of empirical studies are ambiguous, with some supporting the former position (Naeem *et al.* 1995, O'Neill 1976, Tilman and Downing 1994, Vitousek 1982) and others the latter position (Miller 1989, Walker 1989, Wolda 1978, Zaret 1982). Curiously, even though there exist such an ambiguity, it is possible to find studies that continue to use indices of food web complexity (*i.e.,* connectance) as a direct surrogate of ecological instability (*e.g.*, see Holdgate 1996). This is the case even though this "reductionist's" stance is open to numerous criticisms and actually contrary to the findings of many empirical and theoretical studies (*e.g.*, see DeAngelis 1975, Leigh 1965, Pimm 1984, Tilman 1997, Tilman and Downing 1994, Van Voris *et al.* 1980, Yodzis 1981, McCann 2000). The main criticisms of this point of view relate to the crude simplifying assumptions in the models used to derive these conclusions: random combination of organisms all drawn from the same statistical population that are thus equivalent (rather than being historical constructs, assembled over evolutionary-ecological time and selected to coexist); linearity of interactions and the associated assumption of the presence of only one stable point (Austin and Cook 1974, Stone *et al.* 1996); and the lack of attention to transient and *semi-stable* dynamical behaviour (Byers and Hansell 1992, 1996, Hastings and Higgins 1994, Holling 1973, McCann and Hastings 1997, Michalski and Arditi 1995, Neubert and Caswell 1997).

When more realistic spatio-temporal limitations are incorporated into these food web models (*i.e.*, non-random assembly of species; lower levels of connectance; limits in the number of trophic levels; realistic interaction strengths; hierarchical structure of food webs; sigmoidal predation functional responses; patchy, non-random distributions of prey; and constraints upon the efficiency of energy transfer and resource utilisation—DeAngelis *et al.* 1978, Kirkwood and Lawton 1981, Michalski and Arditi 1995, Pimm and Lawton 1977, Yodzis 1981) the results have been invariably inconclusive and complex. It seems that the simplistic extrapolation of results from the small-scale system to the large-scale cannot be reasonably made (see review in McCann 2000).

Also problematic with the reductionist's stance is their almost exclusive reliance upon the asymptotic Liapunov stability formalism as THE stability concept. This is problematic for three reasons: First, the Liapunov stability criterion is a <u>local</u> stability concept. Missing in the Liapunov formalism, at least as it has been used in ecological circles, is the idea of the global boundedness of systems (Holling 1973, Thornton and Mulholland 1974); that is, how *resistant* a system is from being perturbed from its global state, or the capacity of an ecological system to resist change (*i.e.*, an inertia, see below) and so stay within a given range of structural/dynamic characteristics and persist in time and space (Seitz 1994, Zaret 1982). Second, the Liapunov stability does not address the potential of quasi-steady states that may drift and change or even "adapt" with time (again, at least not as it has been used in ecology; Byers and Hansell 1992). Finally, any useful application of the local asymptotic Liapunov (or any other) stability formalism requires an explicit understanding of the *expected* state (*e.g.*, the steady state) and then somehow to measure the distance from this state. Unfortunately, those that adopted this formalism have historically given no attention to understand how such an *expected* state may be described. As a result of these problems, the simplistic conclusions originally given by May (1972a,b) cannot be supported without some rather severe stipulations.

Unfortunately, the status of this debate is rather obscure (Patten 1998). The purpose of this paper is to resurrect this debate and attempt a resolution of the issue using additional information that has more recently become available. To this end, a first approximation of the *expected* patterns of global biological diversity is specified. By biological diversity, we refer simply to *taxonomic richness*[11]. The two primary factors that we consider as the controlling variables of this expected state are: 1) the Energy

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[11] *While other, more extended understandings of biological diversity exist—e.g., information-theoretic diversity, genomic diversity, life history diversity and even behavioural/cultural diversity—here, we focus upon the number of taxa for the following reasons: taxonomic richness has been a primary concept in diversity-stability studies; (consequently) there is greater availability of richness data in the literature; there is a tendency for diversity measures to be inter-correlated.*

richness, and 2) the Perturbation regime of a given system. With knowledge of this expected biological diversity, we then present a general and more useful formulation of the stability concept that allows a clarification of the stability-diversity debate.

A FIRST APPROXIMATION OF THE "EXPECTED" BIOLOGICAL DIVERSITY

Any attempt to understand the stability of a given system, be it reductionist or holist in approach, requires an explicit understanding of the *expected* state of that system. That is, within the context of our question, what is the diversity that is *expected,* given such and such an environment? No reference whatsoever has been made to such an *expected* diversity in the diversity-stability literature. Strangely, this has been the case even though it is widely appreciated that diversity is strongly related to many factors. This oversight represents, in our opinion, a critical flaw in past discussions of this subject. To provide this context and so remedy this situation, we focus upon two such dominant factors, known to influence the diversity of ecological systems: *Energy richness* and *Perturbation* (Rosenzweig 1992, Huston 1994). What follows is a quick summary of this information (we refer the reader to Rosenzweig (1992) and Huston (1994) who have extensively reviewed these and other diversity-related patterns).

Generally, greater biological diversity (i.e., taxonomic richness) is found in more *energy rich* environments (*e.g.*, Wright 1983, Currie and Paquin 1987, Currie 1991, Currie and Fritz 1993, Wylie and Currie 1993; see Figure 4.1a). [Here, we use the term energy rich to mean simply the relative richness of biologically useful resources (*i.e.*, free energy), in contrast to the more restrictive notions of Biomass or Primary Production (the net or gross biomass created per unit time) that are more frequently used. We will refine this concept, below—see equation 1.] This empirical pattern has been generally explained through the niche-packing hypothesis (Preston 1948, 1960 and Rosenzweig 1992). However, over the shorter spatio-temporal scales of ecological systems, this pattern is slightly modified in that biological diversity decreases at very high energy levels, resulting in a maximal diversity at some intermediate level of energy (Rosenzweig 1992, Huston 1994:126). It has been hypothesised that this modal relationship may be due to an increased dynamical variation in highly enriched conditions (*e.g., Paradox of enrichment*; Rosenzweig 1971). Of course, these latter systems frequently represent perturbed systems and so the modal nature of the diversity-energy relationship may also be, in part, due to the effect of perturbations (see below).

Greater biological diversity is also found in environments that are less perturbed (Pianka 1966, Loucks 1970, Zaret 1982, Leigh 1990; see Figure 4.1b). This has been suggested to be the result of extremely variable environments discouraging the development of specialised adaptations, over evolutionary time scales. However, when this pattern has been examined over the smaller spatio-temporal scales of ecological interactions, it too has been found to follow a modal relationship—with highest biological diversity again at some intermediate level of environmental variability. This decrease under the least variable conditions is thought to be due to competitive exclusion by a smaller subset of super-competitive or *over-dominant* species (*e.g.*, Gause's (1934, 1970) *Competitive exclusion principle*). It has been argued that such species are more adaptive (favoured due to differential fitness increases) in low-variability environments because a greater proportion of free energy may be channelled into the maintenance of the specialised physiological/ecological structures/functions, rather than to their diversion to stress tolerance (Rashevsky 1960:192; Rosen 1967:8-10). This idea has been further generalised by Connell and Orias (1964) as the *Intermediate disturbance hypothesis.*

Regardless of the mechanisms that may be causing these two diversity patterns, we can use these empirical patterns to delineate a global, first-order approximation of the *expected* diversity for any given system. An integration of these two factors (energy richness and perturbation) has been previously attempted by Hildrew and Townsend (1987), and Huston (1979). However, the difficulty in simply and systematically quantifying *energy richness* and *perturbation* across a variety of different systems has prevented the development of broad, cross-system generalisations. We remedy this situation by applying a recently suggested approach that allows us to integrate these two factors in a simple cross-system manner (Choi *et al.* 1999, Choi and Patten 2002).

This integration of *perturbation* and *energy richness* may be accomplished by using a simple graphical x-y plane of community standing biomass (B) vs. community respiration (R) as shown in Figure 4.2a. Frequently or strongly perturbed systems tend to have higher R/B ratios (Huston 1979, Margalef 1963, Margalef 1975, Odum 1953, Pianka 1970, Rapport *et al.* 1985, Southwood 1988, Choi *et al.* 1999). This is generally observed because organisms that recolonise a system after perturbations are smaller sized, rapidly growing and reproducing and with higher mass-specific metabolic rates (*i.e.*, "r-selected" organisms, early in a successional sequence). As such, the R/B ratio may be used as a simple system level index of the perturbation regime to which a system is exposed. Similar arguments have been made for the Production to Biomass (or P/B) ratio by Odum (1953) and Margalef (1963). However, we prefer the use of the R/B ratio for three reasons: (1) production is recycled and so difficult to keep track of; (2) respiration is easier to measure; and (3) respiration rates more directly relate to the underlying thermodynamic principles that allow the derivation of a general index of perturbation (for more details, the reader is directed to Choi *et al.* 1999, Fath *et al.*, 2001, Choi and Patten 2002; note that near the steady state, the P/B ratio approximates to the R/B ratio—Appendix 2C).

Within the conceptual model presented in Figure 4.2a, the R/B ratio is simply the slope of the vector (Q). In this context, large slope systems may be considered more *perturbed*, due to their larger R/B ratios. Further, the length of the vector (Q) heuristically describes the *energy richness* of a system as it represents the sum of: (1) the average quantity of biological matter residing within in a system (<B>; i.e., standing biomass), and (2) the average quantity of energy fluxed through the system during the observational period (<R>*t; the amount of biological matter transformed irreversibly to waste heat, that is entropy, in units of biomass):

$$(1) \qquad Q = [\, \langle B \rangle^2 + (\langle R \rangle * t\,)^2 \,]^{1/2}$$

where the symbols "< >" indicate an average over the observational period, t (t=1 year, in all that follows). <R>, a rate, is multiplied by time, t, to convert to energy density units.

Using such a context, it is possible to compare a wide variety of different ecosystems in terms of their *perturbation* and *energy richness* status. For example, we can see a progression of increasing energy richness (Q) from lakes, continental shelf, coral reef, estuaries, tundra, grassland, boreal forest, temperate forest and tropical forest (Figure 4.2b). Within each major class of ecosystem, comparisons of energy richness (Q) and perturbation (R/B) also become possible: *e.g.*, in continental shelf systems, Chesapeake Bay (Sh.Te.1, 2, 3) may be considered a relatively more perturbed system relative to the English Channel (Sh.Te.7).

In this Cartesian framework, we add biological diversity as a third dimension (Figure 4.3a). Because species richness varies as a function of the size of a system that is censused (Figure 4.4; *i.e.*, "Species-Area" relationships; Arrhenius 1921, MacArthur and Wilson 1963, Rosenzweig 1992), biological diversity must first be corrected for this effect. In what follows, species richness is expressed as the number of species found in 10 km^2 (N_{10}) by assuming the species-area relationship to be with a constant slope (in the range of areas studied):

$$(2) \qquad [\ \log_{10}(N_{10}) - \log_{10}(N_A)\ ] \ / \ [\ \log_{10}(10) - \log_{10}(A)\ ] = \text{constant}$$

where, A is the area in km^2; N_A is the number of species found in that area; and the slope constant is obtained from a linear regression of $[\log_{10}(N_A)$ vs. $\log_{10}(A)]$. For flowering plants, the slope constant has a value of ≈ 0.285 (± 0.023, SE; see Figure 4.4). This result and the results that follow are based upon diversity data for 174 countries, published by the World Conservation Monitoring Centre (1992).

The result is a three-dimensional state space that describes the *expected* biological diversity for a given system, what we may call in the most general sense, its *domain of attraction* (Byers and Hansell 1992). Figure 4.3b shows how the diversity of flowering plants varies as a function of these factors. (Note that net primary production (NPP) is used to illustrate this pattern rather than the community respiration rate (R) because NPP estimates are more readily obtained from the literature. This is a crude but adequate approximation as NPP and R are generally of the same order of magnitude; see Figure 4.5).

In Figure 4.6a, we note that the number of flowering plant species is positively correlated with the biological energy richness found in a country $(\approx \langle B\rangle^2 + [(\langle NPP\rangle * t)^2]^{1/2}$; equation 1), with a slight drop in diversity at the most extreme levels of energy richness. This is in line with previous observations of the relationship between diversity and energy richness. Diversity is also negatively correlated to the NPP/B (≈ R/B) ratio, our measure of the perturbation regime (Figure 4.6b), again with a minor decrease in diversity at the lowest levels of *perturbation*. This result is also in line with previous empirical descriptions of the diversity-perturbation relationship. As a result, we may be reasonably confident that the conceptual model we have developed describes, as a first approximation, the expected biological diversity for any given system.

STABILITY

Using the above, albeit crude, knowledge of the expected diversity, the stability of a system may be simply described as the relative proximity to this expected state (*i.e.*, the three-dimensional attractive region described in Figure 4.3b; see also the schematisation in Figure 4.7). When diversity is close to the expected state, it may be considered a stable system; when diversity is far from the expected state, it may be considered an unstable system. Over time, all systems should tend towards this expected space (Choi *et al.* 1999, Fath *et al.* 2001).

We are now in a position to address our primary question. How does biological diversity influence the stability of a system? The answer is unambiguously: it depends. There is no simple answer. This is because the question represents the simplified case where only diversity is allowed to vary while the other state variables (*perturbation* and *energy richness*) are constrained to be unvarying. Certainly, this represents a very limiting and unrealistic stipulation, as simultaneous compensatory and adaptive changes in all ecological characteristics are possible and probable. If however, the *energy richness* and *perturbation* regime of a system is so constrained to be unvarying, what can be said is that any increases in the diversity of a system beyond the expected levels of diversity represents a globally less "stable" state. If the diversity of a system is increased when the diversity is lower than may be expected, the system may be said to become more "stable". That is, any attempt to understand how the global stability of a system is influenced by biological diversity, must at the very least, make explicit reference to the perturbation regime and the energetic richness of the system.

In the less restrictive case where all three state variables (species richness, energy, and perturbation) are unconstrained and so vary with time, it becomes obvious that variations in the Energy richness of a system may also be considered both a destabilising (*i.e.*, *Paradox of Enrichment*, *sensu* Rosenzweig 1971) and a stabilising influence, depending again upon the prior state of the system. Similarly, variations in the perturbation regime may also be considered to be both a stabilising (*i.e.*, *Paradox of the Plankton, sensu* Hutchinson 1961) or destabilising influence depending upon the prior state of the system (Choi and Patten 2002). In fact, this dual nature of the influence of energy and perturbation may account for the widespread belief that biodiversity is greatest at intermediate levels of energy and perturbation, respectively. (Parenthetically, there are no constraints that there be only 3 state variables. In fact, a much higher dimensional space would represent a more realistic situation than the simplistic 3-dimensional surface that we use in this study.)

To conclude, the general confusion that exists in ecology over the concept of stability and its relationship to biological diversity may be easily clarified if we understand that there are both global and local aspects of the concept (Choi and Patten 2002). Our analysis indicates that changing the diversity, energy or perturbation regime of a system may have a stabilising and a destabilising influence, depending upon the prior state of the system. As such, there is a need to focus our efforts at delineating acceptable distances from, or ranges in the locally (ecological) and globally (evolutionary) expected states, such that the adaptive capacity of the system as a whole is compatible with our own tolerances for perturbation, energy richness and species diversity.

ACKNOWLEDGEMENTS

We thank N. Saint-Jacques, B. Patten, I. Craine, H. van Leeuwen, Z. Weng, N. Mookerji, J.-M. Fréchette and M. Proulx for their many insights.

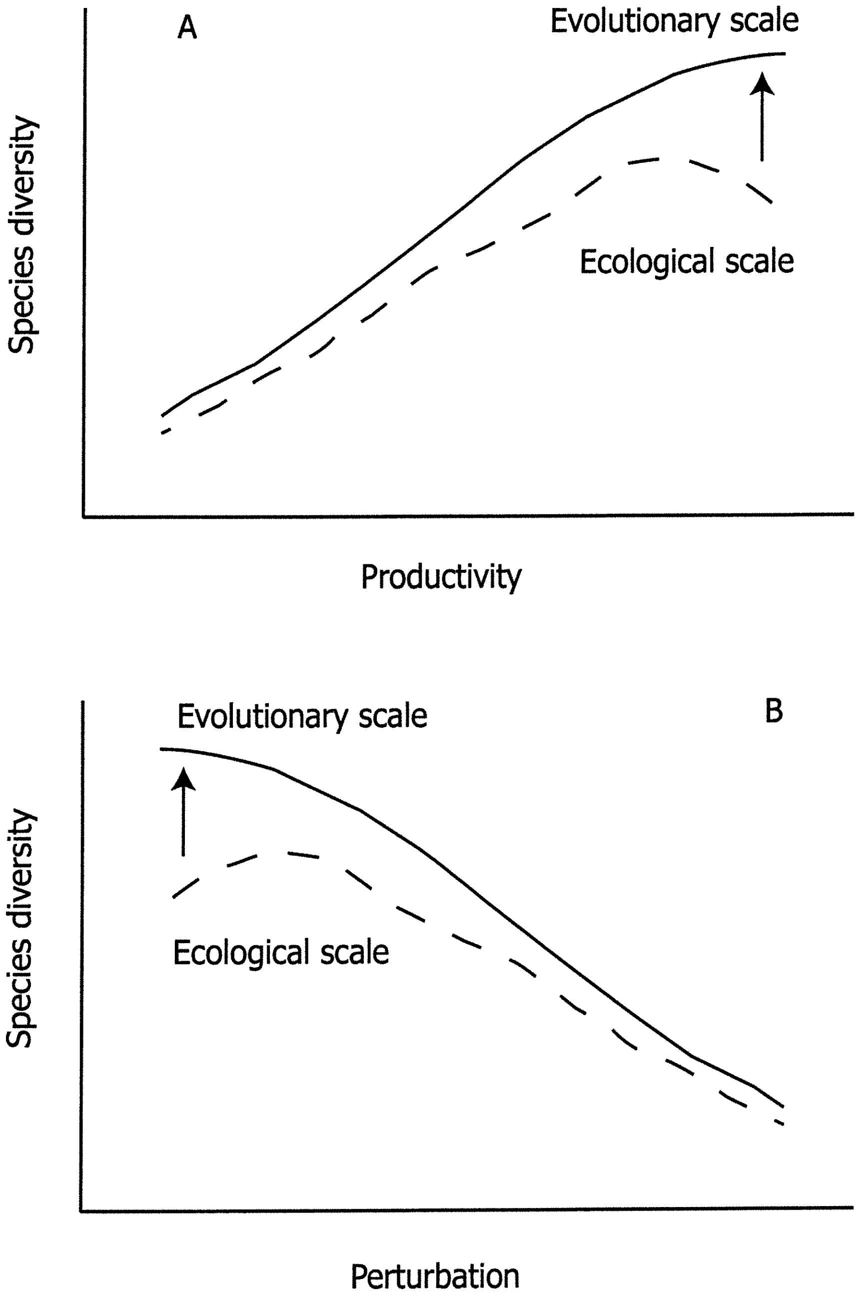

Figure 4.1 Schematisation of the empirically observed patterns of diversity in relation to energy richness (A—top panel) and perturbation (B—bottom panel) gradients. On the larger evolutionary scale, greater diversity is generally found in less perturbed and more energy rich systems. However, at the smaller ecological scales, these relationships are found to be modified: decreases in diversity are found at the highest levels of energy richness and lowest levels of perturbation.

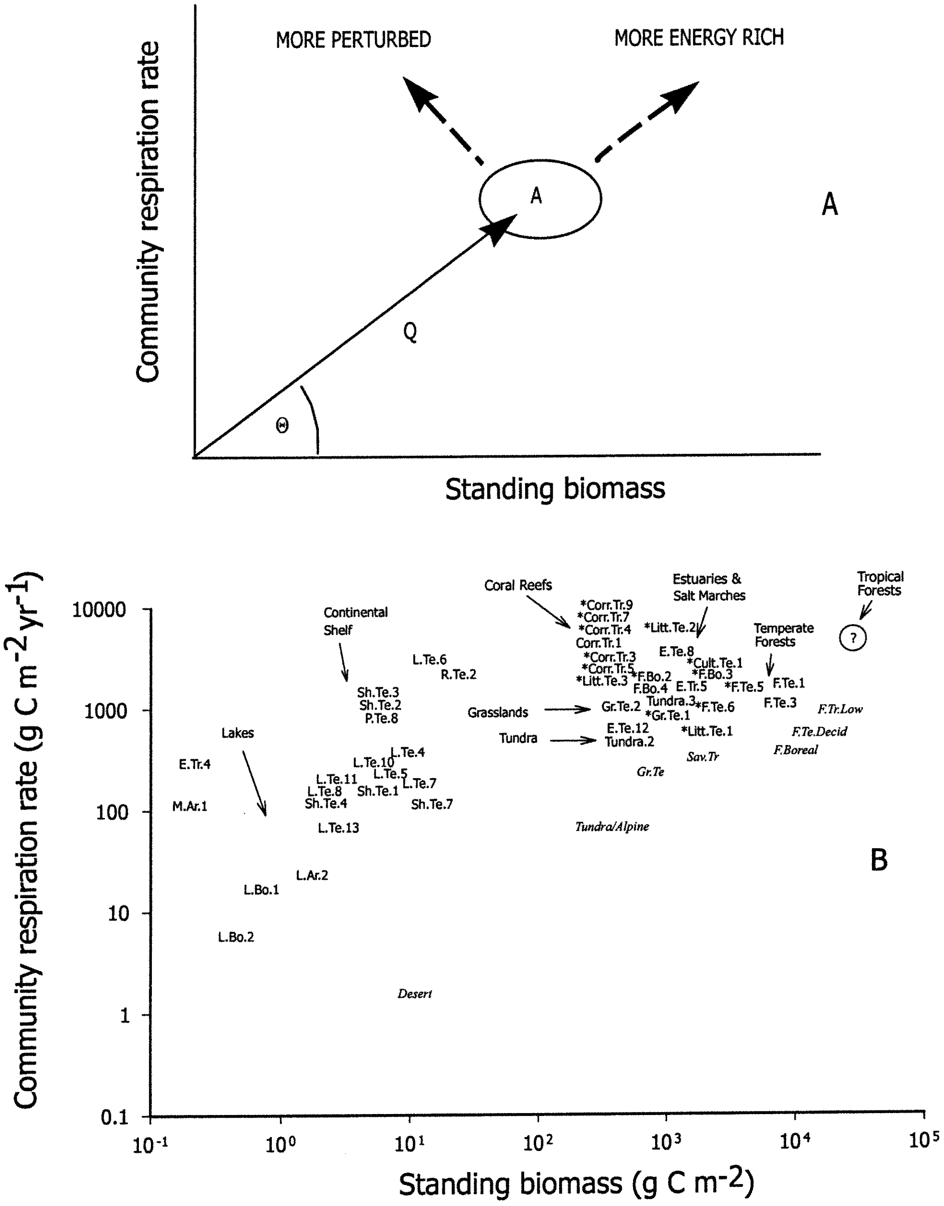

Figure 4.2 **(A)** Respiration rate and standing biomass determine a system's energy richness and perturbation regime. An "expected" species richness may be determined for such a system (*e.g.*, Figure 4.4). **(B)** The distribution of some representative ecosystems in this "state space" (see Appendix 7). An asterisk (*) represents an order of magnitude estimate. *Italics* indicate the relative magnitude of the net primary production (NPP) of representative systems and so delineate the approximate lower bound of community respiration rates of each representative system.

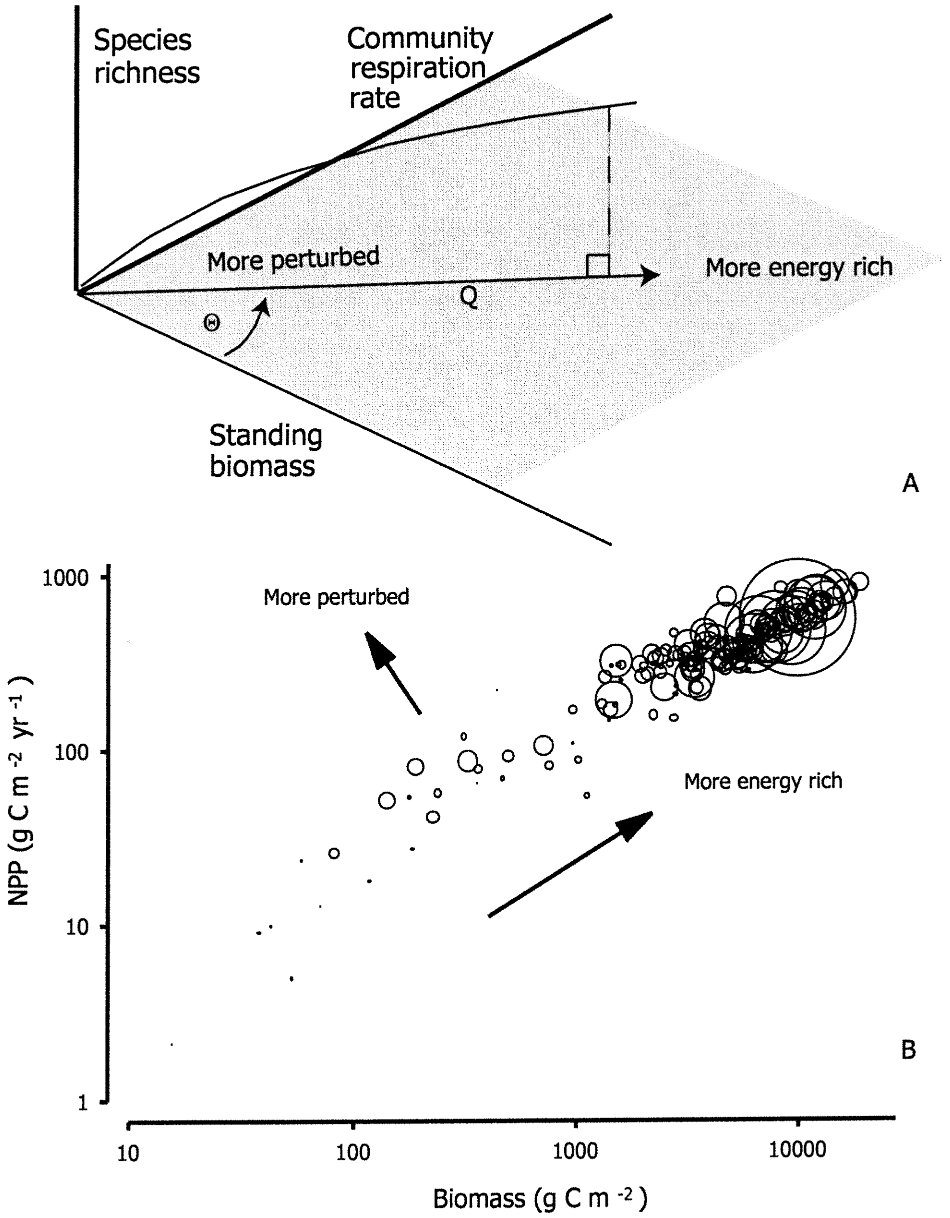

Figure 4.3 **(A)** The three dimensional model depicting the "expected" diversity as a function of energy richness (Q) and perturbation (R/B ratio). **(B)** The radius of circles is proportional to the number of flowering plant species found in each country (N_{10}). Note that instead of the community respiration rate (R), we use the net primary productivity (NPP) as NPP estimates are more readily accessible in the literature. This is an adequate first approximation as a strong relationship exists between the community respiration rate and Net primary production (see Figure 4.5).

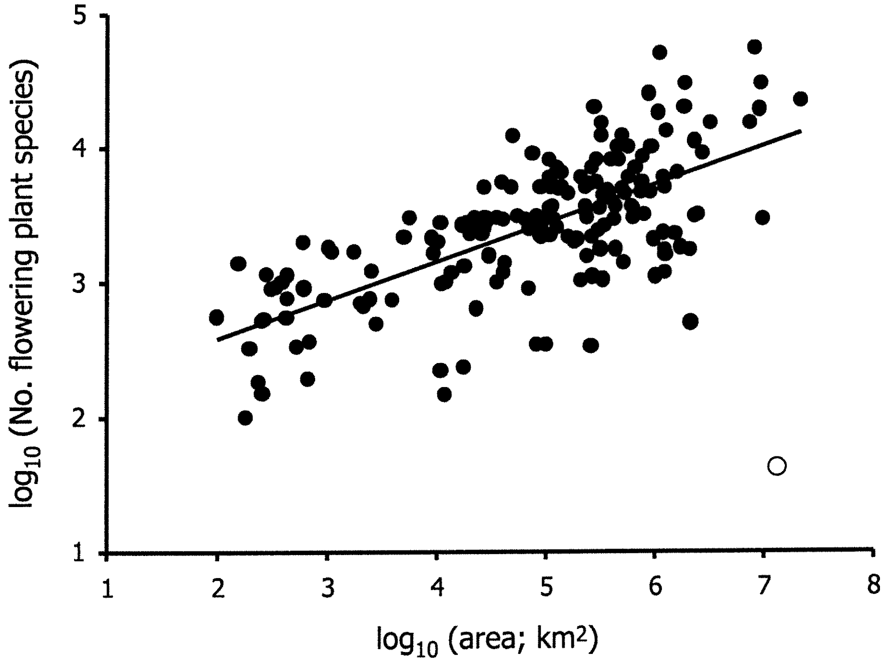

Figure 4.4. The global diversity-area relationship of flowering plant species, broken down by country. The unfilled circle (bottom, right) represents Antarctica which was excluded from the linear regression analysis: [$\log_{10}$ (diversity) = 2.01 + 0.285 $\log_{10}$ (area); R^2=0.460, n=174, p<0.0001]. The standard errors are 0.12 and 0.032, respectively for the intercept and slope.

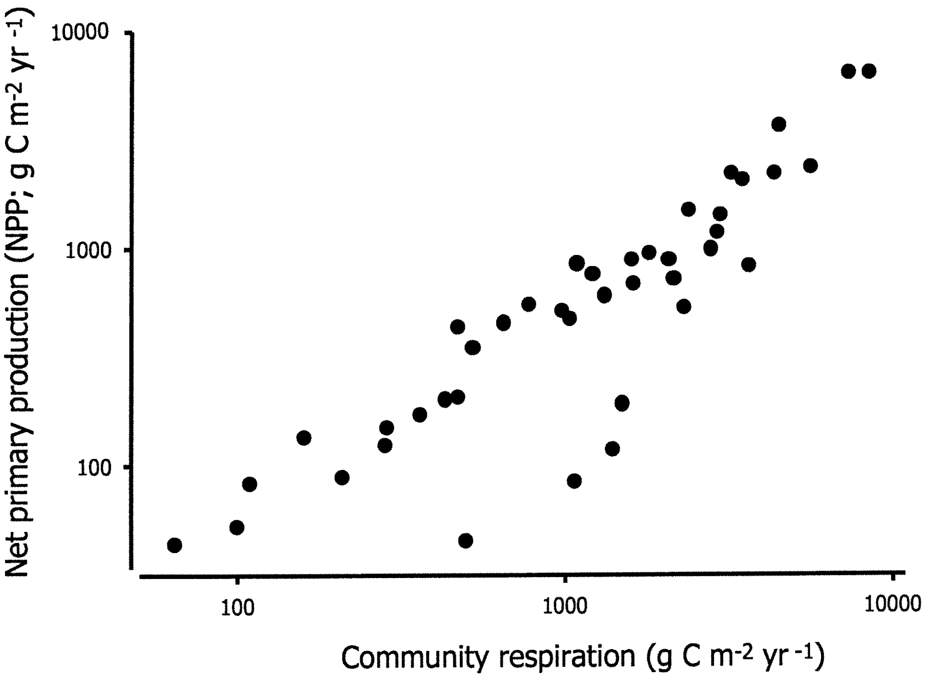

Figure 4.5. Relationship between net primary production (NPP) and community respiration rate (R). The strong positive relationship indicates that NPP may be used as an order of magnitude approximation of R.

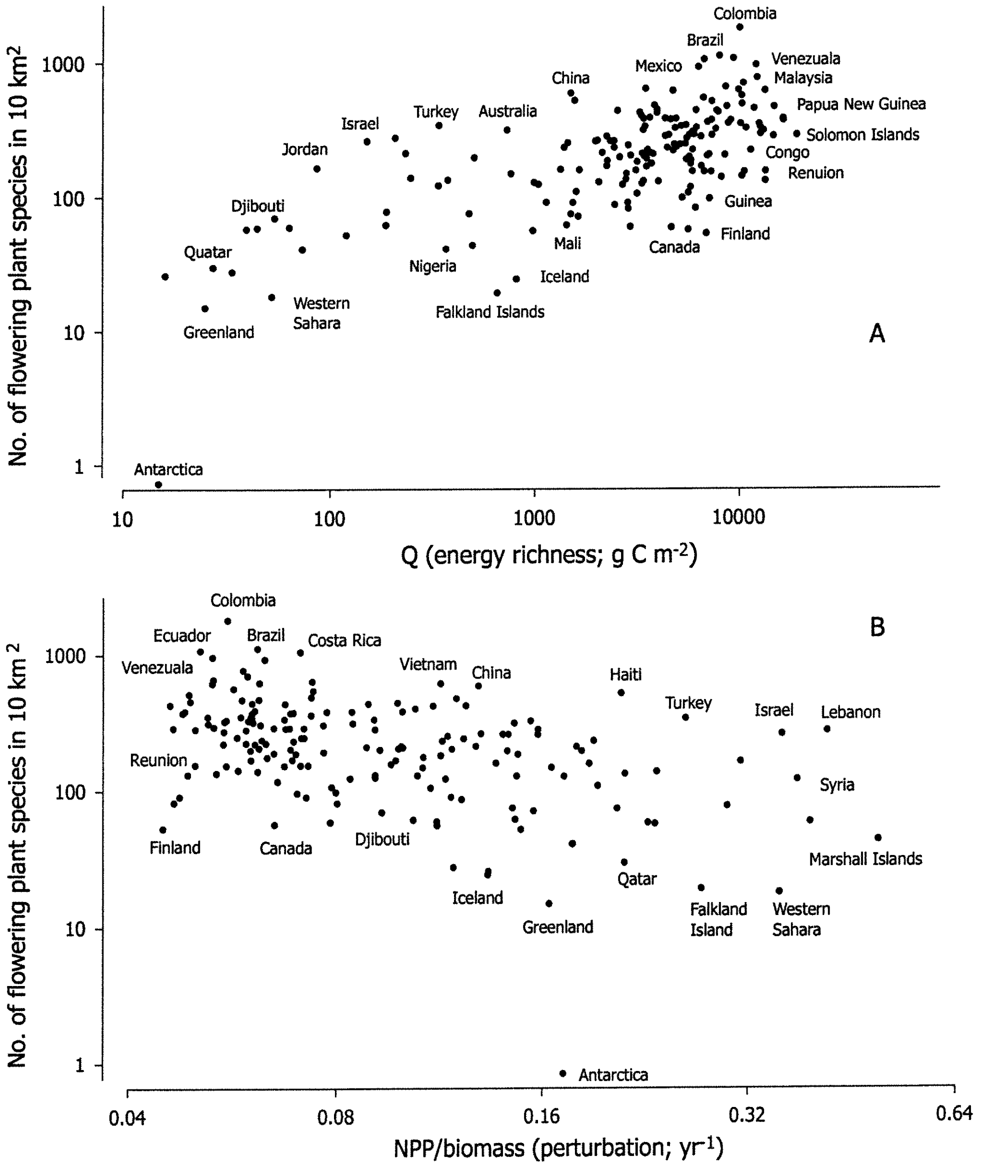

Figure 4.6 **(A)** Energy richness (Q) and N_{10} (the number of flowering plant species in 10 km^2) are positively correlated at the global level, as expected: $\log_{10}(N_{10}) = 1.14 + 0.36 * \log_{10}(Q)$; $n=174$, $R^2=0.40$, $p<0.0001$. The standard errors of the coefficients are: 0.12 and 0.03, for the constant and the slope, respectively. **(B)** "Perturbation" (NPP/B) and N_{10} are negatively correlated as was also expected: $\log_{10}(N_{10}) = 1.62 - 0.74 * \log_{10}(NPP/B)$; $n=174$, $R^2=0.21$, $p<0.0001$. The standard errors are 0.11 for both the constant and the slope. Antarctica was excluded from the above statistical analyses. Biodiversity estimates were obtained from data published by the World Conservation Monitoring Centre (1992).

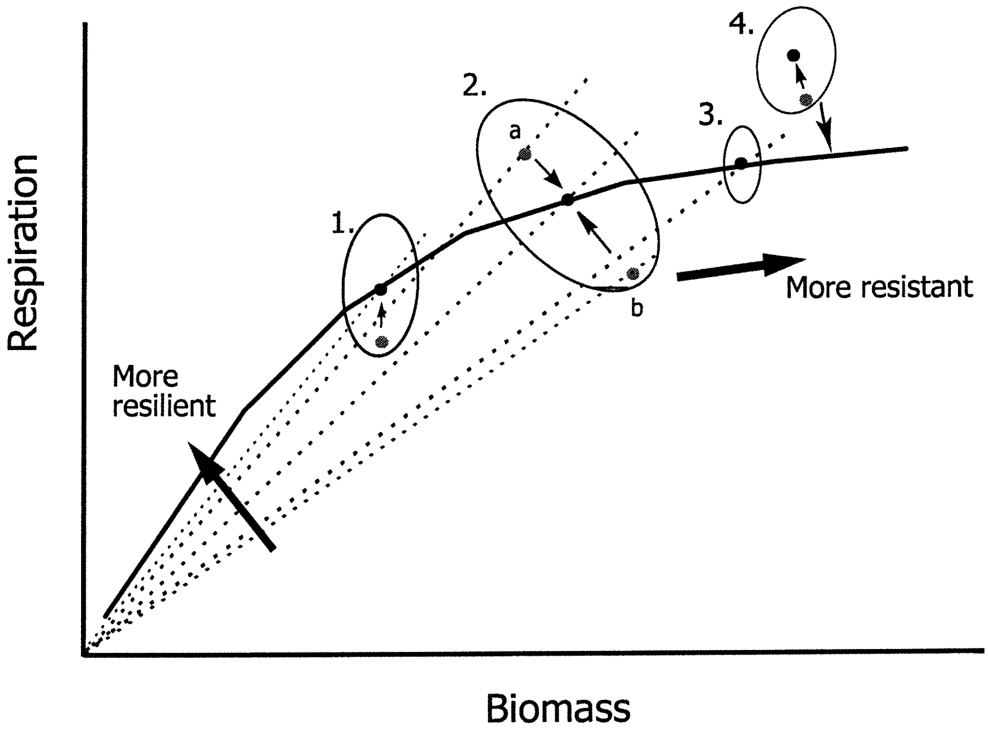

Figure 4.7. Schematic of the stability of systems in the state space of respiration (R) and biomass (B). Due to form of this relationship, high resilience systems (*e.g.*, system 1—with a high R/B ratio) are also low resistance systems (low energy; Q); and low resilience systems (*e.g.*, system 3—with a low R/B ratio) represent more resistant systems (high energy; Q). Any local deviations from this global evolutionary pattern (*e.g.*, system 4) represent a globally unstable situation and a return towards the global pattern becomes more probable. Within each system, deviations from the system-specific expected behaviour represent a more ecologically unstable situation. As can be seen, ecologically and evolutionarily favoured directions for change can be antagonistic or mutualistic, depending upon the specific configuration of the system concerned. Furthermore, at the ecosystem-specific level, the centroid of system 2 (or also system 4) which is intermediate in resilience (relative to condition 2a) and intermediate in resistance (relative to condition 2b) may be said to be the more "adaptive" configuration of that system. Modified from Figure 6 in Choi and Patten 2002.

— Chapter 5 —

LAKE ECOSYSTEM RESPONSES TO RAPID CLIMATE CHANGE[12]

> *Communities dominated by smaller animals must process energy, nutrients, and contaminants more rapidly; they will show more dramatic spatial and temporal changes in population size; and they will be less integrated and interactive because of the restricted existence of their members in space and time. Community size structure is one of the fundamental characteristics of an ecosystem. It is a pity that it should be so little studied.*
>
> *Peters 1983*

ABSTRACT

The consequences of rapid climate change are examined in terms of two main effects: variability effects and magnitude effects. How life history selection is influenced by rapid climate change is examined in these simple terms. Focussing upon body size as a quantifiable and strong correlate of life history variation, an attempt is made to describe these influences. By arguing that the processes that influence life-history selection similarly influence biological diversity, an attempt is made to understand the influence of rapid climate change upon biological diversity.

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INTRODUCTION

Rapid climate change will force numerous changes to temperate aquatic ecosystems. Whole suites of ecologically important factors will change: temperature; evapotranspiration; the availability of water and limiting nutrients; the frequency and magnitude of precipitation, wind, storm and fire events; the length of the ice-free or growing season; the depth and strength of mixed layer development during the growing season; and the period of nutrient limitation during summer stratification of the water column (Lewis 1987, Shuter 1992, Hornung and Reynolds 1995). To simplify our discussion, these changes are broken down into two inter-related classes: (1) alterations in the variability of climatic patterns (*e.g.*, the frequency of extremes in temperature events); and (2) alterations in the mean trends of climatic patterns (*e.g.*, the magnitude of temperature). The influence of these effects upon the life history characteristics of organisms may be described with the use of a simplifying assumption: that biologically useful free energy may be diverted to one of two paths: (1) biomass elaboration (growth and reproduction; *i.e.*, anabolism) and (2) maintenance metabolism (*i.e.*, catabolism). In the following, we will try to describe how these *variability* and *magnitude* effects modulate the diversion of free energy through these two pathways. Such an understanding will then be used as a basis to generate qualitative predictions of the influence of rapid climate change upon biological diversity.

VARIABILITY EFFECTS

What is the influence of elevated variations in climatic patterns upon biological system (*i.e.*, variability effects)? Such increases in the variability of climatic factors (*e.g.*, local extremes of temperature, wind events, precipitation and storm events) represent a perturbation to the biota, in the most general sense (Choi and Patten 2002). Perturbations directly influence the life history of organisms by modifying their size and age dependent survivorship, growth, reproduction and metabolism. Generally, the immediate consequence of a large-scale disturbance (*e.g.*, let us focus upon the variance spectra of temperature fluctuations due to its dominant role in biological and climatic systems) is physiological stress that forces greater allocation of resources to biomass maintenance rather than biomass elaboration. If the disturbance is extreme and/or frequent enough, widespread mortality also results. The consequence of these processes is the dominance of maintenance-related metabolic rates (*e.g.*, respiration rates, R) over biomass elaboration (B). That is, any system exposed to elevated levels of climatic variations may be expected to demonstrate elevated intensities of metabolic rates (Choi *et al.* 1999, Choi and Patten 2002).

In more classical ecological terms, the consequence of the above, disturbance-related mortality is a liberation of resources that were previously unavailable due to their being used or stored in the living biomass. Thus disturbance, in moving a system away from its carrying capacity, also liberates "free energy" (*i.e.,* energy available for work; see Lotka 1922, Holling 1986). This "free energy" can be most rapidly exploited by small organisms as they have extremely high rates of biomass elaboration (growth, reproduction) and metabolism (respiration; Hemmingsen 1960, Fenchel 1974, Robertson 1979), as well as extremely high intensities of metabolic and turnover rates. Thus immediately following such energy liberating perturbations, R/B ratios are also known to be elevated (Margalef 1963, Choi *et al.* 1999, Choi and Patten 2002). With time, the larger, more slowly growing and reproducing organisms may also increase in dominance, while simultaneously, the total available free energy will decrease as it becomes incorporated into the biomass of these larger and longer-lived organisms. This is the classical description of the process of ecological succession (Clements 1936, Odum 1953, Margalef 1963, Matsuno 1978, Whittaker 1975, Patten and Odum 1981, Rapport *et al.* 1985). Therefore, any system that is repeatedly exposed to large variations in climatic extremes may be expected to be dominated by "early-successional" organisms (higher intensities of metabolic rates and smaller body size).

As anectdotal evidence, we can argue that deeper and larger-volumed lakes may be considered more insensitive to large-scale climatic variations and their indirect effects (floods, thermal structure, oxygen stress and changing pH), simply due to the greater size (Lewis 1987; Choi *et al.* 1999; see also Figure 5.1). Thus, a simple consequence of this reasoning is that we may expect smaller-sized (high metabolic intensity) organisms in smaller sized lakes. This indeed is found to be the case (*e.g.*, see Choi 1994). For example, Chen (1991) found shallower lakes to contain fish that matured more quickly (*i.e.,* size at maturity was smaller) relative to deeper lakes. Stunted populations of fish are frequently found in shallow lakes (Roff 1986). Similar patterns of life history

Compare w/ earlier
paper

selection have been reported for riverine fish, along a gradient in river stability (Schlosser 1990). Rapport *et al.* (1985) discussed the shift in size of fish species towards smaller sizes with an increase in the stress or disturbance in many aquatic ecosystems. When the fish species communities at a small geographic scale are examined, small-sized species are more frequently observed in smaller and shallower lakes (Figure 5.2; see also Rahel 1984 for similar data). Amongst zooplankton in the Québec Laurentian lakes, the same pattern is found (Figure 5.3). Similar types of patterns have been documented in the terrestrial literature and are known as r- and K-types of life history selection (MacArthur and Wilson 1963, Pianka 1970, McNab 1980, Taylor *et al.* 1990).

In summary there does seem to be some evidence that climatic variability effects will result in biota that are smaller sized and with greater intensities of metabolic rates.

MAGNITUDE EFFECTS

How do alterations in the mean trends (magnitude effects) of climate change alter the biota? To study this question, we focus upon the primary role of ambient temperature upon the biota, as it represents an easily quantied index and important determinant of climatic change.

In the simplest of terms the influence of elevated temperatures is to elevate metabolic intensities. The consquence of sustained temperature changes (on ecological time-scales) is to drastically alter the metabolic load upon organisms and so also the allocation of free energy to biomass elaboration. The manner in which this metabolic load changes with respect to temperature is generally in good agreement with an Arrhenius formulation (Sharpe and DeMichele 1977, Lin 1995):

$$(1) \qquad dR/dT = k_1 + \exp(k_2 + k_3 / T)$$

where R is the respiration rate; T is temperature in Kelvin; and k_i are constants.

Using the Bertalanffy (1957) formulation of growth rate (*i.e.,* biomass elaboration) for its simplicity, we can describe the effect of an increase in temperature upon the growth rate of organisms in the following manner:

$$(2) \qquad dw/dt = Aw^a - Cw^c$$

where w is animal weight and t is time. The first term represents the size dependence of anabolism (assimilation of energy). Thus A, the coefficient of anabolism, is a function strongly dependent upon resource availability which is frequently described by a Michaelis-Menten functional relationship (Crowley 1975, Sharpe and DeMichele 1977, Lundberg and Persson 1993). The second term represents the size dependence of catabolism (respiration). Thus C, the coefficient of catabolism, is a function strongly dependent upon temperature and generally follows an Arrhenius formulation.

The above formulations indicate that under most conditions, the direct effect of a temperature increase will be to increase metabolic load and so reduce the rate of growth of organisms. When such metabolic loads are sustained, its influence can be strong, resulting in reduced organism size (*i.e.*, biomass elaboration, B) and elevated maintenance metabolism (*i.e.*, respiration rates, R). That is, sustained exposures to high temperatures are expected to result in smaller sized organisms with elevated intensities of metabolic rates. (Temperature changes can also modify resource availability and therefore the first term, A, but we will ignore this effect for the sake of simplicity).

Empirical observations seem to support this expectation. A simple test of this prediction can be made by examining the size distribution of organisms grown in different temperature environments under laboratory conditions. This has been done by numerous researchers (*e.g.*, Mayr 1956, Ray 1960, Partridge *et al.* 1994) and thoroughly reviewed by Atkinson (1994). They demonstrate that the temperature effect is very strong in the vast majority of cases. The same pattern is also found under more natural conditions. Shuter (1992) summarises data showing a decrease in the age at maturity of several fish species with an increase in the number of degree-days. Lindsey (1966), in examining the maximum size of fish species along a latitudinal gradient, found an increased preponderance of smaller-sized species closer to the equator. The same was found with many groups of amphibians and reptiles. Similar results have been demonstrated in marine planktonic communities along a latitudinal gradient by Sheldon (1984).

Smaller, shallower lakes are generally warmer than deeper lakes (Figure 5.1). Thus, small body size may be expected in shallow lakes, not only due to increased disturbance (*variability* effects, above) but also due to direct temperature influences (*magnitude* effects). That is, the patterns of size reduction in shallower and smaller lakes described in Figures 5.2 and 5.3 are likely due to the influence of both magnitude (temperature) and variability effects.

In summary, there also seems to be some evidence that mean trends of climatic variations (e.g., increases in temperature) will also result in biota that are smaller sized and with greater intensities of metabolic rates.

SYNTHESIS

In an attempt to integrate variability effects and mean effects, consider the temporal dynamics of system-level metabolism. There exists an upper limit to the total amount of energy that can be respired (dissipated) in a given system. The manner in which this energy is dissipated over time is a complex function of temperature, disturbance, quantity and quality of available free energy, biotic composition (*e.g.*, size/age/species structure of organisms) and biotic interactions (predation, competition, parasitism, mutualism). As such, this function is an extremely complex and nonlinear process, a fact that biological time series demonstrate quite readily (*e.g.*, see Berman *et al.* 1995, Pascual *et al.* 1995; Chapter 1).

→ no upper limit ? gamma curve ?

In this complex dynamical system, temperature can be seen as one of the dominant forcing functions: when temperatures are high (and all else is equal), ecosystem-level respiration rates will be higher. That is, temperature behaves as a variable that controls ecosystem respiration rates (*e.g.*, as a complex Arrhenius function; see above). The temporal variation in these rates may be expressed in terms of their "domains of attraction" of energy dissipation at a given temperature (Figure 5.4; see May and Oster 1976). When temperatures increase, more complex temporal patterns of community respiration may be expected, due perhaps to more variable population dynamics. This was observed by Halbach (1973) where he demonstrated an increase in the oscillations of rotifer abundance as temperature increased—a pattern strongly suggestive of a bifurcation sequence. Further, he observed an extended desynchrony in their reproductive cycles and a reduced size at maturity of the rotifers with an increase in system temperature. A greater dynamical variation in energy dissipation with increased temperatures may be represented by a horizontal shift in the probability distribution of temperatures (Figure 5.4 top left panel).

Thus, a tropical system may be represented by system b relative to a more polar system, a (Figure 5.4, top). Some evidence exists that supports these predictions. Over a long-term study of Arctic char in seven simple Arctic lakes (a low temperature system), Johnson (1994) found extremely low recruitment rates and very strong *modal* and *large* length frequency distributions (this was not a sampling artefact). The fish in the modal size classes had variable ages and so the length frequency seemed to be a strong and stable characteristic of the populations. After perturbation from heavy fishing, the return times to the original size frequency distributions were found to be quick and repeatable. This led him to believe that conditions were highly stable and that homeostatic processes were involved in maintaining the stability in the size frequency distribution. Here, the body-size distributions were strongly repeatable and convergent. In contrast, the greater preponderance of smaller organisms in warmer latitudes indicates that more variable population dynamics with greater oscillations in population cycles (Peters 1983: p. 182) may be expected nearer to the equator.

The variability effects may be conceptualised as an increase in ? the variance in the controlling variable (temperature). This effect is indicated by the contrast between systems c (low variability—*e.g.*, mainland systems, large lakes) and d (high variability—*e.g.*, island systems, small lakes) in Figure 5.4 (bottom panels). Thus, the total system metabolism may be expected to be more variable in systems that experience a greater variation in climatic factors or in systems that are less robust to the effects of large-scale perturbations (*e.g.*, small lakes, islands vs. large lakes, mainlands). This does not seem to be a remarkably difficult assumption to accept.

The examples given above indicate that rapid climate change can have a relatively straightforward impact upon the distribution of body sizes in a system. Patterns in environmental (climatic) variability and the trends in temperature change may be seen to interact in determining the size structure of organisms in a given community or ecosystem. Such patterns in the distribution of numbers or biomass of organisms with respects to body size as those described by Sheldon *et al.* (1972), Sprules *et al.* (1983), Rodriguez and Mullin (1986), Boudreau and Dickie (1992) and Holling (1992), may very well be connected with these mechanisms. Recent work by Holling (1992) and Choi *et al.* (1999) indicate that these patterns are very robust and vary in systematic ways with different regimes of disturbance.

BIODIVERSITY

The importance of the above ideas in the context of biodiversity hinges upon the strength of the relationship between life history diversity and biodiversity. The notion of biodiversity is a complex idea that is more commonly quantified in terms of taxonomic (*e.g.*, species) richness. However, it is not limited to such a narrow scope: it is a multifaceted idea that also incorporates elements of genetic, behavioural/cultural, morphological, dietary, reproductive, and life history characteristics.

Here, we hypothesise that biodiversity is very strongly related to the diversity in niches that a system is capable of sustaining. A system capable of sustaining a large diversity of life history traits is also a system capable of supporting a wide range in organism size. As a result, elevated temperatures (system b, Figure 5.4) or variations in temperatures (system d, Figure 5.4) may be statistically expected to support such a wide range in body sizes, life history characteristics and also, biological diversity.

Latitudinal trends in species richness (Currie 1991) confirm the first prediction (temperature effect). Thus, increased temperatures may bring increased species diversity and niche diversity.

However, the second prediction of a monotonic increase in species diversity with an increase in disturbance is not so easily supported. The well-known species-richness to habitat area curves (MacArthur and Wilson 1963) seems to support this prediction in that a monotonic decrease in the number of species per unit area is found as lake size increases (Barbour and Brown 1974—where lake size is used as an index of the system's capacity to buffer environmental/climatic variations, Choi *et al.* 1999). However, a number of studies also exist that indicate that taxonomic richness is highest not under maximal but rather intermediate frequencies or magnitudes of perturbation (Hutchinson 1961, Odum 1975, Petraitis *et al.* 1989, Choi and Patten 2002). According to these studies, there seems to exist a limit to the applicability of this rule: too much or not enough perturbation results in reduced taxonomic diversity. That is, a maximal biological diversity (and size range) seems to be supported in systems that experience disturbance with a "reddened" (Steele 1985) or "pink" (Schroeder 1991) variance spectra.

Whether this maximum biological diversity corresponds to a fauna and flora that are culturally considered to be aesthetic and desirable is not a given. It is quite possible that a system dominated by a large number of bacteria may have high biological diversity but that this situation may not be considered desirable. The importance of the above in an applied sense is that it allows biodiversity to be precisely quantified/measured for a given ecosystem and relates it to a simple feature, the disturbance regime that the system experiences. By determining what kind of biodiversity is preferred and quantifying the disturbance associated with the ecological assemblage that is desired, a clearer and more effective management policy may be outlined and put into practice. It must be strongly emphasised that the basic premise of such an approach is the expectation of "surprises" (Schroeder 1991) as these patterns are being described at the level of statistical ensembles of events. The goal of diversity management must, therefore, be for the long term and for the large-scale ensembles of ecosystems rather than for a time-specific and local-scale systems.

In summary, the effects of rapid climate change were categorised into two functional groups: variability effects and magnitude effects. Examples were given of the consequences of each effect upon the size of organisms. Organism size was highlighted as a tangible and readily quantifiable feature of organisms that has the added significance that it is strongly related to the life history strategy of organisms. Thus, in examining how the size of organisms and their life history habits are influenced by rapid climate change, we can also make a first approximation of the influence of rapid climate change upon life history diversity and biodiversity.

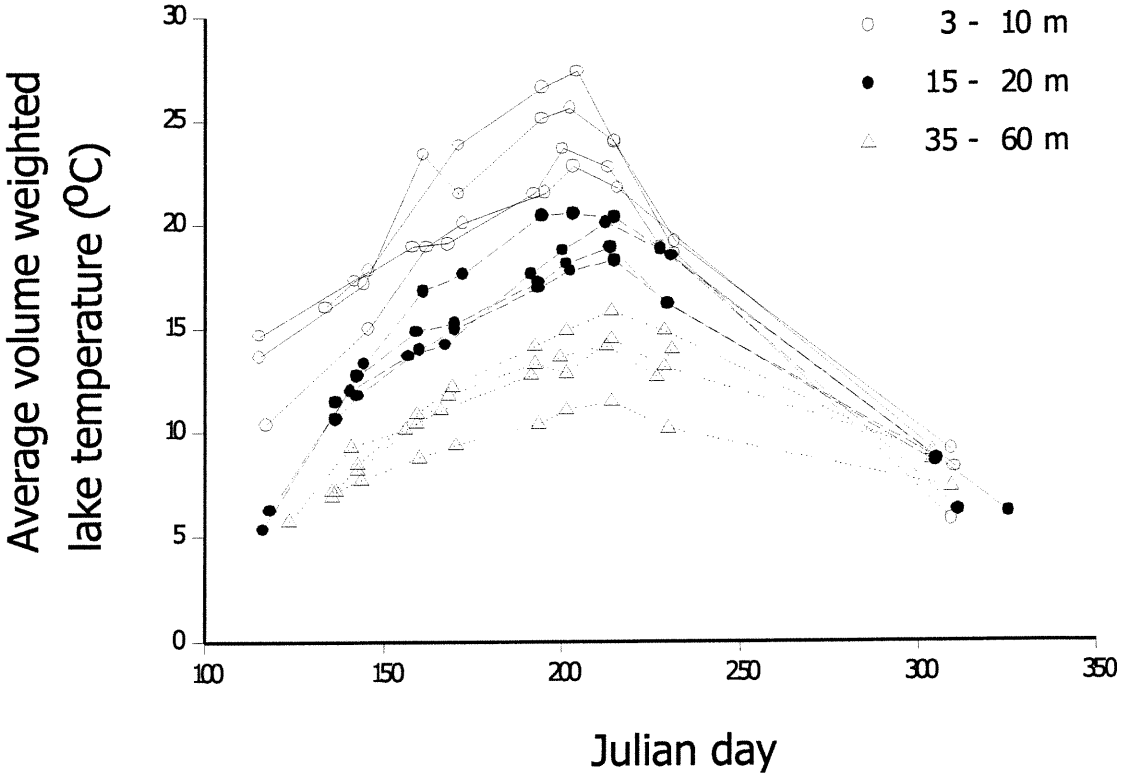

Figure 5.1. Seasonal variations in temperature for lakes with different maximum depths.

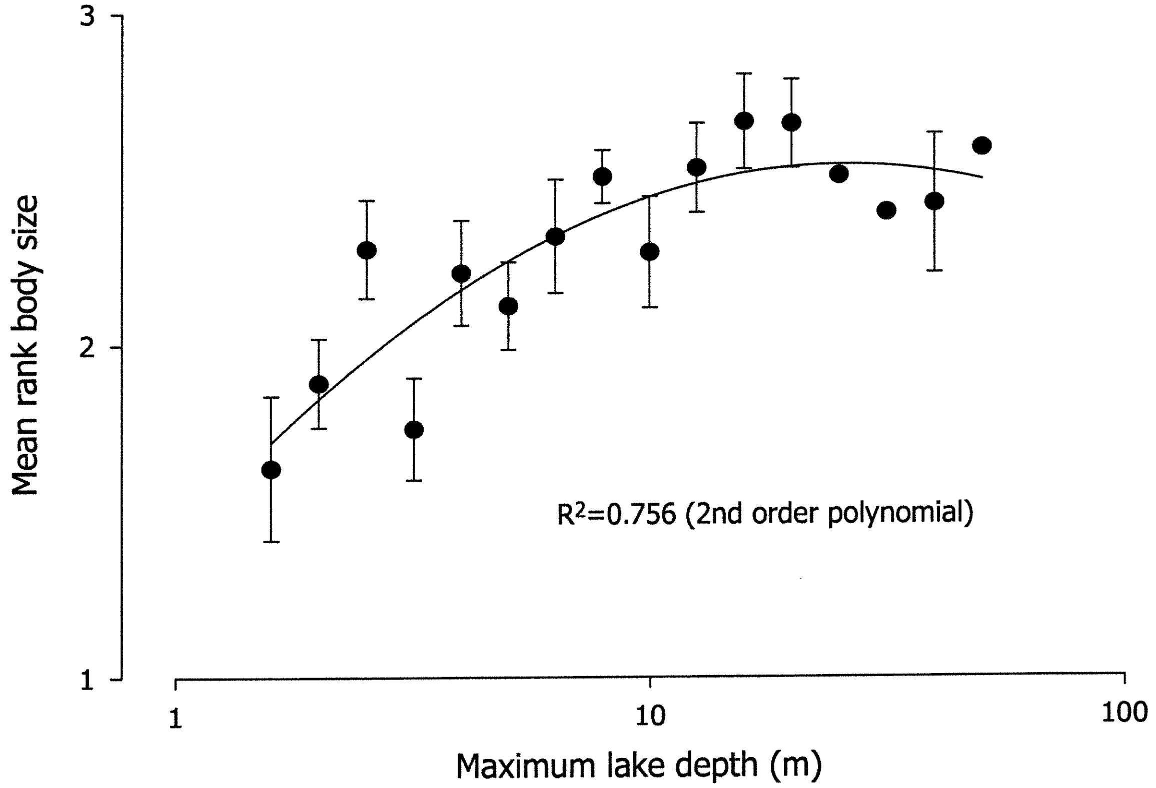

Figure 5.2. The arithmetic mean rank of body size of fish species as a function of lake maximum depth. Mean rank size was calculated by categorising the maximal size of a species into the groups: 0-10 cm, 10-20 cm, 20-40 cm, 40-80 cm, 80 cm+, as per Lindsey (1966) and using data compiled by Scott and Crossman (1973). Species lists and lake depth information are from Harvey (1978, 1981) and Harvey and Coombs (1971). Lakes (n=107) are grouped by increasing lake depth; error bars represent 1 standard error. Modified from Choi (1994).

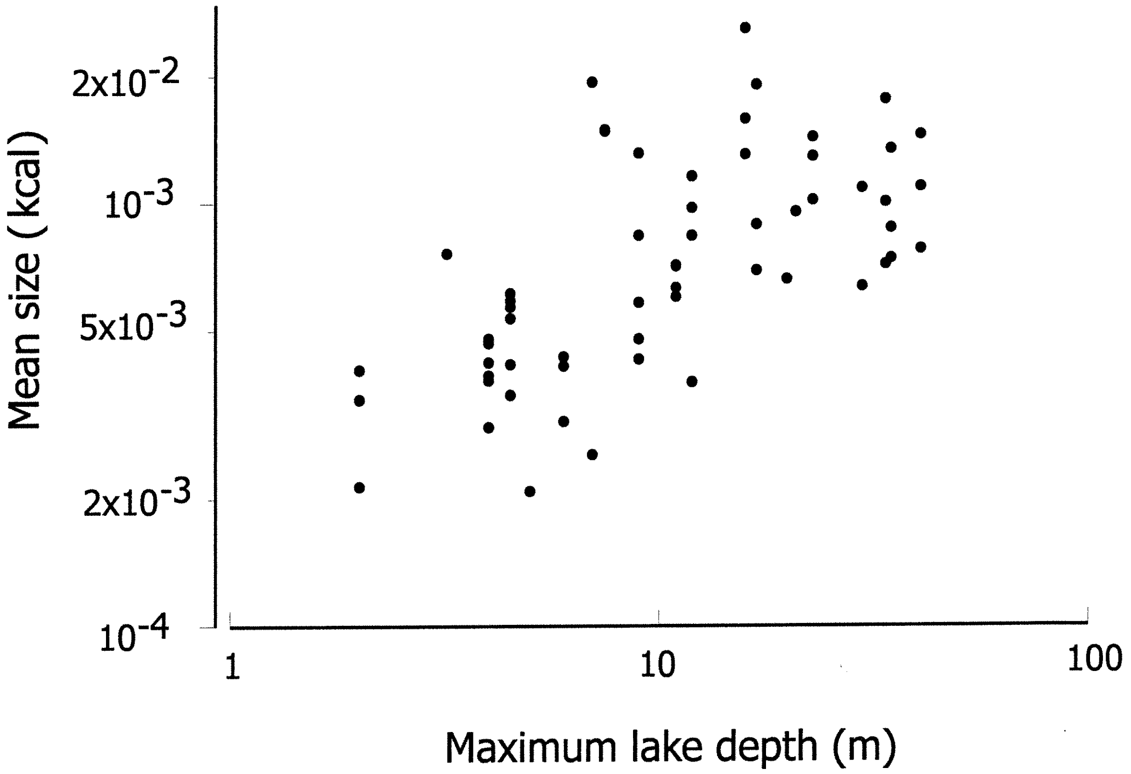

Figure 5.3. Mean body size of zooplankton (in kcal equivalents) as a function of the maximum depth of a lake. Samples taken from the Québec Laurentian lakes during the ice-free season. Each sample represents one sampling date. A total of 30 lakes were studied.

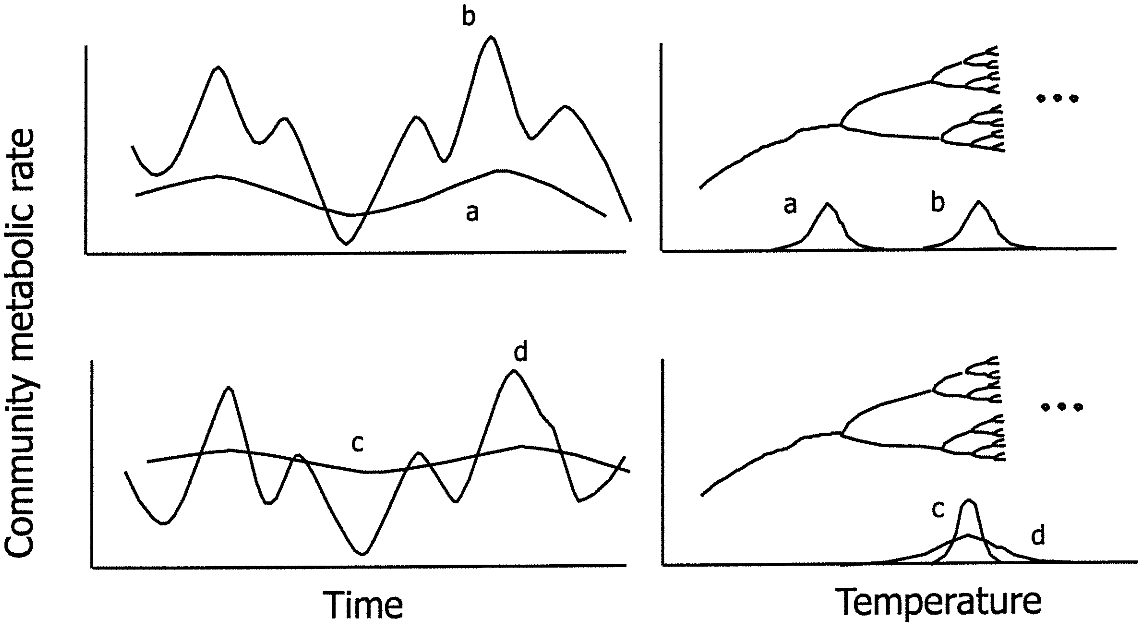

Figure 5.4. Community respiration as a function of the probability distribution of temperatures. The first comparison, (a) vs. (b), contrasts magnitude effects upon the dynamical variation of community respiration (*e.g.*, Arctic vs. Equatorial). The second comparison, (c) vs. (d), contrasts variability effects upon the dynamics of community respiration (*e.g.*, mainland vs. island or large volume lake vs. small volume lake). Systems (b) and (d), in exhibiting greater dynamical variation, may be able to sustain a greater diversity of life history strategies and biodiversity in general. However, see discussions on the importance of "resistance" and "adaptability" in Chapters 4 and 6.

— Chapter 6 —

SYNTHESIS

When the sound and wholesome nature of man acts as an entirety, when he feels himself in the world as in a grand, beautiful, worthy and worthwhile whole, when this harmonious comfort affords him a pure, untrammelled delight: then the universe, if it could be sensible of itself, would shout for joy at having attained its goal and wonder at the pinnacle of its own essence and evolution. For what end is served by all the expenditure of suns and planets and moons, of stars and Milky Ways, of comets and nebula, of worlds evolving and passing away, if at last a happy man does not involuntarily rejoice in his existence?

Goethe (1805; translated by Hollingdale 1969:30)

ABSTRACT

In this concluding chapter, we review the results, elaborate and extend the major implications that emerge from a thermodynamic analysis, and synthesise them into a coherent body of ideas that may be used to describe and analyse living systems. The sequence of ideas presented in this chapter follows in rough order that of the preceding chapters.

First we begin with a phenomenological, scale-free, thermodynamic approach to study the relationship between size and abundance of organisms because of its power to go beyond the (1) spatial, temporal and organisational complexities of living systems, and (2) the intrinsic circularity of ecological concepts. The result was an understanding of why these patterns are observed in so many different systems (Chapter 2)—it is a fractal-like characteristic of energy-dissipating systems that are spatially, temporally and organisationally complex. In fact, the size-abundance relationship indicates that ecological systems may be considered a subset of "critically self-organised systems". The empirically observed constraint in the range of the scaling exponent of the relationship (≈ -1) was found to coincide with the state where minor changes to the size structure of a system would result in rapid changes (*i.e.*, "critical") in total system-specific dissipation rates. As a result, the empirically observed range in parameter values of the scaling exponent seems to exist in the domain that may be called the most "adaptive" to global fluctuations in energy flow. This result supports Bak *et al.*'s (1989) original hypothesis that such self-organised "critical" systems may indeed demonstrate strong adaptive capacity.

The above results provide a theoretical and empirical rationale for the measure of perturbation via the R/B ratio. When examined in a network-thermodynamic context, it is explicitly shown that perturbations represent the influence of processes/interactions *external* to a system upon the processes/interactions *internal* to it. The balance between these *internal* and *external* processes/interactions is explicitly shown to be the consequence of two antagonistic thermodynamic principles that themselves derive from a scale-dependent asymmetry of the action of the Second Law of thermodynamics: *local-order* vs. *local-disorder*. These relationships are detailed.

In the face of a continuum in the degree of uncertainty between system-environment interactions, there exist two strategies that allow the persistence of a system: resilience (rapid response) or resistance (buffer and dampen) to uncertainties in system-environment interactions. An optimal balance or trade-off between these two strategies may exist that depends upon the specifics of the type of system-environment interactions (*i.e.*, its perturbation regime, or more generally, its dominant gradient). This optimal balance may be termed the "*Most adaptive state*". The capacity to adapt in the face of uncertainty in system-environment interactions, well known by evolutionary biologists as the "*Red Queen's hypothesis*", is argued to be the fundamental concept that integrates our understanding of complex living systems.

PERTURBATION

The power of the thermodynamic approach is the formulation of processes and patterns in terms of "potential" functions (*i.e.,* gradients, and their eventual dissipation). This allows us to ask, "How *should* a system change?" Remembering this focus upon "potentials", we may define the degree of perturbation as:

$$(1) \qquad \text{Degree of perturbation} = \Psi\,(\,\text{observed}\,\{U\} - \text{expected}\,\{U\}\,)$$

a function, Ψ of the difference between the observed and expected ecological state of a system that are thermodynamically relevant, U. Any deviations from the expected {U}, represents a "potential" function (in the physical sense) that should decrease with time. In Chapters 2 and 3, we suggested that U may be defined by the set:

(2) U = {Respiration, Biomass}

In particular, the ratio of these two state variables, the R/B ratio, represents a key thermodynamic index—the intensity of entropy production. This index has the very useful characteristic of decreasing with time, due to the Second Law of thermodynamics. In the thesis, this characteristic was argued to be usefully represented by the "least specific dissipation" (LSD) principle of Prigogine (1955), an extension of the Second Law to systems open to energy flows, where linearity assumptions are appropriate between energy gradients and flows (Chapters 2, 3):

> *[The least specific dissipation principle] indicates the direction of evolution of a thermodynamic system kept out of equilibrium by weak and constant forces. As the system is not allowed to reach the ideal state of minimum dissipation, that is of maximum and constant entropy, it chooses the next best alternative and remains in a state of minimum [specific] dissipation or minimum [specific] entropy production"*
>
> *Babloyantz (1986:113)*

This intensity of entropy production is an index of the intensity of biological activity, much as temperature is an index of the intensity of molecular activity (see below). This index is directly related to the patterns of size-abundance due to the very strong allometric scaling of respiration rates. When examined via randomisation methods in the range of naturally observed size-abundance patterns, the mass-specific respiration rates were found to approach a minimum with scaling exponents > -1 (Figure 2.6). This means that change in the direction of less negative scaling exponents (*i.e.*, of ever decreasing intensity of biological activity or increases in the numbers of larger-sized organisms) are thermodynamically favoured, regardless of the spatial, temporal or organisational scale of the focal system.

This thermodynamic tendency towards ever decreasing intensity of biological activity (*i.e.*, low R/B ratios; large average size; or as it was also called in Chapter 3, enhanced local-order), embodied in the LSD principle is opposed by the effect of environmental uncertainty stemming from interactions with other systems, sub-systems and super-systems (*i.e.*, perturbations, stressors; the degradative action of the Second Law of Thermodynamics via the OTF scenario, in Chapter 2; or "local-disorder" in Chapter 3). The empirically observed exponent of the size-abundance relationship is in a dynamic quasi-steady state that is modulated by the antagonistic interplay between the action of the LSD principle (local-order) and the OTF scenario arising out of perturbations (local-disorder). The result of these antagonistic interactions between *internal* and *external* processes are more commonly known as "successional" change in community ecology (*i.e.*, the balance between *internal* growth and *external* perturbations); and K- and r-type life history selection in population ecology (*i.e.*, the balance between *internal* growth causing a "stable" age, size and reproductive structures vs. *external* perturbations causing "variable" size and age structures).

Empirical tests of the utility of this integrated index of the perturbation regime were attempted by comparing the R/B ratio to dominant abiotic indices of a system's sensitivity to perturbations. Due to the complex nature of real systems, isolating a single factor is difficult unless the perturbation is dominant. The size of a lake was chosen as such a dominant characteristic. The assumption being that the larger a lake, the less sensitive it is to perturbations. This represents a relatively straightforward assumption, as large lakes are simply more robust to fluctuations due to statistical size-volume averaging effects (*e.g.*, temperature fluctuations, chemical change). Thus, lower R/B ratios were expected in larger lakes; this prediction was confirmed in Chapter 2, indicating that the thermodynamic index (the R/B ratio) may be a functional measure of the degree of perturbation of a system.

SELF-ORGANISED CRITICAL SYSTEMS

Iterated local interactions (*e.g.*, continuously repeated rule based interactions between organisms—predation, parasitism, competition, commensalism, mutualism, *etc.*) produce spatial/temporal/organisational patterns that are self-similar at all scales and are known as "*fractals*" (Mandelbrot 1967, Schroeder 1991). Self-organised critical (SOC) systems represent an important class of fractals that are characterised by the power scaling of the frequency of energy-dissipating events as a function of the magnitude of energy-dissipating events. The size-abundance relationship represents such a fractal-like pattern (Chapter 2). This is because the individualistic interactions between organisms (predation, parasitism, competition, commensalism, mutualism, *etc.*) produce the size-abundance pattern, found at all spatial, temporal and organisational scales. Further, the allometric scaling of metabolic rates makes it possible to interpret the size-abundance relationship as a magnitude of metabolic rate vs. frequency of metabolic rate relationship. Because of this simple relationship, ecological systems may be considered to be a member of the set of SOC systems:

$$(3) \qquad \{\text{Ecological systems}\} \subset \{\text{Self-Organised Critical Systems}\}$$

This relation is important because SOC systems are known to have some key traits whose ecological implications are intuitive and important: (a) SOC systems are macroscopically near some quasi-steady state of energy inputs and outputs; (b) the degree of perturbation from this steady state may be measured as (1 minus the coefficient of determination of a log-linear fit of the size-abundance relationship); (c) the intrinsic complexities of the interactions involved make predictions possible only in a probabilistic sense; and (d) most controversially, SOC systems are "adaptive" systems (see below).

The size-abundance relationship delimits the approximate upper bound in the numerical carrying capacity of organisms, an upper bound that is a log-linear function of organism size. Any deviations from such a log-linear state may be expected to return to this fractal-like attractive state (if indeed this represents an SOC-type pattern). The relative deviation from this state (*i.e.*, 1 minus the coefficient of determination of the log-linear relationship) is therefore a potential measure of the relative degree of perturbation in a given system. This index was found to correspond well with the thermodynamic index of perturbation (the R/B ratio). That the results of the (near-linear, non-equilibrium) thermodynamic analysis are complementary to the SOC analysis is a very interesting finding; it implies an intimate relationship between these two approaches that have previously developed independently.

While such systems are robustly stable in the statistical sense, there is an indeterminacy (*i.e.*, non-proportionate relationship) between the magnitude of any specific cause and its effects. Even the smallest of perturbations can create an "avalanche" of cascading effects at all spatial, temporal and organisational scales. This indeterminacy between the magnitude of a cause and its effect is due to the sensitivity to initial conditions found in complex (pseudo-nonlinear and nonlinear) dissipative systems. A simple biological example of this indeterminacy is the uncertain effect of invading species, the lag before a massive population explosion of invading species, or the unpredictable occurrence of pest and disease outbreaks (*e.g.*, spruce budworm, influenza, measles, the plague).

Finally, SOC systems have been said to be poised near a state where rapid adaptive change is possible. Chapter 2 showed how the rates of total community energy dissipation change exponentially for slopes ≈ -1. That is, the system exists near a state where rapid changes in energy dissipation rates are possible with small changes in the scaling exponent, or more simply, in a state of most “adaptability” (Conrad 1983). Globally, this allows the system to rapidly adapt to variations (uncertainties) in energy inflow and outflow (Rosen 1967:105-108). That is, fluctuations in energy influxes or deficits are rapidly relaxed, resulting in the macroscopic pattern of a steady state that we can identify in the size-abundance relationship.

LOCAL-ORDER VS. LOCAL-DISORDER

When the spatial, temporal and organisational complexities of systems are explicitly addressed in a network thermodynamic context (Chapter 3), the R/B ratio (storage-specific dissipation) was shown to represent an index of the relative balance between the principles of "local-order" (*i.e.*, the indirect action of the Second Law upon a focal system $x^{(0)}$; "negentropy" of Schrödinger (1945); LSD of Prigogine (1947)) and "local-disorder" (*i.e.*, the direct action of the Second Law upon all systems). The balance between these two antagonistic principles, where the processes internal to a system (growth and development) are in some quasi-steady state with the processes external it (exploitative or perturbing influences).

Any system can thus be characterised by a mean and variance of the R/B ratio (*e.g.*, a lake measured repeatedly over time). When local-disorder (perturbing, external influences) dominates, the R/B ratio is elevated and so may be said to be in a state of greater "uncertainty". When local-order dominates (internal processes), the R/B ratio is reduced; such a system may be said to be in a state of lesser "uncertainty". When the magnitude of the R/B (the intensity of energy dissipation) is large, the assumed linear relationship between the gradients and the flows becomes less reliable. This means that the intrinsic pseudo-nonlinearities and nonlinearities of system dynamics may be expected to become more dominant and that a classic bifurcation sequence of the attractive states of (U) may be expected as the R/B ratio increases (Figure 3.3)—*i.e.*, greater uncertainty.

The immediate consequence of any alterations/manipulations (*e.g.*, nutrient enrichment) to a system is to disturb the balance between local-order and local-disorder, which has the effect of increasing the uncertainty of the relations between all systems (across all hierarchical levels). Thus, the paradox of enrichment (that enrichment increases dynamical uncertainty) may be expected, <u>in the short term</u> (ecological scales). However, <u>in the long term</u> (evolutionary scales), it was also shown how such manipulations that increase the relative storage (biomass) of a given system could represent a stabilising influence for that system, in that the buffering capacity of the system also increases (see below).

These results are directly applicable to our current struggle to search for a functional example of sustainable exploitation/growth, the current incarnation of the concept of maximum sustainable yield. Maximum sustainable exploitation/growth represents our desire to exploit natural resources as much as possible while simultaneously maintaining these resources for future exploitation (and the currently dominant socio-economic system). As such, it represents an extension of the paradox of enrichment, but to more realistic (complex) situations where many interacting factors are at play. In such a context, the search for "sustainable exploitation/growth" represents a search for the removal of any future uncertainties in the availability of resources—a search destined to have the same result as that for a perpetual motion machine. This is because the very act of exploitation is a destabilising influence that increases the uncertainty of the whole dynamical system. Thus, the term "sustainable exploitation" is an oxymoron.

However, sustainable exploitation as a guiding principle for structuring human interactions with its environment represents a more pragmatic stance—much as the search for a perpetual motion machine has helped develop more efficient engines, so too might the search for sustainable exploitation also help develop more efficient human exploitation of our environment, such that some of the uncertainty associated with our exploitative practices may be reduced. This of course is possible only when all interacting systems become adapted to such relationships. Adaptive responses being on the scale of evolutionary (conservative estimate) to ecological time (optimistic estimate), the rate and extent of human/economic exploitation must be reduced to explicitly account for these much slower processes.

DEALING WITH UNCERTAINTY: RESILIENCE AND RESISTANCE

There exist two main strategies in the face of uncertainty (*e.g.*, Rosen 1967:166-169; Holling 1973). One is to respond rapidly to the various manifestations of uncertainty; the other is to resist them. In the evolutionary biology literature, these are known respectively as, the "scramble" strategy—to take advantage of available resources as much as possible because you will never see them again (*e.g.*, the dominant human strategy), and the "hedge-betting" strategy—to tide over or adsorb environmental fluctuations, waiting for a better day (*e.g.*, turtles). In the ecological literature, the former strategy has dominated over the latter as a mechanism advocated to explain the reduction of uncertainty (and has even become almost synonymous with the concept of "stability"; DeAngelis 1980, 1992). Unfortunately, numerous terms have been used to represent these concepts. We used "resilience" to represent the strategy of rapid response because it has gained strong associations with the largest eigenvalue of the community matrix as a measure of the "return time" to some local steady state, after minor fluctuations (system-environment uncertainty). We used "resistance" to signify the strategy of the hedge-better for the reason that it corresponds to the capacity of a system to adsorb and resist environmental fluctuations (system-environment uncertainty).

What is important is that in a thermodynamic context, the relevant state variables U = {respiration, biomass} may be used to quantify the degree of resilience and resistance attributable to any given system:

$$\text{(4)} \quad \text{Resilience} \quad \alpha \ \text{Respiration / Biomass}$$

$$\text{(5)} \quad \text{Resistance} \quad \alpha \ [\,\text{Respiration}^{2} + \text{Biomass}^{2}\,]^{1/2}$$

The dimensional relationship between respiration and biomass (Figures 4.4, 4.7) constrains resilience and resistance to be inversely related functions (units of biomass^{-1} vs. biomass^{1}, respectively; see also Chapter 3). This inverse relationship is important because it is only at some compromised, intermediate level of resistance and resilience that a given system may be said to be the most adaptable to environmental fluctuations: When resilience is too great, the system is too prone to extreme (magnitude and frequency) environmental fluctuations (*i.e.,* there is not enough resistance to environmental fluctuations). The consequence of this is to increase the dynamical uncertainty of such systems (*e.g.*, leading to elevated rates of local extinctions and invasions). When resistance is too great, the capacity to track/follow environmental fluctuations is decreased (*i.e.*, not enough resilience to respond to environmental fluctuations). That is, the responsiveness to perturbations is inadequate (too slow, too rigid) for the system's integrity to be maintained.

ADAPTABILITY IN THE FACE OF UNCERTAINTY: THE RED QUEEN'S HYPOTHESIS

In the previous section, we argued that systems of intermediate resilience and resistance represent the most adaptive configuration for systems that are continuously being perturbed/disrupted, due to the embedded nature of their interactions in the web of life. This concept of adaptability is of course one of the central foundations of evolutionary biology (*e.g.*, Lamarck, Darwin, Wallace) which has since been re-expressed in an alternate context as the "Red Queen's hypothesis" by Van Valen (1976; see also Holling 1973). The hypothesis refers to the Red Queen in Lewis Caroll's, "Alice in wonderland", who had to keep running to stay still. That is, due to uncertainties in system-supersystem (*i.e.*, system-environment) interactions, one must continue to adapt to stay in the game of life.

We are thus arguing that the point of balance between the principles of local-order and local-disorder, determines the nature of the trade-off between resilience and resistance, and is measurable via the R/B ratio. What is intriguing is whether this point of balance also coincides with the "critical" aspect of SOC systems. By "critical", Bak *et al.* (1989) referred to the manner in which the spatio-temporal auto-correlation function goes to infinity near the steady state (*i.e.,* when the size-abundance relationship approaches the log-linear form, with exponent ≈ –1). This means that spatially or temporally local interactions have consequences that are non-local—*i.e.,* spatially, temporally, and organisationally co-ordinated on a global scale. This was taken to mean that such systems were most adaptive to fluctuations in energy input/output in that they may be more rapidly relaxed. Results of randomisations (Chapter 2) indicate that indeed this may be the case as the rate of change of the R/B ratio (with respect to the exponent of the size-abundance relationship) is indeed maximal near the state where most natural systems exist (exponent ≈ –1).

THE INFLUENCE OF DIVERSITY UPON UNCERTAINTY

There exists a long tradition of biological thought that has attributed biological diversity (*i.e.*, species richness) with the capacity to modulate the stability characteristics of ecological systems (Chapter 4). Exactly what this influence may be has however been a matter of contention.

We hypothesised in Chapter 4 that the number of organisational units (*e.g.*, species richness) may be included as another biological state variable:

$$\text{(6)} \qquad U = \{\text{respiration, biomass, diversity}\}$$

As with the case of U = {respiration, biomass} of equation 2, the degree of perturbation (or uncertainty) may be said to be proportional to the deviation from the expected {U}, except that it is now a system with 3 state variables (equation 6). A greater deviation from the expected {U} represents a greater potential for change and therefore a more unstable or uncertain system.

A first approximation of such an expected {U}, that is its "attractive set", was attempted in Chapter 4. The precision and resolution of the data currently available for such an approximation remain far from being completely satisfactory; however, the potential of such an approach is still apparent. For example, a given spatial-temporal-organisational system may be said to exist in a 3-dimensional region {U*}, from equation 6. The distance of the centroid of such a system to the global attractor represents an index of the global instability of the system, in that the greater the distance, the greater is the potential for change in that system (see Figure 4.7). Within the 3-dimensional region {U*}, the relative distance of a system to its centroid may be said to represent the local instability of the system, in that the greater the distance from the centroid, the more deviant it is from the average behaviour of the system and so again, the greater the potential for change of the system (Figure 4.7). Immediately we can see that changes that increase the local stability of the system can at times be antagonistic to the global stability of the system.

Changes in the number of species found in a system can alter the distance from the expected state and so also the degree of perturbation of a system. Exactly how such changes will influence the degree of perturbation of a system is of course dependent upon the prior state of that system. If the prior state were depauperate of species (relative to what is expected), increases in diversity would only make it more stable and more probable. Thus, the question of how diversity influences the stability of a system represents the constraint where {respiration, biomass} are invariant with only {diversity} free to change. In reality, this is an unrealistic constraint as all state variables are free to change.

RAPID CLIMATE CHANGE

The possibility of rapid global climate change represents a looming reminder of the ephemeral nature of our existence and of the environment in which we exist. The potential effects of such an over-powering source of system-environment uncertainty represents a compelling issue that begs for an examination.

In Chapter 3, it was argued that the balance between the principles of local-order and local-disorder may be indexed by the R/B ratio. When local-disorder dominates, such a system is said to be a perturbed system. When local-order dominates, such a system is said to be a less perturbed system. This generalisation is important because it applies to any system, regardless of its spatial, temporal and organisational scale. As a result, we may identify with any given system a mean and variance of the U = {respiration, biomass, (diversity)} that characterises its average or "expected" behaviour, where {(diversity)} is here treated as a passive state variable. The question that was asked was: How does temperature influence the R/B ratio, at a variety of different spatial, temporal and organisational scales (and as a consequence the biological diversity of systems)?

In physical systems, the "temperature" of a system is an index of the average kinetic energy of molecules (or, in terms of velocity, temperature α root mean square molecular velocity). The R/B ratio is an analogous index of the average kinetic energy of biological systems (*i.e.*, the "velocity" of dissipative energy flows in biological systems). It is in fact very well known that the intensity of metabolic activity at the physiological level increases with temperature, within given bounds (Klieber 1961, Lin 1995). Thus, any increases in the magnitude of temperature will have a relatively straightforward effect of an increase in the R/B ratio. This was empirically verified and referred to as a "magnitude effect".

However, there exist fluctuations of temperature across various space-time scales (hourly, daily, yearly, decadal, and larger). Such fluctuations were referred to as "variance effects" in that they describe the influence of environmental variability/uncertainty upon the R/B ratio. It was argued that variance effects (*i.e.*, environmental uncertainty) will increase the R/B ratio at the level of ecological communities, much as physiological uncertainty ("stress") will also increase the physiological R/B ratio, or at the population/cohort level, environmental uncertainty will increase the R/B ratio (and decrease its inverse correlates, the size and age structure) of organisms. This argument is supported by the results of Chapters 2 to 4 and the anecdotal information presented in Chapter 5.

The importance of the R/B ratio is that elevated intensities of metabolic activity (high R/B ratios) coincide with elevated dynamical and structural variability. This was demonstrated theoretically and empirically (see Chapters 2 and 3). When placed in such a context, we can see that global climate change can be seen to have local and global repercussions upon the stability of systems. Locally (that is, in the smaller spatial-temporal-organisational scales of ecological systems), the uncertainty of the system is increasing (elevated R/B ratios) due to climate change, via both magnitude and variability effects. However, globally (in the long term, evolutionary scale), both the respiration rate and the standing biomass increase as a function of the temperature. As biomass increases faster than respiration rates (Figures 4.2B, 4.4B and 4.7), a reduced R/B ratio may be expected at elevated temperatures, and an associated decrease in the dynamical uncertainty, <u>over the long term</u> (as the system approaches the globally attractive state). In other words, global climate change can be seen as another but more global manifestation of the paradox of enrichment.

Associated with such changes (*i.e.,* an increase in the energy richness, of systems) over the long run, species richness may also be expected to increase, as shown by the nature of the global attractor U={respiration, biomass, diversity} in Figures 4.4 and 4.6. We re-emphasise that such changes to the biological diversity are expected on the scale of evolutionary processes. In the shorter term, greater variability in extinction/extirpation and speciation/immigration rates may be expected. That is, greater dynamical and structural uncertainty is expected until the new attractive state is approached. Any desire to maintain such systems in a pseudo-static state (such as our desire to preserve the same community composition even in the face of large-scale changes, caused by humans or otherwise) represents a cause that would require enormous expenditures of energy to maintain such a mal-adapted system.

Seen in such a fashion, increased local uncertainty (in the short term) may even be said to serve as a mechanism to arrive more rapidly upon a new and more adaptive and therefore globally more stable state. This is because local uncertainty provides a source of "novelty", much as mutations and genetic recombination provides novelty in the Red Queen's game of life.

FUTURE DIRECTIONS

There are of course many ideas that need further refinement, exploration and empirical development. Most notably, the magnitudes and variations in values of the L, X and J, that is, the phenomenological coefficients, gradients and flows of real ecological systems must be characterised (Chapter 3). Simulation studies on such networks are another avenue of research that would allow a more robust appreciation of the stability characteristics of such systems and to verify that indeed such networks will follow SOC dynamics; this is especially case in the context of the diversity-stability relationships that were predicted in Chapter 4. There also exists a possibility of linking these results with the relative abundance/rarity of organisms, known as abundance-frequency relationships (*e.g.*, the broken stick distribution, *etc.*).

Finally, the maintenance or enhancement of the integrity or "health" of ecological systems has become another major principle for the guidance of human activities. However, what integrity really means and how it may be measured is quite uncertain. There is promise in the results of this thesis that hints to a clarification of this concept. This is because it is possible to numerically delineate the "average" behaviour of ecological systems using our thermodynamic approach and so with time (*i.e.*, more data) express a probability level for the degree of deviation from this average behaviour. These are future directions of research that hold much promise.

CONCLUSIONS

The mutually complementary nature of the results that have been examined throughout the body of this work illustrates the potential of a scale-free, thermodynamic approach to usefully go beyond the traditional limitations imposed by the spatial, temporal and organisational complexities of real systems and the self-referential (circular) nature of ecological concepts. This utility was shown by the study of the patterns of size and abundance of organisms, from which it was determined that ecological networks may be considered to be in some quasi-steady state between two antagonistic principles: local-order and local-disorder. This antagonism was shown to be due to the asymmetric influence of the Second Law of thermodynamics in hierarchically organised systems. The realised point of balance between local-order and local-disorder was argued to represent a state of greatest adaptive capacity, in the face of continued system-environment uncertainty. This result was verified using a thermodynamic analysis of the stability of the size-abundance relationship, a result that is quite likely related to the adaptive characteristics of self-organised critical systems.

The practical results that emerge from this study are the clarification and justification of the indices of environmental uncertainty and as a consequence a more general concept of ecological stability. Such a measure was shown to be useful in the resolution of a variety of ecological questions, notably that of the relationship between biological diversity and stability which becomes a relatively simple one when viewed from this context. Further, the most adaptive state was suggested to correspond to a trade-off between resistance and resilience. This was argued to explain and synthesise the Intermediate disturbance and Intermediate productivity hypotheses of biological diversity. The paradox of enrichment was also shown to be quite general with the consequence that again some intermediate level of enrichment (and exploitation) may represent the most adaptive strategy for the human system, a strategy that may be considered the most sustainable case, in the face of system-environment uncertainty.

GLOSSARY OF KEY TERMS AND CONCEPTS

Adaptation—The process of change due to the interaction of *assertive* (internal; local-order) and *integrative* (external; global-order) tendencies.

Assertive tendencies—Empirically (phenomenologically), the tendency to self-assert, compete, separate, dominate, individuate, *etc.* and so increase the autonomous, modular, independent nature of holons (Koestler 1969). This is analogous to the *local-order* principle (Choi *et al.* 1999). See also *Most adaptive state.*

Complexity—The minimal amount of information needed to describe a system's structure (Komolgorov 1965). It is a notion that depends upon the number and intensity of interacting systems.

Emergy—The available energy [in joules, J] used directly and indirectly to make a service or product. Its unit is the emjoule [ej] (Odum 1996; the 'em' alluding to '*em*bodied'), and is dimensionally those of energy [ML^2T^{-2}]. Emergy, though having energy dimensions, is not a conservative quantity as it requires a reference state, much as exergy. This reference form is usually solar energy. Solar emergy is expressed in solar emjoules (sej), and related to other forms of energy by dimensionless stoichiometric coefficients, solar transformity, expressed in solar emjoules/joule (sej J^{-1}). Emergy does not "flow" along transfer pathways, nor is it "used up," "dissipated," or "lost in transfer."

Environ—Term introduced by Patten (1978, 1985) to describe, looking upward-outward, the incoming and outgoing environments of *holons* circumscribed by the boundaries of open systems in which the said holons are component parts. Input environs are afferent transactive networks extending in past time from the system input boundary to a component-level holon in the present, and output environs are efferent networks extending through future time from the component-level holon in the present to the system output boundary. Environ theory thus defines two system-bounded environments associated with each holon within the system, and is mathematically an ecological extension of economic input-output analysis. Environs are nested networks across levels of hierarchic and holarchic organization.

Environmental uncertainty—The lack of predictability of subject-environment interactions. While it is a relative concept (dependent upon the subject system of interest), pragmatically, it is an index of the lack of periodicity or regularity of environmental conditions, or more generally, the variability of environmental conditions (*i.e.*, perturbations). That is, in pragmatic usage, there is an implicit assumption of a "fixed" space-time-organisational frame of reference.

Exergy—Energy that can be used (*i.e.*, available) to do work. In chemical thermodynamic terms, it is useful *free energy* and has energy units and dimensions.

Unlike energy, however, exergy is not conserved because any unused energy fraction at any point in a system may always be used by a more efficient or qualitatively different process (*e.g.*, "technology").

Feedbacks—The return of information from a system that modifies its function. Feedbacks are generally categorised as being deviation amplifying (also "positive feedback"), and deviation reducing ("negative feedbacks"). In the ideal (simple) case, the former results in destabilisation and the latter in stabilisation of processes. These idealisations are called "feedback mechanisms" in the thesis, to distinguish from their "feedback effects" which represent the emergent consequences of complex and numerous direct and indirect feedback mechanisms. While the former are reductionistically deterministic in the ideal case (although non-linearities in behaviour limit such determinism), the latter are emergently probabilistic concepts.

Generalised thermodynamic feedback model—Any thermodynamically open system fluctuating about some local quasi-steady state experiences the following cycle of states:

1. (+) thermodynamic gradient =>
2. (+) thermodynamic flow =>
3. (–) thermodynamic gradient =>
4. (–) thermodynamic flow =>
5. (+) thermodynamic gradient => Step 1.

where, "=>" signifies "causes" or "leads to", in the thermodynamic sense (*i.e.*, probabilistically). The autocatalytic steps (1, 2) detail the formation of entropy creating "dissipative structures". Steps (3, 4) detail the "relaxation" (gradient breakdown) due to the action of "dissipative structures." The consequence of the action of "dissipative structures" (via OTF) is a thermodynamic local quasi-steady state where rate processes slow down as much as possible (*i.e.*, the LSD). It is thus a simple and general negative (stabilising) feedback cycle, applicable regardless of the scale or complexity of the system. This phenomenological feedback mechanism has also been recognised by Bertalanffy (1950), Ulanowicz and Hannon (1987), Schneider and Kay (1994) and many others as the LeChatelier-Braun principle.

Hierarchy—Term pertaining to levels of organization, usually defined as an epistemic property to simplify complexity. The question of whether hierarchies are "real" or only mental constructs is usually sidestepped and generally remains unresolved. Hierarchy models are well known in ecological literature (*e.g.*, Allen and Starr 1982; O'Neill *et al.* 1986) as the basis for such concepts as "scale" and "grain" expressed in terms of both space and time. Hierarchies of "*scale*" are nested (supersets, sets, subsets, ... *etc.*) whereas hierarchies of "*control*" (as in the military—generals, colonels, majors, lieutenants, ... *etc.*) are not.

Holarchy—Term pertaining to the nested structure of holons, as in *scale* hierarchies. Analogous to the term *hierarchy*, but created to remove from this the connotation of a lineal, chain-like order and thereby emphasize a more anarchistic or polyarchistic nature of across-scale organization (Koestler 1969, Regier and Kay 1996).

Holon—Term introduced by Koestler (1969) which is the juxtaposition of two concepts: *holos* (Greek for "whole") and *on* (suffix indicating a particle or part—*e.g.*, neutron, proton). A holon is a "Janus-faced" (two-way) open system, one that is simultaneously a whole (to its sub-systems, looking hierarchically downward-inward) and a part (in relation to its super-systems, looking upward-outward). See also *Most adaptive state.*

Information handling systems—Following the usage of Professor Henry Regier (University of Toronto, pers. comm.), many biological systems exhibit highly refined, context sensitive or non-linear controls over rate processes. These are more commonly known as catalysts and enzymes (accelerate rates) and poisons and inhibitors (decelerate rates). These controls are non-linear in that they have an effect that is not linearly proportional but rather accelerational or decelerational, and so allow a more rapid modulation of processes. Such refined information handling structures and their complexly embedded webs of interactions represent the essence of that which we call living systems. Variations in size-abundance patterns represent one such information handling/managing system (see especially Figure 2.6). Via the simple, *Generalised thermodynamic feedback model*, deviations from the steady state are "detected" and "corrected" by the activities of the biological system. When the net available free energy increases, there is an associated increase in the gradient in the system. Increased potential gradients tend to increase the intensity and the total energy lost from the system (*e.g.*, heat), which in turn dissipates the gradient, and in turn decreases the degradative outflows. The controlling/modulating mechanism may be seen in the form of the size-abundance relationship that can quickly accelerate or decelerate the flows through the ecological system. It represents a very sensitive phenomenological "processing valve" that quite effectively maintains a quasi-steady state. While specific organisms or classes of organisms may play even more refined roles in the modulation of energy flows, theirs are more context-specific mechanisms that require more in-depth study and so are consequently less generalisable.

Information overload—Concept attributable to David B. Brown (Department of Zoology, University of Toronto, Canada; R.I.C Hansell, pers. comm.). It describes the phenomenon of a system that becomes too saturated with information (*e.g.*, irregular, erratic, or mixed environmental signals or biotic interactions) to process it coherently. It responds incoherently, or breaks down and does not respond at all. Information overload forces an *adaptive* response; alternate or novel attractors (*e.g.*, phenotypes/genotypes, behaviours, species) are turned to as current ones become inviable.

Integrative tendencies—Empirically (phenomenologically), the tendency to integrate, diminish, or restrain the assertive tendencies of sub-systems in favour of the assertive tendencies of the super-system within which the holons are nested. This is analogous to the local-disorder principle (*i.e.*, interactive uncertainty or perturbational influences; Choi *et al.* 1999, Choi and Patten 2002). See also *Most adaptive state.*

Irreversibilities—Processes that contribute to entropy production. The term, "*Dissipation*" is used synonymously by Prigogine. The term, "*Degradation*" is used synonymously by Kay.

Least specific dissipation (LSD)—The intensity of entropy production *decreases* with time for systems that are near some local quasi-steady state (Onsager 1931a,b; Prigogine 1955). This quantity is usefully approximated by the ratio of respiration rate to biomass (R/B ratio; Choi *et al.* 1999) and more generally as the ratio of system boundary output to system storage (Fath *et al.* 2001).

Most adaptive state—Each holon is subject to *internal-assertive* tendencies and *external-integrative* tendencies. The negotiated *balance* between these tendencies (*i.e.*, a quasi-local steady state) was suggested by Koestler to be indicative of a "healthy" state ("adapted" in the thesis). An imbalance (*i.e.*, an over-exaggeration of the *Integrative* or the *Assertive*) was suggested to be a pathological state (*e.g.*, psychological disorders). As a system deviates further and further from such a balance, the degree of non-linearity of system dynamics is argued to increase and as a consequence, so also its likelihood of rapidly and adaptively finding (or "negotiating") a new balance. This meta-mechanism of finding a new balance is at the heart of this thesis.

Negentropic principle—Popularised by Schrödinger (1945), the tendency for living organisms to become more ordered and to maintain that order for a time (*i.e.*, decrease their local entropy; "*local-order*" in the thesis) against the universal pattern of the Second Law of Thermodynamics for order to be destroyed with time (entropy to increase; "*local-disorder*" in the thesis). Living organisms accomplish this apparently anti-entropic feat (locally) by actively "exporting" excess disorder at the expense of the universe (globally). That is, living systems "create" a local fluctuation or a local reversal in the global action of the Second Law of Thermodynamics. A simple physical example is the localised reversal of the directionality of currents in flowing waters (sometimes known as "eddy currents").

Order through fluctuation (OTF)—In the presence of a free-energy gradient, statistical asymmetries or inhomogeneities of free-energy densities become coherent flows of energy inside the system ("*organized structures*"; Glansdorff and Prigogine 1971; Nicolis and Prigogine 1977). As internal energy flows are never completely efficient (*i.e.*, the Second Law), they act as gradient dissipating structures.

Perturbation—Term used synominously with *Disturbance* to indicate an exterior phenomenon that affects the system and causing some system response. The biological response to environmental perturbations is suggested to be useful, *integrated* index of all such perturbations that are individually quite difficult to measure, let alone integrate.

Phenomenological—in the thermodynamic sense: that specific mechanisms responsible for a phenomenon may be numerous and varied but their empirical (macroscopic) patterns are still repeatable and generalisable.

Photorespiration—the immediate loss of photosynthetically fixed carbon due to enzymatic limitations during conditions of high O_2 and low CO_2 concentrations.

Respiration—The focus of the thesis is upon eco-physiological respiration rates—the combined metabolism of ensembles of interacting organisms (be they cohorts, subpopulations, populations, communities, landscapes, ecosystems, *etc.*). Regardless of scale, respiration has only one generally accepted meaning—the biochemical oxidation (*i.e.*, "catabolism") of organic molecules in plants and animals that provides biochemically useful free energy (generally in the form of high energy phosphate groups—ATP). Thus it represents a fundamentally biochemical/physiological concept. There are many ways of estimating respiration rates (*i.e.*, direct and indirect calorimetry) depending upon the specifics of the biochemical pathways involved. Generally, indirect methods of calorimetry are used due to the inherent difficulties of direct calorimetry of large, complex and motile systems (Swan 1975). Thus, indirect calorimetric methods measuring gas production (CO_2) or utilisation (O_2) are generally used to estimate waste heat production, using empirically derived conversion factors. Thus, all methods (some being more appropriate than others depending upon the specifics of the system concerned) attempt to quantify the metabolic transformation of free energy into waste heat. As such, while one is never directly measuring Exergy degradation, one obtains a practical index of the “irreversibilities” (*sensu* J.J. Kay; see Introduction). In the language of Network theory (*sensu* B.C. Patten; Appendix 2), these respiratory losses of free energy represent "boundary outflows" (waste heat) in that they do not return to the originating system. As such, respiration rates represent the rate of free energy lost permanently to the originating system, and the specific respiration rate represents the relative intensity of these losses attributable to the structure (the biomass of the originating system). When mass and energy/exergy flows exist, the accounting process becomes more complicated, in that there is the possibility of cycling of matter and energy (*e.g.*, urea, and other “wastes”), but respiration rates still represent the ultimate "boundary outflows" of useful free energy attributable to the originating system. That is, respiration rates do not cease to be a valid index of entropy production rates when there are other flows of energy/exergy/entropy/mass (*e.g.*, the wastes) as these flows are still part of the system until they are ultimately dissipated into “boundary outflows” of entropy via relevant transformational processes (*e.g.*, fossil fuel utilisation by humans, waste recycling, *etc*). Other forms of energy transfer such as radiative, conductive, convective and phase-change related heat losses/gains certainly may play an important part in the energy balance of organisms but their alterations always have an associated metabolic cost. It is these metabolic costs, these metabolically related irreversibilities that are the focus of this thesis.

Red Queen's Hypothesis—In *The Adventures of Alice in Wonderland*, the Red Queen said one must keep running just to remain in place. The "hypothesis" from evolutionary biology refers to the necessity of continuously adapting in the face of ever changing context to stay in the game of life (van Valen 1976; Choi *et al.* 1999; Choi and Patten 2002). In the face of ever-changing sets of interactions, the likelihood of continued existence is a function of trade-offs between refined information-handling capacity (specialization) to avoid disaster at one extreme, and flexibility (generalization) at the other extreme: to be opportunistic and able to rapidly capitalize on new signals or information and so cope with drastic changes in information content.

Second law analysis—The direct application of the Second Law of Thermodynamics to the analysis of energy transformations, generally in the context of cost and efficiency optimisations in engineering applications (Gaggioli 1980). The currency that is used in this mode of analysis is *exergy* (the available or useful free energy). As such, Second law analysis represents a detailed accounting of how processes alter the *quality* of energy. This is in contrast to a "First law analysis" that is a detailed accounting of the *quantity* of energy flows through systems. Thus, for example, the accounting of energy flows for a given food web such as those illustrated by Lindemann (1942) represents a First law analysis (*i.e.*, the conservation of energy). In contrast, Schneider and Kay's (1994) analysis of the change in the quality of high quality incoming solar energy (shortwave) to low quality outgoing radiation (longwave) as it passes through various ecosystems, represents a Second law analysis.

SOHO systems—An acronym for Self-regulating Open Holarchic Order systems (Regier and Kay 1996). The concept extends the holon concept to systems explicitly open to matter/energy/information exchange (though this is implicit in the two-way-looking faces of holons). The concept is referred by Bertalanffy's (1950, 1968) General Systems Theory and incorporates the empirical observation of self-organizational tendencies in such systems. The self-organizational property is generally attributed to the negative entropy concept of Schrödinger (1945).

Transformity—A dimensionless quotient of two energies or energy flows that serves as a stoichiometric coefficient relating the quantities involved. For example, the solar transformity is the ratio of the solar energy required to generate a product or service to the actual energy in that product of service. Transformities have the units of emergy/energy (sej J^{-1}). Transformities are system-specific because systems vary in both number and kind of external energy inputs and also in the connectance pattern and transformation efficiencies of their internal transfer pathways.

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— Appendix 1 —

LEAST SPECIFIC DISSIPATION

The Least specific dissipation principle is a thermodynamic criterion of evolution. It applies to systems that experience a weak and continuous energy gradient. Developed by Onsager (1931a,b), Prigogine (1955), Glansdorff and Prigogine (1971), Prigogine and Nicolis (1971), the principle specifies that any general energy dissipating system, in the face of a small but continued energy gradient, will tend towards a state of least specific energy dissipation. The proof of this principle is as follows:

The mass-specific rate of entropy change in a system (ds/dt) may be partitioned into two terms: the mass-specific rate of entropy production due to irreversible processes inside the system (i); and the mass-specific rate of entropy flow due to an exchange between the system and the external environment (e):

(1) $ds/dt = d_i s/dt + d_e s/dt$

The entropy production ($d_i s/dt$) cannot be directly measured, but it is constrained to be larger than 0, due to the Second Law of thermodynamics. There are no such constraints for the entropy flow ($d_e s/dt$) but it may be approximated by heat calorimetry as specific heat dissipation or simply as the ratio of community respiration to biomass (R/B ratio; see footnote 11 in Appendix 2C). The general observation that increased order is found in living systems may be attributed to the dominance of the entropy transferred to the environment over the entropy production inside the system (*i.e.*, $|d_e s/dt| > |d_i s/dt|$). This is found to be generally true except perhaps under extremely rapid periods of biological activity (Lurié and Wagensberg 1979; *e.g.*, the earliest stages of embryonic activity, or immediately after a large-scale perturbation) when $d_i s/dt$ can also be large due to intensive growth and differentiation. As one approaches some quasi-stationary (steady) state ($ds/dt \approx 0$), the entropy production may be approximated with greater validity by the entropy flow ($d_i s/dt \approx - d_e s/dt$; *i.e.*, the R/B ratio).

The specific entropy production ($d_i s/dt$) can be represented as the sum of the product of flows (J) and forces (X) for all irreversible biological processes (k):

$$(2) \qquad d_i s/dt = \Sigma_k (J_k / X_k)$$

The power series expansion of these flows (J) with respects to the forces (X) near some local steady state is given by:

$$\begin{aligned}(3) \qquad J_k(\{X_m\}) = J_k(0) &+ \Sigma_m (\partial J_k/\partial X_m)_0 X_m \\ &+ \tfrac{1}{2} \Sigma_{mn} (\partial^2 J_k/\partial X_m \partial X_n)_0 X_m X_n \\ &+ \text{higher order terms} \ldots\end{aligned}$$

which when linearised becomes:

$$(4) \qquad J_k = \Sigma_m L_{km} X_m$$

where, $L_{km} = (\partial J_k/\partial X_m)_0$ are the so-called "phenomenological coefficients". In the steady state with respect to variations in the forces (X), the cross coefficient are equal ($L_{km} = L_{mk}$) due to the so-called "Onsager reciprocal relations" (Onsager 1931a,b). The entropy production term of equation 2 thus becomes simplified to:

$$(5) \qquad d_i s/dt = \Sigma_{km} (L_{km} X_k X_m)$$

In the case of k=2 irreversible processes, equation 5 becomes:

$$(6) \qquad d_i s/dt = L_{11} X_1^2 + 2 L_{12} X_1 X_2 + L_{22} X_2^2 \geq 0$$

where $L_{12} = L_{21}$ due to the Onsager relation. The inequality $d_i s/dt > 0$ is due to the Second Law of thermodynamics. The derivative of the entropy production with respects to the force X_2 is:

$$(7) \qquad \partial (d_i s/dt) / \partial X_2 = 2 (L_{21} X_1 + L_{22} X_2) = 2 J_2$$

Since the system is near a steady state, $J_2 = 0$ and as $d_i s/dt \geq 0$, $d_i s/dt$ has an extremum which is a minimum. This means that the thermodynamic steady state of a system in the presence of a weak energy gradient is characterised by a local minimum in the specific rate of entropy production.

— *Appendix 2* —

ENVIRONS AND NETWORKS

A. DYNAMIC MODEL

Conservative (energy or matter) flows and storages within an n^{th} order dynamical system can be decomposed via differential or difference equations descriptions into n input environs or n output environs, where n is the number of intrasystem components whose storages (*e.g.*, biomass or energy density), x_k, k = 1, ..., n, serve as state variables. An n-component system has 2n environs within it. Half of these are output environs, propagating forward in time from boundary inputs (**z**) to boundary outputs:

$$\text{(1a)} \qquad d\mathbf{x}/dt = \mathbf{F}\,\mathbf{w} + \mathbf{z} = \mathbf{0} \qquad \text{(at steady state)}$$

The other half are input environs, traceable backward in time to boundary inputs from boundary outputs (**y**):

$$\text{(1b)} \qquad d\mathbf{x}/dt = -\mathbf{F}^{\mathbf{T}}\,\mathbf{w} - \mathbf{y} = \mathbf{0} \qquad \text{(at steady state)}$$

By boundary flows, we refer to the flows that do not go to other systems of the same hierarchical level but rather to environmental sources and sinks that represent the next larger hierarchical level of organisation (see Figure 3.1). A useful perspective is that boundary inputs originate output environs (1a) and boundary outputs are terminals of input environs (1b). Boldfaced symbols indicate matrices or vectors. The state vector is $\mathbf{x}^{(0)}_{nx1} = (x_k^{(-1)})$, with energy dimensions $[ML^2T^{-2}]$. Parenthesised superscripts will, when used, denote hierarchical level. For example, $\mathbf{x}^{(0)}$ above applies to the focal, whole-system level and $x_k^{(-1)}$ refers to this system's k'th component; a $^{(+1)}$ superscript would refer to the $\mathbf{x}^{(0)}$-system's environment. The first time derivative is $d\mathbf{x}/dt$, dimensioned $[ML^2T^{-3}]$; these dimensions denote power. $\mathbf{F}_{nxn} = (f_{kj})$ is a matrix of conservative energy flows $[ML^2T^{-3}]$ from components j to k, where j, k = 1, ..., n; the principal diagonal elements are corresponding total flows, or throughflows, through each component k: $f_{kk} = -T_k = -\sum_{j(\neq k)=1}^{n} f_{kj}$. $\mathbf{w}_{nx1} = (1_k)$ is a vector of ones [dimensionless, 1], and $\mathbf{0}_{nx1} = (0_k)$ a vector of zeros (with power dimensions). $\mathbf{z}_{nx1} = (z_k)$ is a vector of boundary inputs, with dimensions of power $[ML^2\,T^{-3}]$. $\mathbf{y}_{nx1} = (y_k)$ is a vector of boundary outputs, also dimensioned $[ML^2T^{-3}]$.

B. ENVIRON THEORY

In the theory of environs, which defines environments as interactive networks, every open system at any level of organization has associated with it two environments, one afferent (input environment, derived from equation 1b) and the other efferent (output environment, derived from equation 1a). These two environments together with their defining system are, at any given moment, partition elements (*i.e.*, identifiers) of physical reality. This means that in the input environment of a system, at some present (or usually initial) time, resides an infinite regress of events and interactions receding backward to the beginning of time. These events and interactions are uniquely associated at that time with that system and none other. On the output side, a unique future of events and interactions is uniquely generated by the system moment by moment. These have their origins at that time with that system and none other. Thus, unique portions of both pasts and futures in the universe come to a focus on each existent open system, and the three units together are inseparable, as given by the sufficient conditions of openness (for matter) and nonisolation (for energy).

The environments of component-level systems, say $x_k^{(-1)}$ (see Figure 3.7, where $k = \{1, 2\}$), can be traced within the boundaries of the focal-level systems, say $x_i^{(0)}$, in which they are members because it is these that are fully described by dynamical equations like (1a), and less frequently, (1b). In other words, the infinite regresses to past and future inherent in the concept of system-defined environments are truncated at the boundaries of the next-higher-level systems; the indefinite environments of $x_k^{(-1)}$, say, are cut off at the border of the encompassing system, $x_i^{(0)}$, and because this system is fully described (*e.g.*, equations 1a, b) so can be (as truncated "environs") its $k = 1, ..., n$ components' n input and n output environments, giving 2n environs in all. The sets of input environs of all the component parts within the entire system comprise a partition of the whole into n nonoverlapping units. Similarly, the set of output environs forms a second such partition.

Environs are explicit networks that carry energy and matter around the established circuits of ecosystems. Output environ analysis concerns the mapping of boundary inputs generated outside the whole-system level, $z_i^{(0)}$, into throughflows, $T_k^{(-1)}$, and storages, $x_k^{(-1)}$, associated with component-level systems. Input environ analysis backtraces boundary outputs, $y_i^{(0)}$, to their throughflows, $T_k^{(-1)}$, and storages, $x_k^{(-1)}$, of origins. In both cases it is the tracing over direct and indirect pathways in the intrasystem$^{(0)}$ network that is of interest because it reveals the importance of network indirect effects, as discussed in the Introduction.

For throughflow analysis, equations (1) are converted to the forms:

$$\begin{aligned} &(2a)\quad d\mathbf{x}/dt = \ \ (\mathbf{G} - \mathbf{I})\,\mathbf{T} + \mathbf{z} = \mathbf{0} &&\text{(at steady state)} \\ &(2b)\quad d\mathbf{x}/dt = -(\mathbf{G}' - \mathbf{I})\,\mathbf{T} - \mathbf{y} = \mathbf{0} &&\text{(at steady state)} \end{aligned}$$

where, $\mathbf{G}_{nxn} = (g_{kj}) = (f_{kj}/T_j)$, $\mathbf{G}'_{nxn} = (g_{kj}') = (f_{kj}/T_k)$, and $\mathbf{T}_{nx1} = (T_k)$ is the vector of throughflows; $\mathbf{I}$ is the identity matrix; $g_{kk} = g_{kk}' = 0$. Letting $\mathbf{N}_{nxn} = (\mathbf{I} - \mathbf{G})^{-1}$ and $\mathbf{N}'_{nxn} = (\mathbf{I} - \mathbf{G}')^{-1}$, the forward- and back-mappings of inputs and outputs, respectively, to throughflows are given by:

$$\begin{aligned} &(3a)\quad \mathbf{T} = (\mathbf{I} + \mathbf{G} + \mathbf{G}^2 + \dots + \mathbf{G}^m + \dots)\,\mathbf{z} = \mathbf{Nz} \\ &(3b)\quad \mathbf{T} = (\underbrace{\mathbf{I}}_{\substack{\text{boundary}\\ \text{inputs}\\ (m = 0)}} + \underbrace{\mathbf{G}'}_{\substack{\text{direct}\\ \text{flows}\\ (m = 1)}} + \underbrace{\mathbf{G}'^2 + \dots + \mathbf{G}'^m}_{\substack{\text{indirect}\\ \text{flows}\\ (m > 1)}} + \dots)\,\mathbf{y} = \mathbf{N'y} \end{aligned}$$

In both cases, in environs with well-developed networks, the sums of terms with powers m = 2 usually significantly exceed the direct-flow term, where m = 1. Throughflow-specific output environs are computed from **N**, and input environs from **N'**.

For storage analysis, equations (1) are converted to the forms:

(4a) $d\mathbf{x}/dt = \mathbf{Cx} + \mathbf{z} = \mathbf{0}$ (at steady state)
(4b) $d\mathbf{x}/dt = -\mathbf{C'x} - \mathbf{y} = \mathbf{0}$ (at steady state)

where $\mathbf{C}_{nxn} = (c_{kj}) = (f_{kj}/x_j)$, $\mathbf{C'}_{nxn} = (c_{kj}') = (f_{kj}/x_k)$, and $\mathbf{x}_{nx1} = (x_k)$ is the vector of storages; $c_{kk} = c_{kk}' = -\tau_k^{-1}$, the turnover rate of the k'th subsystem. Letting $\mathbf{Q}_{nxn} = -\mathbf{C}^{-1}$ and $\mathbf{Q'}_{nxn} = -\mathbf{C'}^{-1}$, the forward- and back-mappings of inputs and outputs, respectively, to throughflows are given by:

(5a) $\mathbf{x} = -\mathbf{C}^{-1}\,\mathbf{z}$
(5b) $\mathbf{x} = -\mathbf{C'}^{-1}\,\mathbf{y}$

Because $\mathbf{C}$ and $\mathbf{C'}$ are dimensional, $[T^{-1}]$, power series like (3a, b) cannot be formed. To achieve these, nondimensional coefficients are constructed as $\mathbf{P} = \mathbf{I} + \mathbf{C}\Delta t$ and $\mathbf{P'} = \mathbf{I} + \mathbf{C'}\Delta t$, where Δt is a discrete-time interval. Then, the (5a, b) mappings of inputs and outputs, respectively, into storages can be written:

(6a) $\mathbf{x} = (\mathbf{I} + \mathbf{P} + \mathbf{P}^2 + \ldots + \mathbf{P}^m + \ldots)\,\mathbf{z} = (\mathbf{Q}\Delta t)\,\mathbf{z}$
(6b) $\mathbf{x} = (\underbrace{\mathbf{I}}_{\substack{\text{boundary}\\ \text{inputs}\\ (m=0)}} + \underbrace{\mathbf{P'}}_{\substack{\text{direct}\\ \text{flows}\\ (m=1)}} + \underbrace{\mathbf{P'}^2 + \ldots + \mathbf{P'}^m + \ldots}_{\substack{\text{indirect}\\ \text{flows}\\ (m>1)}})\,\mathbf{y} = (\mathbf{Q'}\Delta t)\,\mathbf{y}$

As with throughflows, in environs with well-developed networks the sums of terms with powers m = 2 usually greatly exceed the direct-flow term, where m = 1. Storage-specific output environs are computed from **Q**, and input environs from **Q'**.

C. LINEARISED THERMODYNAMICS OF HEIRARCHICAL NETWORKS

To better understand the relevance of the Second Law to dynamical system networks, an algebra of needed concepts is presented below. Due to generality of the environ formalism, we will deviate from the standard thermodynamic approach by making no reference, suggestion, or assumption as to the reductionistic form of the transport and reaction processes involved (e. g., diffusion, heat flow, temperature change, electron or ion transport, *etc.*). We treat each system at any level as a complex set of reaction processes that are phenomenologically summarised in terms of their associated flows and gradients (also known as "forces"), and these relate to the dynamical equations. This amounts to a simple application of nonequilibrium, near-linear thermodynamics as developed and elaborated by Onsager 1931(a,b), De Donder and Van Rysselberghe 1936, Prigogine 1947, Spanner 1964, Katchalsky and Curran 1967, and Glansdorff and Prigogine 1971, among others.

Let S be the entropy of a system $x_i^{(0)}$, and dS/dt its rate of change. The storage-specific rate of change can be partitioned into two terms: entropy production by <u>int</u>ernal irreversible processes, $d_{int}S$, and boundary exchange of entropy between the system and its <u>ext</u>ernal environment, $d_{ext}S$:

(7) $dS/dt = d_{int}S/dt + d_{ext}S/dt$

The storage-specific rate of entropy production, $d_{int}S/xdt \equiv d_{int}s/dt$, cannot be measured directly, but it is constrained by the Second Law of Thermodynamics to be > 0. No such constraint exists for the specific rate of entropy flow, $d_{ext}S/xdt \equiv d_{ext}s/dt$. However, this quantity can be approximated by calorimetry[13] as storage-specific heat dissipation, $\sum_{k=1}^{n} y_k^{(-1)} \Big/ \sum_{k=1}^{n} x_k^{(-1)}$. For living systems, this latter quantity is conveniently measured as the ratio of respiration to biomass (R/B ratio; Choi *et al.* 1999).

Increased order in living systems is generally attributed to the dominance of entropy transferred to the environment over internal entropy production, $|d_{ext}S/dt| > |d_{int}S/dt|$. This is generally true except under periods of rapid biological activity (*e.g.*, early stages of embryonic development, or immediately after a strong perturbation; Lurié and Wagensberg 1979). Then, $d_{int}S/dt$ can also be large due to intensive growth and differentiation. The closer the approach to some <u>local</u> steady state, $dS/dt = 0$, such that from equation (7), $d_{int}S/dt = -d_{ext}S/dt$, the closer can specific entropy production due to irreversible processes within the system ($d_{int}s/dt$) be approximated by the specific rate of

---

[13] *Fundamentally, the relationship between entropy production (dS) and heat transfer (dQ) is: dS = dQ * 1/T; where T is temperature (Kelvin). Because of the influence of temperature, the measurement of metabolic waste heat production as index of entropy production ("dissipation",* sensu *Prigogine 1955; "irreversibilities",* sensu *Professor J.J. Kay, pers. comm., University of Waterloo) is truly valid when temperature is constant. In the range of application of the freshwater lakes studied in the thesis, temperatures ranged from about 10 to about 22 degrees Celsius at the surface. The maximum "error" attributable to these temperature variations represents an error of 1/(273+10) = 0.0035 to 1/(273+22) = 0.0034, or about 3% to 4% error. Relative to the methodological errors in the determination of respiration rates and field sampling errors (e.g., Appendix 3), this amounts to a negligible effect. What this means is that for most biological applications, the waste heat measured represents a pragmatic and easily measured index of entropy production rates ("irreversibility",* sensu *Kay).*

entropy flow to the exterior ($-d_{ext}s/dt$). (We emphasise that we are focussing upon a local (quasi) steady state, relevant to the characteristic space, time and organisational scales of the system being treated).

For each component-level (local) system, say $x_k^{(-1)}$ within a focal (global) system $x_i^{(0)}$, the net storage specific flow through the local system, J_k dimensioned $[T^{-1}]$, can be expressed as the sum of a function, F, of all the $j = 1, \ldots, n$ gradients, X_j, with which x_k directly or indirectly interacts (*e.g.*, see Figure 3.7). That is:

$$(8a) \qquad J_k = \sum_{j=1}^{n} F(X_j)$$

which, when linearised near some local steady state, gives:

$$(8b) \qquad J_k = L_{k1}X_1 + L_{k2}X_2 + L_{k3}X_3 + \ldots + L_{kk}X_k + \ldots + L_{kn}X_n$$

or more compactly,

$$(8c) \qquad J_k = \sum_{j=1}^{n} L_{kj}X_j$$

The L_{kj} parameters, termed phenomenological coefficients, represent empirically determined constants of proportionality for the relative influence of the gradients $X_j^{(-1)}$, for all $j=1, \ldots, n$ component-systems upon the flow $J_k^{(-1)}$ through component-system $x_k^{(-1)}$.

The gradients $X_j^{(-1)}$ may be represented as a function of their storage $x_j^{(-1)}$, which when linearised near the steady state, gives:

$$(9) \qquad X_j = k_j\, x_j$$

where k_j is a proportionality constant. Thus, when linearity assumptions are appropriate, the gradients X_j may be considered proportional to the storage x_j of a component-level system.

Using these quantities, the irreversible storage-specific dissipation rate, $d_{int}s^{(0)}/dt$, of the focal system $x_i^{(0)}$ may be represented as the sum of products of storage specific through flows, J_k, and gradients, X_k, for all k = 1, ..., n sets of irreversible processes making up the interior of the focal system:

$$(10a) \qquad d_{int}s^{(0)}/dt = \sum_{k=1}^{n} J_k X_k$$

Or, represented alternatively as a function of the gradients using equation (8c), the storage-specific dissipation rate of the overall system becomes the sum of products of the internal gradients, $(X_k X_j)$, and their cross-couplings (L_{kj}):

$$
\begin{aligned}
(10b) \qquad d_{int}s^{(0)}/dt = {} & L_{11} X_1^2 + L_{12} X_1X_2 + L_{13} X_1X_3 + \ldots + L_{1n} X_1X_n \\
& + L_{21} X_2X_1 + L_{22} X_2^2 + L_{23} X_2X_3 + \ldots + L_{2n} X_2X_n \\
& + L_{31} X_3X_1 + L_{32} X_3X_2 + L_{33} X_3^2 + \ldots + L_{3n} X_3X_n \\
& \qquad \ldots \\
& + L_{n1} X_nX_1 + L_{n2} X_nX_2 + L_{n3} X_nX_3 + \ldots + L_{nn} X_n^2
\end{aligned}
$$

In the neighbourhood of linear relations between the flows (J_k) and gradients (X_k), and given the applicability of Onsager's reciprocal relations, $L_{kj} = L_{jk}\ \forall j, k$, this simplifies to:

$$\text{(10c)}\quad d_{int}s^{(0)}/dt = \begin{array}{llll} L_{11}X_1^2 & + 2\,L_{12}X_1X_2 + 2\,L_{13}X_1X_3 + \ldots & + 2\,L_{1n}X_1X_n \\ & + L_{22}X_2^2 \quad + 2\,L_{23}X_2X_3 + \ldots & + 2\,L_{2n}X_2X_n \\ & \qquad\qquad + L_{33}X_3^2 \quad + \ldots & + 2\,L_{3n}X_3X_n \\ & & \ldots \\ & & + L_{nn}X_n^2 \end{array}$$

or more compactly:

$$\text{(10d)}\quad d_{int}s^{(0)}/dt = \sum_{k=1}^{n} \sum_{j=1}^{n} L_{kj}X_kX_j, \qquad \text{where } L_{kj} = L_{jk}\ \forall j, k$$

Alternately, by substitution with equation (9), we obtain an expression of the specific dissipation rate of the focal system in terms of the storage of the component-systems:

$$\text{(10e)}\quad d_{int}s^{(0)}/dt = \sum_{k=1}^{n} \sum_{j=1}^{n} L^{*}_{kj}x_kx_j$$

where $L^{*}_{kj} = L_{kj}\,k_j$ and $L^{*}_{kj} = L^{*}_{jk}\ \forall j, k$. These phenomenological coefficients L^{*}_{kj} are therefore analogous to the community (interaction) matrix of ecological communities in that they indicate the relative influence of one system upon another. The only difference being that the state variables, x, are represented as the storage (biomass) of systems and not the numerical abundance of species.

Because $d_{int}s^{(0)}/dt$ is constrained by the Second Law to be > 0, the following algebraic constraints upon the phenomenological coefficients may be recognised (*e.g.*, see Katchalsky and Curran 1967, p. 91):

1. $L^*_{kk}x_k^2 > 0$; all L_{kk} (interpreted as "conductivities", or "permeabilities") are positive-valued since any x_j can be made to vanish.
2. $L^*_{kk}L^*_{jj} > L_{kj}^2$; the magnitudes of cross-coupling coefficients, L^*_{kj} $(k \neq j)$, are limited by the magnitudes of the conjugate coefficients, L^*_{kk} and L^*_{jj}. This is because the determinant of the matrix, $\mathbf{L}^* = (L^*_{kj})$, of phenomenological coefficients must be greater than or equal to 0, det $\mathbf{L}^* \geq 0$.

Consider, for example (Figure 3.7), a two-system interaction within a focal system $x_i^{(0)}$, where there is a continuous flow through the primary subsystem $(x_1^{(-1)})$, and the other $(x_2^{(-1)})$ is at steady state: $J_2 = 0$; $X_2 = k_2x_2 = 0$. The specific dissipation rate for the whole system becomes (from equation 10a):

(11a) $d_{int}s^{(0)}/dt = J_1 X_1$; (because $J_2 = 0$)

or, in terms of storage:

(11b) $d_{int}s^{(0)}/dt = J_1 k_1 x_1$

and gradient X_2 becomes a simple function of gradient X_1 because of the coupling of the two systems expressed by the phenomenological coefficients L_{21} and L_{22} of the output environ of $x_1^{(-1)}$ to the input environ of $x_2^{(-1)}$:

(12a) $$J_2 = L_{22}X_2 + L_{21}X_1 = 0 \quad \Rightarrow \quad X_2 = -(L_{21}/L_{22})X_1$$

or, in terms of storage,

(12b) $$J_2 = L^*_{22}x_2 + L^*_{21}x_1 = 0 \quad \Rightarrow \quad x_2 = -(L^*_{21}/L^*_{22})x_1$$

This result is important in that it shows how the primary gradient, the storage x_1, "actively" displaces the secondary gradient x_2 away from the steady state (*i.e.*, "creates" storage) via the interaction coefficient L^*_{21}. This displacement is directly (and linearly) proportional to the magnitude of the primary gradient x_1, and consequently causes an "active" flow ($J_2 = 0 \Rightarrow J_2 \neq 0$) through system x_2. Indeed, what is especially interesting from the biological point of view is exactly when such "active" interactions moves a system to an ever increasing gradient (potential; *i.e.*, "aggradation"; Schrödinger 1945, Bertalanffy 1950, Spanner 1964, p. 261).

Due to the interaction between the two systems, the flow (J_1) is in turn reduced by an amount, $(L^*_{21}L^*_{12}/L^*_{22})x_1$, where $L^*_{11} \geq L^*_{21}L^*_{12}/L^*_{22}$ (property 2, above):

(13) $$J_1 = L^*_{11}x_1 + L^*_{12}x_2 = [L^*_{11} - (L^*_{21}L^*_{12}/L^*_{22})]\, x_1$$

but the total dissipation of the whole system actually increases by a factor x_1:

(14) $$d_{int}s^{(0)}/dt = [(L^*_{11} - (L^*_{21}L^*_{12}/L^*_{22})]\, x_1^2$$

This means that interactions with other component-systems can alter a system's local flow (J_2) and as a consequence, the global entropy production. Any useful (or "ordering") effect of such interactions increases as a linear function of the primary gradient (x_1; equation 13), while the total rate of energy dissipation of the focal system, $x_i^{(0)}$, increases as the square of the primary gradient (x_1^2; equation 14) rather than simply as a linear function (equation 11b). Thus, any linear increase of the "local-order" of a system $x_k^{(-1)}$ will be associated with a quadratically increasing "cost" in the dissipation of gradients of the global system $x_i^{(0)}$ (that is, “global-Disorder”). This means that the creation and maintenance of local-order can be considered a thermodynamic mechanism by which global gradients are dissipated in accordance with the Second Law.

However, this "local-order" is also subject to Second-Law degradation, in a hierarchically recursive manner: Second Law dissipation at level $x_i^{(0)}$ creates local gradients in $x_k^{(-1)}$ while simultaneously being subject to the Second-Law degradation of the gradient in $x_k^{(-1)}$, which in turn creates local gradients in $x_l^{(-2)}$, and so on, …, in a cascading sequence. There is therefore, a fundamental and cascading **asymmetry in the action of the Second Law** at different hierarchical levels.

— Appendix 3 —

METHODS OF ESTIMATING OF RESPIRATION AND PRODUCTION

In the following, some of the incubation methods of measurement of respiration and production are briefly reviewed. These quantities are important in that they shed light on large-scale autotrophic and heterotrophic metabolic activity.

In studies of pelagic systems, light-dark bottle incubations are the most commonly used means of measuring metabolic processes. However, the extrapolation of such small-scale incubations (300 mL bottles or smaller) to estimate lake-wide metabolic processes is extremely problematic for two main reasons. Firstly, such extrapolations are not tenable without an understanding of the spatio-temporal variations in these processes - a subject of study that is still not very well understood. Secondly, incubation chambers drastically change the hydrodynamic conditions of the plankton studied. Turbulent, convective and diffusive mixture modulates the ambient resource, light and temperature regimes, thus modifying the growth, mortality and metabolic activity of the natural planktonic community (De Vooys 1979). Reduction of turbulent mixing is particularly important as it results in rapid sedimentation of organisms within a bottle also constrains their presence at a constant depth regime. This results in photo-inhibition, photorespiration and self-shading in the bottles incubated near the surface (each of which can reduce carbon production by up to 50 %; Hall and Moll 1975). While this problem is circumvented in algae able to use HCO_3^- (as well as C4 plants), the vast majority of algae are C3 plants and unable to avoid this photo-respiratory loss of energy. Photo-inhibition (light shock) of algae from deeper waters can dramatically change the physiology of the algae and so also the photosynthetic rates (De Vooys 1979). The above problems associated with bottle incubations represent an important limiting factor in the quantification of community metabolic activity (Alvarez Cobelas and Rojo 1994).

In situ measurements promise to alleviate some of the above problems of incubation methods. The electron transport system (ETS) assay is one such method (Bamstedt 1980). It quantifies the enzyme activity of the terminal rate limiting step found in mitochondrial respiration: the co-enzyme Q-cytochrome B complex that delivers a free electron from the Krebs cycle (catabolism) to an electron receiver (O_2, NO_x, SO_4^{2-})—the oxidation of organic matter and the phosphorilation of ADP. Packard developed this method in 1971 and many variations of the method are now in use (*e.g.*, Owen and King 1975, Broberg 1985, del Giorgio 1992, Huovenin *et al.* 1994).

In ecology and physiology, it is a popular method because it is robust (*i.e.*, not sensitive) to handling stresses during sampling (del Giorgio 1992), requiring only short handling times (<20 minutes) and represents over 90% of all biological O_2 consumption (Toth *et al.* 1994) in the biosphere. The disadvantages to the method include the following: chemically intensive (and expensive) in that it uses of a large number of chemicals (16 in the original method) most of which require freshly (daily) prepared reagents (Packard 1971); time and equipment intensive (del Giorgio 1992); the use of empirically derived and variable correction factors to convert to oxygen units (the relationship between ETS activity and respiratory activity is modified by pH, temperature and the species examined, *e.g.*, Toth and Drits 1991, Toth *et al.* 1994); the subsequent conversion of oxygen to carbon units using variable respiratory and photosynthesis quotients (see above); and gives only respiration rates (production must be measured separately). Overall, the method offers a means of avoiding painstaking and error-ridden incubations but it is still too new and untested. Too many intermediate steps of conversion and correction are necessary to obtain a measure of carbon production rates. Thus, error rates may be high unless time and resource expensive calibrations are made very frequently.

The Winkler method (1888, in Wetzel and Likens 1991:70) is the most frequently used chemical method of measuring dissolved oxygen concentrations in the ecological literature. Dissolved oxygen is fixed by a reaction with manganous hydroxide, which reacts with iodide when acidified to produce an equimolar quantity of iodine. This iodine is titrated with sodium thiosulphate in the presence of starch. Many variations of the method exist, the most common being: azide (Alsterberg), permanganate (Rideal-Stewart) and Pomeroy-Kirschman-Alsterberg modifications are the most commonly used to control for other oxidising elements (*e.g.*, Fe^{3+}, organic matter).

The precision of this method is in the range of ± 0.05 mg L^{-1} to ± 0.02 mg L^{-1} (Wetzel and Likens 1991:71, 211). This translates to about ± 20 to 10 mg C m^{-3} in terms of the resolving power of the method. Strickland and Parsons (1972) indicate that the method is applicable for productivities between 3 to 2000 mg C m^{-3} hr^{-1}. This sensitivity is near the detectable limit for the less productive lakes found on the Canadian Shield (*e.g.*, see data in del Giorgio and Gasol 1995). Further precision may be gained using micro-Winkler techniques that utilise much smaller quantities of reagents. Longer incubations are problematic due to the recycling of O_2. The advantage of this method is that it is very well established and simple. The disadvantages of this method include: time consuming titrations; incubations and associated bottle effects; and the ~~use of~~ use of conversion factors (respiratory and photosynthetic quotients) to obtain carbon units.

Another potential method is the use of oxygen sensitive electrodes (platinum anode and gold-plated cathode). They are an extremely rapid means of measuring dissolved oxygen concentrations. Such polarographic sensors are surrounded by an electrolyte solution and housed by an oxygen permeable membrane. When oxygen diffuses into the electrolyte solution, a current is produced that is proportional to the concentration of oxygen in the water. Their drawbacks are that their sensitivity is limited by the need to continuously replenish the oxygen near the electrodes by a rapid flow of water across the membranes. Further, sensitivities of most electrodes below 1 mg L^{-1} are unreliable. Precision ranges from ± 0.2 to 0.001 mg L^{-1}, depending upon the price of the model. The substantially higher sensitivities of the more expensive meters are accomplished with the use of smaller microelectrodes (less than 100 um diameter), but frequent re-calibration is also required with these more sensitive probes. This method is very desirable but a micro-probe is prohibitively expensive (more than $2000).

The measurement of oxygen production measures the activity of photosystem II of the light reaction (acyclic photophosphorylation). It does not take into account the photosynthetic activity of the photosystem I of the light reaction (cyclic photophosphorylation). Thus the use of oxygen evolution as a measure of primary production is problematic. Further, to measure respiration with oxygen consumption is also problematic in that many other electron donors exist, especially under anaerobic conditions (lower redox potentials) which can be a problem if incubations are long or if metabolic rates are high. Due to these problems and depending upon which compounds (carbohydrates, proteins or lipids) are oxidised, the conversion of oxygen measurements into equivalent carbon units requires the use of respiratory and photosynthetic quotients. Unfortunately, these conversion factors vary depending upon species composition, physiological state, light, temperature and CO_2 conditions and other environmental conditions (Strickland 1960). Wetzel and Likens (1991:210) indicate that the photosynthetic quotient of 1.2 and a respiratory quotient of 1 may be used for rough approximations, but they are known to vary from up to 0.5 to 3.5 (A. Zimmerman, unpublished data, personal communication). For example, a constant respiratory quotient of 0.85 was used by del Giorgio and Peters (1994). This alone represents a minimum of at least 15 % uncertainty in the magnitude of carbon flux, relative to Wetzel and Likens' suggestion of 1. This error compounded with experimental error can greatly decrease the reliability of this method, especially under low metabolic rates.

An alternate approach to the measurement of production and respiration is by directly measuring carbon uptake and release. Carbon is fixed into carbohydrates by autotrophs in the dark reactions of photosynthesis and released during respiratory activity. This approach is attractive in that it directly measures this uptake without having to use uncertain conversion factors. However, the use of inorganic carbon as a measure of metabolic activity is also problematic in that under anaerobic conditions, organic carbons (*e.g.*, methane) can be respired and not just DIC.

The most widespread technique of carbon uptake/release is the radiocarbon method: tracing the uptake of $H^{14}CO_3^-$ (labelled sodium bicarbonate) developed by Steedman-Nielson (1951). The general approach is to estimate ^{12}C assimilation by equating the ratio of (^{14}C available) / (^{14}C assimilated) to the ratio of (^{12}C available) / (^{12}C assimilated) over an incubation of about 3-4 hours. The sensitivity of this method is extremely high and so it is generally the method of choice especially in low-productivity environments. Further, it lends itself to a size-fractionation method.

The main difficulty with the technique is that ^{14}C primary production estimates have been found to be much less that Winkler estimates of gross primary production (up to an order of magnitude less!). Currently, it is believed that ^{14}C production estimates are intermediate between net and gross primary production (Peterson 1980). This is mainly due to the fact that C uptake by phytoplankton is not the same as C assimilated into algal biomass. Further, algal cells are leaky in that there is a constant loss of dissolved organic and inorganic carbon from the cytoplasm to the extracellular environment (30 to 1% of cytoplasm; Watt 1966, Storch and Saunders 1978). This recyclage of carbon will underestimate gross primary production rates, even in very short incubations.

Bacteria (with generation times in the order of 20-40 min + under optimal conditions) are also quite capable of competing for nutrients and so make them less available for algal production. Predation and leakage of cytoplasmic fluids upon cell lysis also contribute to an under-estimation of gross primary production. Dark uptake of ^{14}C in even short-term incubations of 4 hours has also been shown to be high (10-50% of light uptake; Prakash et al 1991). There is also a preferential uptake of $^{14}CO_2$ over other forms of DIC by the vast majority of algae and so the use of $H^{14}CO^{3-}$ is also problematic (De Vooys 1979). Finally, such incubation methods assume a linear rate of carbon uptake during the period of study when in fact Michaelis-Menten type dynamics may be more appropriate (*e.g.*, Moloney and Field 1991).

Numerous other difficulties with the ^{14}C method exist. Daily production estimates must be measured by staggered incubations (about every 4 hours, Wetzel and Likens 1991: 212), and so is very time intensive. The chemicals used (scintillation cocktails, radioactive carbon) are harmful and expensive. It is dependent upon measures of total inorganic carbon concentrations, which is alternately calculated from alkalinity, temperature and pH or measured directly by titration or gas analysers. Further, the use of correction factors due to isotopic effects and counter efficiency adds to the various sources of compounded error. Most importantly, it is impossible to estimate respiration rates or gross and net production rates, as respiration rates cannot be measured. Thus, while this method is attractive due to its extreme sensitivity it is useful only as a heuristic estimate of planktonic production.

A more direct and simpler measure of production and respiration is to directly measure changes in inorganic carbon content using an in-situ incubation approach. The changes in inorganic carbon content can easily be measured by infrared gas analysers or gas chromatography (Wetzel and Likens 1991:116), titration and also by calculation. Simple chemical titrations using only a limited number of cheap chemicals can give estimates with errors on the order of ± 1 ppm for a limited range of DIC. Calculation methods are more prone to error as they depend upon four independent measures: alkalinity, pH, conductivity and temperature, each of which may compound the error significantly (*e.g.*, Quay *et al.* 1986).

Direct measurement of DIC concentrations in incubation experiments (*e.g.*, by gas chromatography) is the most direct method (Salonen 1981, Stainton 1973, Lampert 1984:439-441). However, the direct measurement of DIC in incubations also has its share of problems—the most important being that of the degassing of CO_2 during the transfer of a water sample (*e.g.*, from an incubation bottle). This degassing occurs due to lowered pH from respiratory activity that forces the conversion of DIC into gaseous CO_2. This is especially a problem in high DIC waters.

The gas chromatographic (GC) method can detect changes in DIC of less than 1% (errors in the range of ± 0.7%; R. Carrignan, pers. comm.). This method compares well with titration methods, which have measurement errors in the range of 0.6% to 2%. Infra-red spectroscopy has been quoted to have errors in the range of <0.2%;

unfortunately I do not have access to such a machine. The sensitivity of less than 1% should be sufficient to detect most metabolic processes within a 24-hour period. Oligotrophic Canadian Shield lakes in Québec have been found to have metabolic rates on the order of 10 mg C m^{-3} day^{-1} (*e.g.*, del Giorgio 1992, Likens 1975). Lac Croche has been found to have DIC levels of about 60 mmol m^{-3} (~ 720 mg C m^{-3}; R. Carrignan, personal communication). Thus, the lowest of the metabolic rates represent about 1.3%, which should technically be detectable by the GC method. Preliminary studies indicated that this was so. After practice, error rates of ~0.5% were obtained, however error rates increased with increasing DIC concentrations in lakes with greater preponderance of calcareous bedrock.

— *Appendix 4* —

ESTIMATING RESPIRATION, PRODUCTION AND STANDING BIOMASS FROM SIZE-ABUNDANCE RELATIONSHIPS

The description of the allometric nature of the physiological rates have been pioneered and extensively reviewed by numerous authors (*e.g.*, Kleiber 1932, Hemmingsen 1960, Fenchel 1974, Blueweiss *et al.* 1978, Banse and Mosher 1980, Peters 1983, Ikeda 1985). The synecological application of these autecological patterns to the distribution of biomass has been attempted by various people. For example, Strayer (1986) estimated assimilation rates of a lacustrine benthic community using the same approach (see also Schwinghamer *et al.* 1986). Inferences upon standing-crop biomass and production of fisheries and primary production have been attempted by Platt and Denman (1978), Sprules and Knoechel (1983), Paloheimo (1988), and Boudreau and Dickie (1992). Platt *et al.* (1984) using the biomass size distribution of the North Pacific Central Gyre, have estimated an upper bound to planktonic production and respiration that are comparable with other methods of estimation. Borgmann (1987) and Thibeaux and Dickie (1992, 1993) have used allometric predation models to predict the distribution of the biomass of a trophic level from another level. This potential has been empirically confirmed by Sprules and Goyke (1994) and Sprules and Stockwell (1995) for lakes Michigan, Ontario and Erie. These latter studies suggest that an allometric approach may be an extremely powerful and cost-effective means of ecosystem and fisheries management (but see Cyr and Pace 1993, Cyr and Peters 1996, who test and dispute this potential).

Today, such an allometric approachs are used for many divergent purposes (see Yodzis and Innes 1992). For example, the central assumption of bioenergetic models begins with the use of an allometric representation of mass and energy fluxes. Studies of life history evolution depend almost completely upon the allometric representation of energetic costs and fitness functions (Angerbjorn 1985, Brown *et al.* 1993, Lundberg and Persson 1993). Field (1991) simulated carbon and nitrogen flows in the planktonic food web. Griesbach *et al.* (1982) examined pesticide accumulation by adopting an allometric approach.

It must be clearly understood that the results of such studies must be accepted with caution. Behavioural interactions, ecological interactions (*e.g.*, immigration, emigration), evolutionary and life history constraints in addition to physiological condition and environmental stress may strongly modify these patterns (*e.g.*, see Cyr and Pace 1993).

Due to the strong allometric relationship between organism size and respiration rate, the community respiration rates may be roughly estimated with knowledge of the size-abundance relationship (Platt *et al.* 1984, Ahrens and Peters 1991a,b). Such an approach is facilitated by the availability of numerous automated particle counting and sizing apparati (Sheldon *et al.* 1972; Sprules and Stockwell 1995). Respiration may be estimated as $R_T = \Sigma_i N_i R_i$, where N_i is the number of individuals in the i^{th} weight class; and R_i is the estimated respiration rate of an individual in the i'th weight class. $R_i = k\, m_i^{0.751}$ with the values of k taken from Peters (1983:29; see also Moloney and Field 1989, and Ikeda 1985 for comparisons); k=0.018 (for mass = 10^{-12} to 10^{-7} g) and k=0.14 (for mass = 10^{-7} to 10^{2} g). Q_{10} are usually between 1.63 to 1.89 (Ikeda 1985). Conversion factors are as in Boudreau and Dickie (1992). Some examples of their application may be found in Platt *et al.* (1984) and Joint and Pomeroy (1988).

However, studies that actually test empirically, this method are few in number. One such study was done by Ahrens and Peters (1991a,b) where they demonstrated a weak relationship between mean size of the plankton community and respiration rates. The variation in the relationship was enormous (several orders of magnitude). However, I re-examined their data and estimated respiration rates from observed size-abundance distributions (Figure A4.1) and found a surprisingly good relationship. These results are encouraging.

Similar relationships have been found amongst the lakes studied in preliminary studies (Figure A4.2). The ratio of respiration to biomass based upon allometric relationships should be a decreasing function of average size of plankton. However, due to an incomplete size spectrum, I have chosen to use mean zooplankton biovolume as a measure of the average size of the planktonic community. The assumption here is that due to their larger sizes, the zooplankton will dominate the central tendency of the mean size of the plankton.

These results indicate that the size-based physiological influence upon these (community) eco-physiological respiration rates dominates over the ecological interactions that may modify these eco-physiological rates. That is, the application of these allometrically estimated respiration rates seems to be justified and the role of ecological interactions in modifying these rates seems to be limited to the level of structuring the size distributions of organisms in a given system.

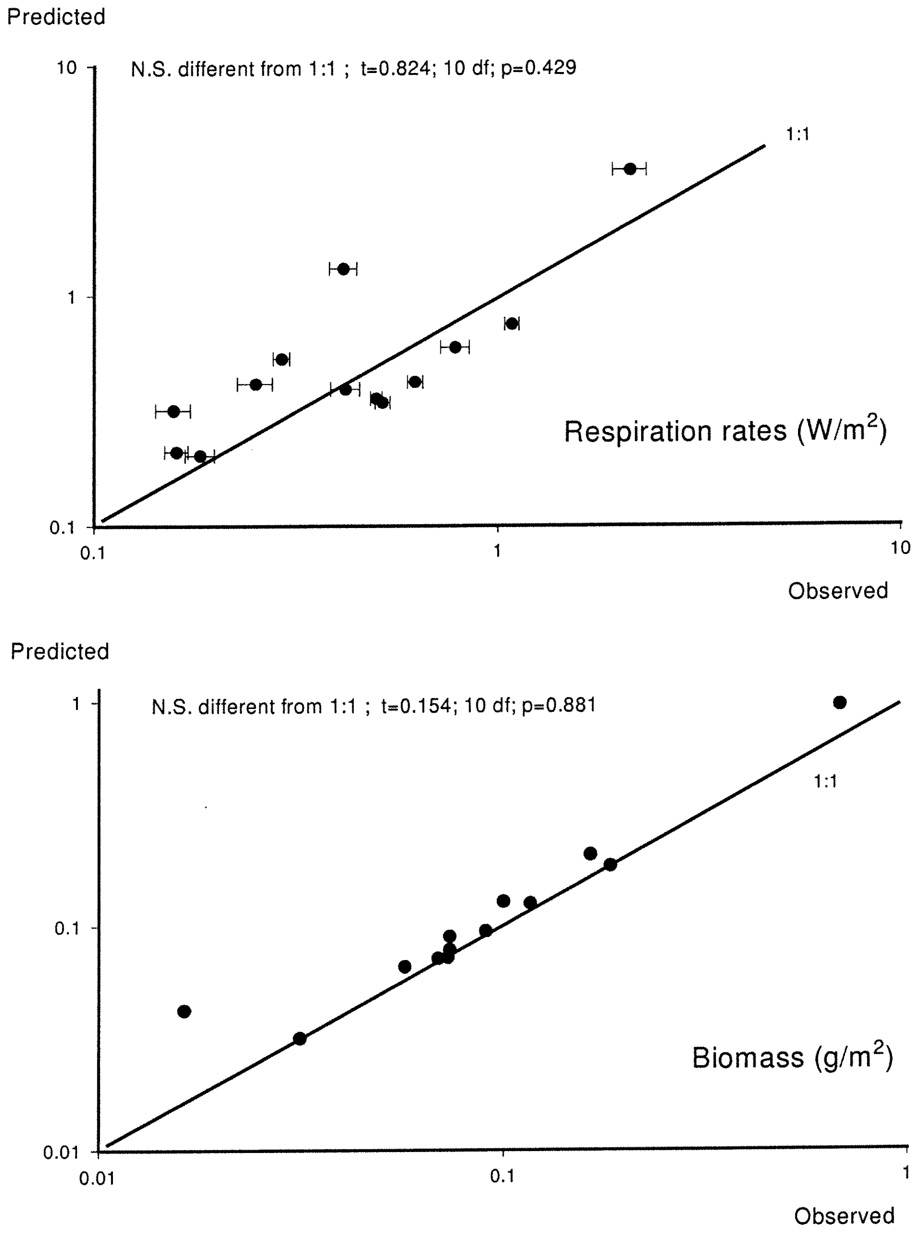
The general approach in estimating net secondary production from an allometric approach has been to utilise empirically determined production to standing crop (average) biomass ratios of large groups of organisms (species, population, assemblage, trophic group) and then to estimate the production from the average biomass of the average standing crop biomass. This approach has been elaborated and generalised by Paloheimo (1988). Unfortunately, this method is more prone to alterations from ecological interactions, which is evidenced by the greater variability of the P/B allometric relationship (Peters 1983:134). Nonetheless, it is a useful means of obtaining order of magnitude estimates of net secondary production (*e.g.*, Sprules and Stockwell 1995).

The allometry of gross primary production is even more poorly described. Although the maximum growth rate of phytoplankton decreases with size, the relationship is quite variable and strongly influenced by ambient nutrient and temperature conditions

(Reynolds 1984:197). I am not aware of any allometric relationships that have been published for photosynthetic rates.

Another potential method of estimating gross primary production is through the empirical relationship between production and respiration. Production being more difficult to measure than respiration makes this a potentially useful method. Net secondary production of a population is approximately proportional to total community respiration (McNeill and Lawton 1970, Humphreys 1979, Robertson 1979, Peters 1983:144), although large differences between taxonomic groups are known. Similarly, at a community level, gross primary production is known to be strongly related to the total planktonic community respiration (del Giorgio and Peters 1994). However, the scatter in the relationship is also quite large (< 1 order of magnitude variation; see Figure A4.3).

Such a method is useful for an order of magnitude estimate—however, there are some complications. del Giorgio and Peters (1994) asserted that the importance of heterotrophic activity increases as lake nutrient levels decrease. In fact, in their study, they found that all but the most eutrophic lakes had higher rates of respiration relative to production. This was not found in my results, and in fact, demonstrate an opposite pattern (Figure A4.3). It is possible that this contradiction may be due to the use of ^{14}C production measures in the study by del Giorgio and Peters (1994), which is known to underestimate production rates.



Predicted from size-abundance distributions
Ahrens and Peters (1991; Hydrobiologia 224:77-87)

Figure A4.1. Comparison of observed and predicted respiration rates and biomass. Estimates are based upon the size-abundance distributions in Ahrens and Peters (1991a,b).

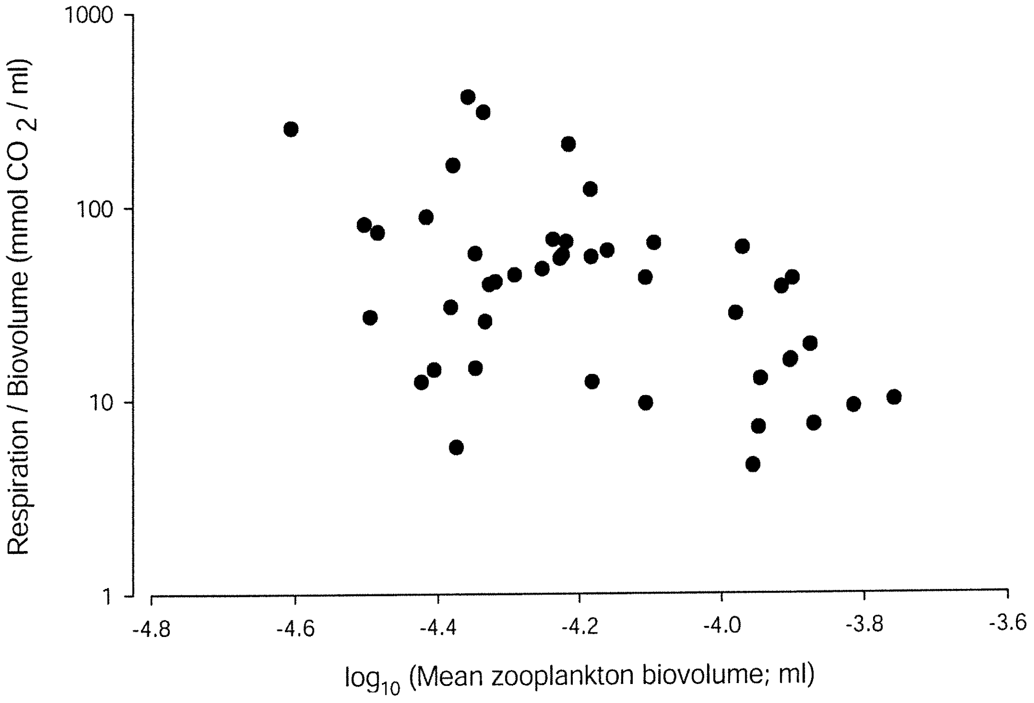


Figure A4.2. A more easily measured index of R/B is the mean size of organisms (zooplankton). The empirical relationship based upon measurements of respiration rates and the biomass of freshwater planktonic organisms (R^2 = 0.24; 87df; p<0.0001). Similar empirical patterns have been demonstrated by Ahrens and Peters (1991a,b).

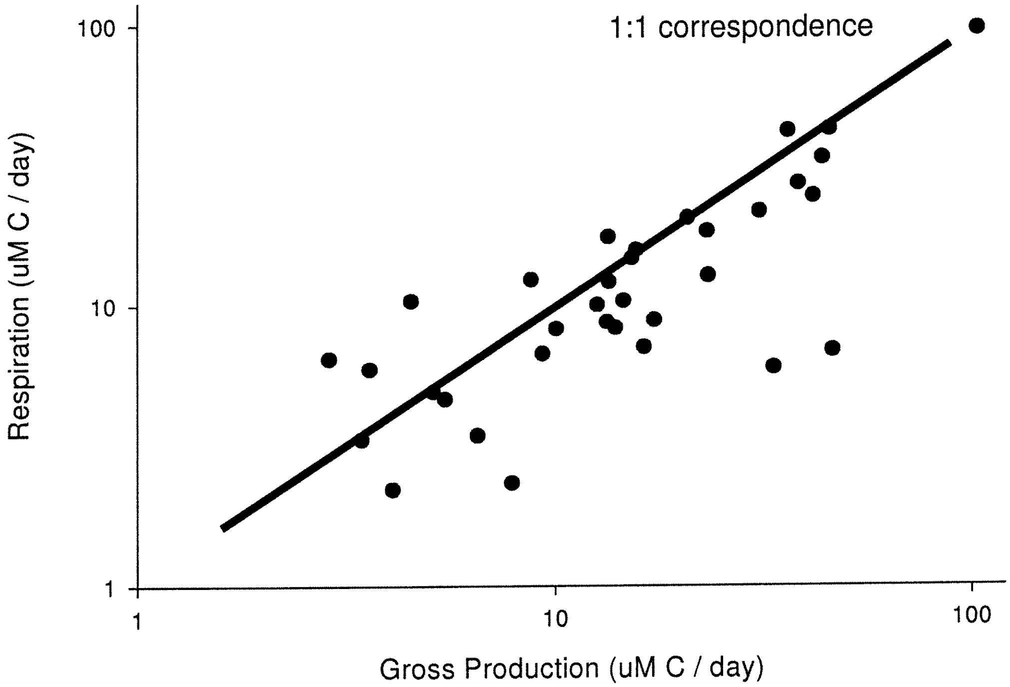


Figure A4.3. The relationship between respiration rates and gross production rates in lakes studied in 1996. The relationship is weakly but not significantly different from the line of 1:1 correspondence (t=1.96; p=0.06; 35 df: log R = 0.123 + 0.778 log P; r^2=0.57).

— Appendix 5 —

FIELD PROTOCOL

Epilimnetic water samples were taken with a Van Dorne (4 L) at a depth of ~ 1-2 m at the point of maximal lake depth. Sub-samples were immediately transferred to 125 mL incubation bottles and capped. Incubation bottles were stored at in-situ temperatures in the dark and transferred to the same depth in Lac Croche for a 24 hour light-dark incubation. Generally, three or four replicates were taken for each treatment. Bottles were fixed with additions of concentrated H_2SO_4 to a pH of < 2 and analysed by gas chromatography at the Université de Montréal at the end of the week.

The water samples from the epilimnion were sampled with an integrated tube for Chl-a and TP determinations (10 litres). A 250 mL subsample was fixed in Lugol's solution for the examination of phytoplankton.

Zooplankton was sampled with an integrated net (64 um mesh, 25 cm diameter conical net), from surface to 1 m above the sediments at the point of maximum lake depth. Subsamples were taken for the determination of biomass, size distributions using the optical plankton counter and taxonomic identification.

Lakes were selected to demonstrate the greatest possible variation in morphometry. Morphometric variation was important because it is a measure of the spatial scale of a system, which in turn is related to its capacity to buffer perturbations.

The DIC method was validated with a very precise modification of the Winkler method and a ^{14}C uptake method using a liquid scintillation technique (Steedman-Nielsen 1951, Schindler and Holmgren 1971, Wetzel and Likens 1991) in Lac Croche (a lake found on the Station de biologie de Université de Montréal). Incubations were conducted in September 1996 for ~ 4 hrs in duration in the epilimnion (1 to 2.5 m depth) during peak light levels (10 am to 2 pm). Metabolic rates were extrapolated to daily rates as per Schindler and Holmgren (1971) and Wetzel and Likens (1991; p.216). An isotopic factor of 1.06 was used for the calculation of ^{14}C uptake rates Wetzel and Likens (1991) and a respiratory quotient of 0.85 was assumed as per del Giorgio and Peters (1994):

Table A5.1. A comparison of different methods of measurement of planktonic metabolism in Lac Croche (September 1996, 1m station; µg C L^{-1} day^{-1}; assuming RQ = 0.85). Standard errors in parentheses. Note that the ^{14}C-method provides a production measure that is not considered gross nor net production.

	Gross Production	**Net Production**	**Respiration**
Winkler-method	42.6 (4.7)	28.9 (4.0)	46.7 (8.6)
DIC-method	48.3 (8.9)	36.5 (5.87)	41.3 (23.3)
^{14}C-method	--------	29.4 (0.3)	-------

These results indicate that there is a close match between all the methods. Note the lower rates of production estimated by the ^{14}C-method, which is between gross and net primary production. The large errors in the DIC-method are due to the short incubations (4 hours) in the comparative study. In the fieldwork, incubations were generally for more than 24 hours in length and so reducing this source of error. This would assume respiration rates are a linear function of time, which is verified in (Figure A5.1).

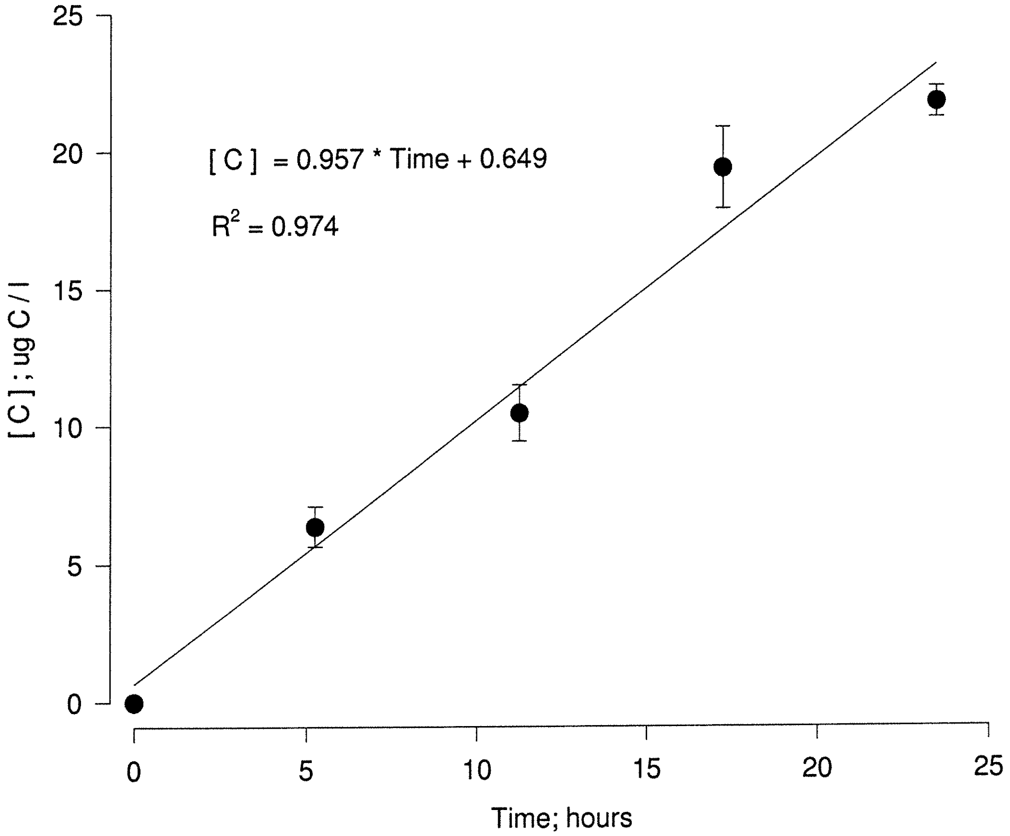


Figure A5.1. Respiration rates over 24 hours is approximately a linear function.

— Appendix 6 —

ALLOMETRY OF SIZE AND ABUNDANCE

The upper bound of the abundance of organisms (N) is known to be a power function of the size of the organisms (m):

$$(8) \qquad N \propto m^{w}$$

where the exponent (w) generally ranges between –1.2 and –0.6 (see Table 2.1).

While empirically well known, we do not know why these patterns exist in so many diverse environments. One of the first known attempts at an explanation may be attributed to Elton (1927) and his concept of the "pyramid of numbers"—the pattern of decreasing numbers of organisms with increasing trophic level (*i.e.*, body size). He attributed this pattern to the sequential loss of energy (dissipation into metabolic heat and faecal matter) at each step of consumption. This idea was further developed as simple mass transfer models, from small to larger organisms (Platt and Denman 1978; Silvert and Platt 1980; Borgmann 1987; Thibeaux and Dickie 1993). In fact, using allometric arguments, the exponent of the size-abundance relationship was predicted to be near –1.22 by Platt and Denman (1978).

Unfortunately, these explanations assume feeding relationships to be unidirectional linear food chains, when in reality, they are very complex webs of interactions and ignore the very important reverse transfer or recycling of mass from large to smaller organisms through the decomposer or detrital system. These latter processes can make up the bulk of metabolic activity in many systems (*i.e.*, the Microbial Loop; Pomeroy 1974; Williams 1984; Cole *et al.* 1988; Jahnke and Craven 1995). Another explanation may be attributed to the process of numerical "self-thinning" that has been observed in monocultures of various plants or cohorts of a given population of animals. In plant populations, this self-thinning rule has been attributed to the competition for space or resources (*e.g.*, light, water, nutrients; Yoda *et al.* 1963). In fish populations, this "self-thinning" pattern has also been demonstrated by Bohlin *et al.* (1994) for cohorts of Atlantic salmon, brown trout and sea trout in Swedish rivers. Thus, under more restricted spatio-temporal conditions, intra-specific competition and size-dependent mortality rates represent mechanisms that may be involved in the generation of the size-abundance relationship. Paralleling the above, Morse *et al.* (1985), examining the arthropod size-abundance relationship in trees, hypothesised that the relationship may be due to the fractal-like increase of habitat space with decreasing spatial scale. However, no particular mechanism can be said to be the definitive cause of this size-abundance relationship.

— *Appendix 7* —

ECO-PHYSIOLOGICAL RATES OF REPRESENTATIVE SYSTEMS

Data used in Chapter 4 (Figure 4.2). Rates are expressed as g C m^{-2} yr^{-1} and the mean standing biomass (B) as g C m^{-2}. R.t is the total system respiration rate; R.a is the autotrophic respiration rate; GPP is gross primary production; NPP is net primary production. The codes are structured as follows: [climatic region].[ecological type].[ID number]. Climatic regions: Te=temperate; Tr=tropical; Ar=arctic; Bo=boreal. Ecological types: E=estuary/brackish water; L=whole lake; P=freshwater pelagic; Lit=littoral; M=marine pelagic; Sh=continental shelf; CR=coral reef; R=river; Tu=tundra; Gr=grassland; Cul=culture and F=forest. Conversion factors are given in Appendix 8. Net Primary Production (NPP) and Average Standing Biomass (B) estimates were calculated from percentage cover of vegetational type (World Conservation Monitoring Centre 1992, Central Intelligence Agency 1996), in conjunction with NPP and B estimates for each vegetational type compiled by the IBP (Rodin *et al.* 1975, Olson 1975, Lieth 1973, 1975).

Location	Code	R.t	R.a	GPP	NPP	B	Source
Char lake—Cornwalis Island (Arctic)	Ar.L.1	28.85					Welch 1974
Char lake—Cornwalis Island (Arctic)	Ar.L.2	13.6		22		1.6	Rigler 1975
Resolute Bay, Canada	Ar.M.1	107.86		60		0.18	Welch *et al.* 1997
Lake Vanda, Antarctica (4m ice)	Ar.P.1				5.1		De Vooys 1979
Taimyr, USSR	Ar.Tu.1				27.3	28.6	Matveyeva *et al.* 1975
Truelove, Devon Island	Ar.Tu.2	497	451	496	45.1	474	Bliss 1975
Truelove, Devon Island	Ar.Tu.3	1071.82	966.52	1050.31	83.79	943.31	Bliss 1975
Tundra	Ar.Tu.4	205	120	208	88		National Academy of Sciences 1974
Coniferous forest	Bo.F.1	1050	680	1320	600		National Academy of Sciences 1974
Coniferous forest—Picea omorika	Bo.F.2				760	690	Ovington and Heitkamp 1960; quoted by McFayden 1964
Coniferous forest—Pinus silvestris	Bo.F.3				800	1840	Ovington 1957
Picea stand	Bo.F.4		870	1814	944	690	McFayden 1964
Lake Krivoe (USSR)	Bo.L.1			16		0.64	Winberg 1972
Lake Krugloe (USSR)	Bo.L.2			5.5		0.408	Winberg 1972
Great Bear Lake (Canada)	Bo.P.1				18.2		De Vooys 1979
Great Slave Lake (Canada)	Bo.P.2				36.5		De Vooys 1979
Alfalfa Field, USA	Te.Cul.1	1300	920	2400	1480		Coleman *et al.* 1976
Ascophylum beds (Nova Scotia)	Te.E.1				920	1600	MacFarlane 1952
Spartina marsh (Georgia)	Te.E.10				1600	840	Westlake 1963
Hudson river (tidal zone)	Te.E.11	500		350	40		Howarth *et al.* 1996
Spartina marsh (Georgia)	Te.E.12		40	470	430	435	McFadyen 1964
British Columbia	Te.E.2			650	450		Woodwell *et al.* 1973

Chara sp. (Caspian Sea)	Te.E.3				500	1000	Kiriva and Shapova 1939; quoted by Westlake 1963
Long Island Sound (New York)	Te.E.4			470	204.8		Woodwell *et al.* 1973
Louisiana (Barataria Bay)	Te.E.5			359.2	170		Woodwell *et al.* 1973
North Carolina	Te.E.6			99.6	52.4		Woodwell *et al.* 1973
Spartina marsh (Georgia)	Te.E.7				1320	840	Odum 1969
Spartina marsh (Georgia)	Te.E.8	3271	2820	3640	820	900	Teal 1962
Spartina marsh (Georgia)	Te.E.9				520		Smalley 1960
Deciduous—poplar	Te.F.1	1465	941	1625	685	8320	Reichle *et al.* 1973
E. Deciduous forest	Te.F.2	2105	1440	2150	720		Burgess and O'Neill 1976
Hubbard brook Forest	Te.F.3	900	572	1040	468	7142	Gosz *et al.* 1978
Mesic Deciduous forest (Tennessee)	Te.F.4	2737	1820	2798	978		Coleman *et al.* 1976
Deciduous woodland—alder	Te.F.5				785	3400	Ovington 1956
Deciduous woodland—birch	Te.F.6				425	1760	Ovington and Madgewick 1959
Field grass (Minnesota)	Te.Gr.1				500	740	Golley 1960
Grassland	Te.Gr.2		470	982	512	400	McFayden 1964
Grassland	Te.Gr.3	1090	430	983	840		Burgess and O'Neill 1976
Short grass prairie (Colorado)	Te.Gr.4	416	178	523	345		Coleman *et al.* 1976
Cedar bog lake	Te.L.1	29.4		129			Lindemann 1942
Lake Naroch (USSR)	Te.L.10			197.5		2.39	Winberg 1972
Mirror lake	Te.L.11	57	21.1	64.6	43.5		Jordan and Likens 1975
Rybinsk reservoir (USSR)	Te.L.12			65		2.466	Winberg 1972
Lake Huron	Te.L.13				85		De Vooys 1979
Lake Superior	Te.L.14				60		De Vooys 1979
Cold Spring	Te.L.2	218					Teal 1957
Kiev reservoir (USSR)	Te.L.3			359		8.69	Winberg 1972
Lake Batorin (USSR)	Te.L.4			232.9		6.5	Winberg 1972
Lake Biwa (Japan)	Te.L.5		1752	2920	1168	12.8	Shoji 1984
Lake Drivyati (USSR)	Te.L.6			177		8.536	Winberg 1972
Lake Krasnoe (USSR)	Te.L.7			157		2.123	Winberg 1972
Lake Mendota (Wisconsin)	Te.L.8				350	8.5	Brock 1985
Lake Myastro (USSR)	Te.L.9			226		4.98	Winberg 1972
Typha sp. (Minnesota)	Te.Lit.1				640	1744	Bray *et al.* 1959
Fucus beds (Woods Hole—full sunlight)	Te.Lit.2				7300	800	Kanwisher 1966
Laminaria community (Nova Scotia)	Te.Lit.3				1750	265	Mann 1972
Sargasso Sea	Te.M.1				134	0.87	Menzel and Ryther 1961
Lake Tahoe, Sierre Nevada (USA)	Te.P.1				36.1		De Vooys 1979
Lake Washington	Te.P.10	158.50		199.53			Waring 1989
Sewage Treatment ponds (California)	Te.P.11				1800	24	Goluake *et al.* 1960
Lake Baikal (USSR)	Te.P.2				113.1		De Vooys 1979
Lake Constance (Bodensee)	Te.P.3				164.2		De Vooys 1979
Lake Clear (California, USA)	Te.P.4				912.5		De Vooys 1979
Lake Erie	Te.P.5				240		De Vooys 1979
Lake Ontario	Te.P.6				185		De Vooys 1979
Lake Michigan	Te.P.7				145		De Vooys 1979
Lake Constance (Bodensee)	Te.P.8		224.48	774.48	550	5.5	Weisse *et al.* 1990
Lawrence lake (Temperate)	Te.P.9	34			43.4		Wetzel and Rich 1973
Young pine (UK)	Te.Pl.1	930	470	1220	750		Coleman *et al.* 1976

Bear Brook (New Hampshire)	Te.R.1	204				1.5	Fisher and Likens 1973
Silver Springs	Te.R.2	1879.6	1197.7	2081	883.3	21.59	Odum 1957
Chesapeake Bay plankton	Te.Sh.1	89.31		182.06			Smith and Kemp 1995
Chesapeake Bay plankton	Te.Sh.2	748.83		1154.16			Smith and Kemp 1995
Chesapeake Bay plankton	Te.Sh.3	336.63		1401.48			Smith and Kemp 1995
English Channel	Te.Sh.4		25	160	135	2	Harvey 1950 and McFayden 1964
Fladden ground N. Sea 1953 Sta. 1-4	Te.Sh.5				100	3.5	Steele 1956
Long Island Sound	Te.Sh.6				470	8	Riley 1956
English Channel	Te.Sh.7	109.6	27.4	109.6	82.2	13.1	Brylinsky 1972
Windward reef, Eniwetok	Tr.CR.1	3504	1460	3504	2044	280	Odum and Odum 1955
Plantation Key Reef	Tr.CR.10		1775	2303	528		De Vooys 1979
Rongelapp Atoll (Marshall, Islands)	Tr.CR.2		1310	1500	190		De Vooys 1979
Kapaa Reef	Tr.CR.3		1600	3000	1400		De Vooys 1979
Arabian Sea Reef	Tr.CR.4		876	4494	3618		De Vooys 1979
Eniwetok	Tr.CR.5		1051	3241	2190		De Vooys 1979
Eniwetok	Tr.CR.6		1051	7358	6307		De Vooys 1979
Eniwetok	Tr.CR.7		2190	4380	2190		De Vooys 1979
Hawaii	Tr.CR.8		2190	8497	6307		De Vooys 1979
Curacao	Tr.CR.9		3320	5650	2330		De Vooys 1979
Sugar cane (Java)	Tr.Cul.1				3450	1700	Giltay 1898
Cystoceira abies marina community (Canary Isles)	Tr.E.1				3836	630	Johnston 1969
Epiphytic algae (Florida)	Tr.E.2		230	430	200		Woodwell *et al.* 1973
Epiphytic algae (Florida)	Tr.E.3			284.8	148		Woodwell *et al.* 1973
India (Cochin backwater)	Tr.E.4			280.8	124	0.2	Woodwell *et al.* 1973
Thalassia sp., tropical turtle grass beds	Tr.E.5		720	1600	880	1320	Woodwell *et al.* 1973
Thalassia sp., tropical turtle grass beds	Tr.E.6				4650	2260	Odum 1956b, Burkholder *et al.* 1959
Hyper Eutrophic lake (Florida)	Tr.L.1	1260		1400	118		Gale and Reddy 1994
Shahidullah Hall Pond (Dhaka, Bangladesh)	Tr.L.2	1335		1383			Khondker and Kabir 1995
Peru Current	Tr.M.1				3650	14	Menzel *et al.* 1971
Ponds	Tu.L.1	19.95		17.78			Waring 1989

— *Appendix 8* —

CONVERSION FACTORS

1 kcal = 1/10 g C; 2 g wet; 1/4 g dry; 1/5 g ash-free dry weight; 4.184 kJ (Crisp 1975)
1 g dry = 22,000 J; 5.268 kcal (Peters 1983)
1 g wet = 7,000 J; 1.673 kcal (Peters 1983)

1 kcal = 4.184 kJ
1 W = 1 J s^{-1}; 20.65 kcal day^{-1}; 7537.2 kcal $year^{-1}$

1 mL O_2 = 0.0446 mmol O_2; 0.699 mg O_2
1 mL O_2 = 20.1 J; 4.804 cal
1 g O_2 = 28.76 kJ; 6.873 kcal; 0.687 g C (Peters 1983)

1 ppm = 1 cm^3 m^{-3} ; 1 g m^{-3}
1 cm^3 = 1 mL; 1 g (wet; assuming unit density)
1 g/m^2 = 1 metric ton km^{-2}; 10^3 kg km^{-2}

— *Appendix 9* —

FIELD DATA

All limnological variables and size-abundance data collected during the course of the fieldwork are here presented.

Morphometric variables:

Lake	Latitude	Longitude	Surface area (ha)	Drainage area (ha)	Maximum depth (m)	Secchi* depth (m)	Thermocline* depth (m)	Perimeter (km)	Fetch (km)	Elevation (m)
Achigan	45-56-33	73-58-39	519	6401	20.8	4.5	5.9	19.45	5.79	208
Berthier	46-15-50	73-28-10			8.3	3.0	4.1			
Chertsey	46-08-13	73-49-06	127	375	39.5	9.5	6.9	8.66	2.9	287
Coeur (en)	45-58-04	74-00-37	45	231	8.0	3.7	4.9	6.4	1.31	354
Connelly	45-53-54	73-57-51	124	860	16.3	3.8	4.9	6.6	1.95	195
Cristal	45-58-29	73-53-28	28	201	18.0	7.0	5.9	2.29	0.8	264
Croche	45-59-35	74-00-27	18.1	104	11.5	5.4	3.5	4	0.42	363
Cromwell	45-59-21	73-59-56	9.4	636	8.8	2.6	3.1	1.9	0.63	340
Desiles	46-05-59	74-01-45	467.4	2332	25.5	6.2	6.7	17.1	4	365
Desjardins	45-54-57	74-04-24	5.8	272	4.5	1.9	n/a	1.1	0.4	351
Dufresne	46-12-16	74-13-32	91.6	411	13.7	6.4	5.6	6.7	1.8	469
Geai	45-59-46	73-59-33	3	36	6.5	1.8	1.9	0.5	0.25	370
Long	45-59-48	74-00-31	16	298	9.0	5.1	3.6	3.6	1.75	364
Mandeville	46-22-05	73-19-45	104		4.8	1.2	3.1			
Manitou	46-03-33	74-22-12	401.1	2530	21.5	5.6	6.5	26	6.1	388
Marois	45-51-05	74-07-50	91.1	658	21.5	4.8	6.2	6.3	2.1	291
Matambin	46-19-30	73-32-20	54		20.0	3.7	4.8			
Montagne Noire	46-11-49	74-16-18	278.6	1305	30.3	6.2	6.4	11.2	3.2	456
Noir	45-58-59	74-01-13	6.2	65	5.0	1.8	2.5	1.1		
Oglivy	45-55-20	74-04-19	16.9	95	30.5	8.1	5.3	2.2	0.8	355
Patrick	46-06-19	73-58-44	159.2	6281	28.0	5.3	5.6	7.8	2.1	349
Pontbriand	46-03-11	73-46-23	192.4	11252	5.0	2.6	6.3	19.6	6.8	155
Quatre	45-59-50	73-58-58	3	49	2.5	1.7	1.5			
Rawdon	46-03-02	73-42-14	46.3	1288	5.0	1.6	2.3	7.5	2.4	150
Raymond	46-00-15	74-09-39	71.1	11720	15.8	2.2	4.3	7.8	1.4	307
Siesta	45-55-39	73-49-07	11.8	624	4.4	2.0	3.0	2.3	1	135
Thibault	45-58-39	74-01-15	5.5	85	2.9	1.2	1.5	1.5	0.53	352
Triton	45-59-15	74-00-28	3	25	3.8	2.7	2.1	0.8	0.3	365

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*Averages over the 1995 and 1996 field seasons.

Chemical variables:

Lake	Mean stability (W/m2)	Maximum stability (W/m2)	Temp. (deg. C) bottom	DO (% sat.) bottom	Conductivity (uS/cm) surface	pH surface	DOC[*] (ppm) surface	DIC[*] (uM) surface	Mean [TP; ug/L] surface	Mean [CHL a; ug/L] surface
Achigan	159.5	197.4	6.2	67	55	7.09	4.6	222	11.5	1.5
Berthier	17.5	34.4	8.5	4	44	6.75	7.2	244	28.9	3.1
Chertsey	253.4	291.7	5.8	64	32	7.08	2.8	167	5.9	0.5
Coeur (en)	10.5	20.4	10.2	4	47	6.45			22.0	1.9
Connelly	100.4	126.8	6.4	51	121	7.31	5.9	347	18.2	1.6
Cristal	137.4	141.0	5.5	34	105	7.21			9.2	0.9
Croche	25.8	62.6	5.4	24	18	6.06	4.4	77	6.6	0.9
Cromwell	16.3	39.8	5.2	12	21	5.99	6.5	207	27.8	3.4
Desiles	298.2	363.1	6.1	72	41	6.87			23.0	4.0
Desjardins	1.2	2.6	19.3	45	47	6.39			50.0	0.9
Dufresne	29.9	31.1	7.1	13	55	6.76			6.8	4.4
Geai	18.0	31.5	4.7	3	13	5.08	7.7	203	31.5	4.5
Long	46.5	52.9	5.8	2	36	6.20			14.5	2.7
Mandeville	0.7	2.4	20.9	59	41	7.70	5.1	192	85.3	4.6
Manitou	114.2	146.9	8.4	63	33	6.91	2.9	151	11.7	1.5
Marois	233.4	250.3	5.2	33	192	7.51			12.0	0.7
Matambin	193.5	243.2	4.7	44	51	6.29			16.2	1.4
Montagne Noire	170.3	213.5	5.8	66	32	7.05	2.6	179	11.1	1.3
Noir	10.6	14.2	7.7	4	15	5.61	9.6	102	31.9	2.9
Oglivy	400.3	430.0	4.0	20	51	6.47			6.5	3.3
Patrick	341.9	402.4	4.9	63	48	6.81			9.5	0.7
Pontbriand	1.4	1.8	18.5	41	53	6.56			17.0	1.1
Quatre	0.4	0.5	18.4	6	21	5.64			38.0	1.7
Rawdon	2.6	5.8	21.0	55	93	7.49			38.5	3.7
Raymond	56.4	76.3	7.3	71	122	7.04	5.0	338	47.1	4.0
Siesta	0.6	1.3	18.9	37	78	7.12	6.7	414	47.2	3.4
Thibault	0.1	0.2	20.4	76	34	6.63	11.7	171	42.8	9.5
Triton	0.2	0.8	16.2	86	19	6.21	5.0	108	20.7	3.3

[*] DOC (dissolved organic carbon) and DIC (dissolved inorganic carbon) are seasonal means from 1996 only. All other values represent the averages over 1995 and 1996. DO is dissolved oxygen levels. Stability is calculated as in Appendix 10.

Size-abundance relationships*:

Lake	n	Slope (mean)	Slope (SD)	Intercept (mean)	Intercept (SD)	R^2 (mean)	R^2 (SD)	$\log_{10}$ (size; mg) (mean)	$\log_{10}$ (size; mg) (SD)
Achigan	10	-0.721	0.053	-1.615	0.131	0.886	0.034	-3.337	0.098
Berthier	8	-0.758	0.091	-1.623	0.118	0.891	0.038	-3.199	0.251
Chertsey	9	-0.752	0.031	-1.386	0.190	0.910	0.014	-3.028	0.084
Coeur (en)	2	-0.999	0.166	-1.739	0.319	0.877	0.081	-3.445	0.280
Connelly	9	-0.692	0.039	-1.711	0.106	0.870	0.030	-3.589	0.067
Cristal	3	-0.780	0.018	-1.500	0.158	0.890	0.013	-2.762	0.571
Croche	36	-0.708	0.072	-1.610	0.161	0.868	0.027	-3.335	0.061
Cromwell	37	-0.721	0.065	-1.778	0.136	0.843	0.034	-3.474	0.076
Desiles	3	-0.841	0.050	-1.397	0.055	0.919	0.020	-3.032	0.047
Desjardins	3	-0.797	0.042	-1.842	0.160	0.854	0.053	-3.834	0.126
Dufresne	3	-0.902	0.250	-1.647	0.101	0.893	0.017	-3.329	0.119
Geai	15	-0.817	0.108	-1.188	0.281	0.868	0.061	-2.523	0.146
Long	3	-0.897	0.147	-1.615	0.129	0.908	0.008	-3.377	0.093
Mandeville	8	-0.678	0.036	-1.914	0.074	0.819	0.045	-3.782	0.144
Manitou	9	-0.684	0.038	-1.541	0.086	0.892	0.029	-3.281	0.041
Marois	3	-0.764	0.080	-1.349	0.101	0.880	0.029	-3.101	0.118
Matambin	3	-0.764	0.091	-1.722	0.135	0.890	0.030	-3.648	0.190
Montagne Noire	9	-0.749	0.016	-1.450	0.160	0.910	0.015	-3.217	0.083
Noir	10	-0.881	0.154	-1.984	0.156	0.794	0.077	-3.993	0.080
Oglivy	3	-0.819	0.062	-1.434	0.011	0.921	0.022	-2.759	0.395
Patrick	3	-0.836	0.027	-1.544	0.048	0.924	0.029	-3.278	0.019
Pontbriand	3	-1.505	0.134	-1.960	0.157	0.795	0.035	-3.411	0.380
Quatre	3	-1.027	0.152	-1.932	0.180	0.831	0.074	-3.885	0.095
Rawdon	3	-0.837	0.095	-1.959	0.072	0.812	0.040	-3.622	0.358
Raymond	7	-0.774	0.065	-1.835	0.164	0.837	0.058	-3.785	0.155
Siesta	9	-0.670	0.021	-1.970	0.066	0.802	0.029	-4.032	0.032
Thibault	10	-0.821	0.102	-1.965	0.163	0.795	0.065	-3.821	0.121
Triton	24	-0.789	0.116	-1.938	0.120	0.814	0.037	-3.846	0.095

*log-log transformed, linear regression parameters.

Incubation experiments*:

LAKE	DATE	Depth	TEMP	DIC (uM)	(SE)	Resp.	(SE)	PNet	(SE)	PGross	(SE)	TP	(SE)
Achigan	04 06 96											9.09	1.98
Achigan	12 06 96											10.49	0.96
Achigan	25 06 96											13.03	7.26
Achigan	09 07 96	2	20.5	222.14	1.55							9.85	1.38
Achigan	09 07 96	2	20.5	222.14	1.55	18.11	1.61					9.85	1.38
Achigan	09 07 96	2	20.5	222.14	1.55	7.85	14.86					9.85	1.38
Achigan	17 07 96	2	20.8	218.40	0.10	45.46	1.38					8.14	1.35
Achigan	17 07 96	2	20.8	218.40	0.10	7.51	9.85					8.14	1.35
Achigan	31 07 96	2		224.45	1.14	7.37	1.62	1.53	1.66	8.90	2.32	19.9	3.17
Achigan	14 08 96	2		221.86	0.87	9.03	2.23	2.22	1.83	11.25	2.89	18.5	3.03
Achigan	14 08 96	2		221.86	0.87	11.68	5.40					18.5	3.03
Berthier	13 06 96											34.01	7.95
Berthier	27 06 96											26.51	9.47
Berthier	10 07 96	2	20.87	221.10	0.49		1.55					46.98	16.6
Berthier	10 07 96	2	20.87	221.10	0.49		5.85					46.98	16.6
Berthier	10 07 96	2	20.87	222.34	0.50	39.51	18.17	8.86	0.07	48.37	18.17	46.98	16.6
Berthier	23 07 96	2	21	246.01	0.56	15.27	4.89					41.97	1.08
Berthier	23 07 96	2	21	246.01	0.56	16.24	6.57					41.97	1.08
Berthier	13 08 96	2		264.63	1.93	13.57	19.56					15.88	0.71
Berthier	13 08 96	2		264.63	1.93	17.75	5.57	10.49	1.22	28.24	5.70	15.88	0.71
Chertsey	12 06 96											8.96	1.44
Chertsey	25 06 96											3.75	0.38
Chertsey	08 07 96	2	20.5	164.62	0.71	14.96	8.68					6.55	1.72
Chertsey	08 07 96	2	20.5	164.62	0.71	5.70	3.86					6.55	1.72
Chertsey	08 07 96	2	20.5	164.62	0.71	5.53	0.74					6.55	1.72
Chertsey	08 07 96	2	20.5	164.62	0.71	4.34	0.44					6.55	1.72
Chertsey	17 07 96	2	20.8	162.11	0.49	1.48	4.81					4.51	0.38
Chertsey	17 07 96	2	20.8	162.11	0.49	5.53	6.25					4.51	0.38
Chertsey	31 07 96	2		171.87	0.51	6.37	2.31	2.81	0.76	9.19	2.44	14.3	4.94
Chertsey	14 08 96	2		169.99	0.42							6.68	1.62
Chertsey	14 08 96	2		169.99	0.42	5.00	1.29	-3.17	1.13	1.83	1.71	6.68	1.62
Connelly	04 06 96											17.61	3.06
Connelly	18 06 96											11.25	4.74
Connelly	26 06 96											13.54	1.44
Connelly	11 07 96	2	20.56	323.17	1.34	45.25	34.00	-11.84	9.59	33.41	35.33	14.43	2.38
Connelly	24 07 96	2		339.88	1.45	44.10	1.77					23.94	2.47
Connelly	07 08 96	2		353.21	0.46		31.67					19.9	1.17
Connelly	07 08 96	2		353.21	0.46	10.14	5.15	-2.21	2.39	7.93	5.67	19.9	1.17
Connelly	15 08 96	2		370.84	1.55	5.71	3.81	-3.13	3.98	2.58	5.51	59.69	1.5
Connelly	15 08 96	2		370.84	1.55	18.12	34.80					59.69	1.5
Croche	20 05 96	1	16.15	93.46				9.44					
Croche	20 05 96	1	16.15	115.15									
Croche	04 09 96	1	20.5	73.44	0.21	2.99	1.94	2.65	0.49	5.64	2.00	8	1.5
Croche	05 06 96											7.31	1.88

Croche	17 06 96											10.87	2.68
Croche	02 07 96	2	21	74.09	0.42	2.90	1.00	0.07	0.33	2.96	1.05	4.26	0.96
Croche	08 07 96	2	20	72.76	0.82	12.95	12.50	2.70	7.79	15.66	14.73	8.07	4.71
Croche	08 07 96	2	20	72.76	0.82	10.62	4.55					8.07	4.71
Croche	09 07 96	2	20	68.92	0.21	12.29	4.15					8.07	4.71
Croche	09 07 96	2	20	68.92	0.21	4.09	0.30	-2.28	0.41	1.81	0.51	8.07	4.71
Croche	09 07 96	2	20	71.63	0.15	7.58	3.50	52.56	13.12	60.13	13.57	8.07	4.71
Croche	09 07 96	2	20	68.92	0.21	15.03	4.00	2.59	1.31	17.62	4.21	8.07	4.71
Croche	09 07 96	2	20	68.92	0.21	4.24	5.00					8.07	4.71
Croche	11 07 96	2		72.11	0.05	20.92	9.05						
Croche	11 07 96	2	23	72.11	0.05	12.27	5.00						
Croche	11 07 96	2	20	72.11	0.05	17.86	11.00						
Croche	11 07 96	2	15	72.11	0.05	20.17	7.00						
Croche	11 07 96	2	13	72.11	0.05	1.78	4.16						
Croche	16 07 96	2	21	72.35	0.27	1.90	0.72	1.58	0.67	3.48	0.98		
Croche	22 07 96	2	21	81.60	0.77	17.86	0.71	-16.81	2.93	1.04	3.02	4.82	0.93
Croche	29 07 96											4.97	0.27
Croche	07 08 96	2		80.97	0.17	4.06	0.71	0.66	0.27	4.72	0.76		
Croche	12 08 96	2		85.43	1.09	10.98	11.08	1.10	2.47	12.09	11.35	8.55	0.93
Croche	16 05 96	3	7.18	143.38	2.45								
Croche	20 05 96	3	8.72	143.71		3.94		1.04		4.98			
Croche	21 05 96	3	8.72	134.60				14.00					
Croche	22 05 96	3	8.72	132.79									
Croche	02 07 96	4	12.54	156.51		5.75		-4.58		1.17			
Croche	07 08 96	4		108.48	2.50	12.29	2.56	-2.84	2.50	9.45	3.58		
Croche	20 05 96	5	6.05	232.41									
Croche	02 07 96	6	12.5	257.48		2.27		-1.50		0.77			
Croche	20 05 96	7	5.17	314.57									
Croche	07 08 96	8		501.06	6.12	13.96	7.14	2.71	10.13	16.67	12.39		
Cromwell	05 06 96											23.97	2.32
Cromwell	17 06 96											26.38	2.89
Cromwell	02 07 96	2		164.25		5.30		25.51		30.81		36.43	12.54
Cromwell	12 07 96	2	19.87	155.27	0.01	39.58	11.55	6.85	2.99	46.42	11.93	29.43	2.17
Cromwell	16 07 96	2	21	141.66	1.92	13.54	2.00	-1.30	2.33	12.25	3.07		
Cromwell	22 07 96	2	21	171.07	0.55	19.22	3.86	-10.55	1.43	8.66	4.11	28.6	2.03
Cromwell	29 07 96	2		210.74	0.02	7.49	1.90	-1.43	1.62	6.06	2.50	30.93	5.73
Cromwell	08 08 96	2		305.19	3.44								
Cromwell	12 08 96	2		267.19	0.89	8.46	2.67		3.23		4.19	41.04	13.88
Cromwell	22 05 96	3	14	107.31	0.25								
Cromwell	02 07 96	4		287.19		4.65							
Cromwell	08 08 96	4		552.00	0.73			10.60	3.10				
Cromwell	02 07 96	6		258.07									
Cromwell	08 08 96	6		864.30	3.33								
Geai	11 06 96											31.85	8.8
Geai	20 06 96											52.58	10.16
Geai	04 07 96	2		226.83								29.43	7.36
Geai	18 07 96	2	22	211.84	1.38							30.83	3.87
Geai	18 07 96	2	22	211.84	1.38	19.11	35.25					30.83	3.87

Geai	30 07 96	2		175.54	0.94	3.19	3.21	2.22	0.87	5.41	3.33	35.91	0.97
Geai	06 08 96	2		198.94	3.29							36.69	1.77
Geai	06 08 96	2		198.94	3.29	5.79	3.00	1.61	3.46	7.40	4.58	36.69	1.77
Geai	04 07 96	4		477.51									
Mandeville	13 06 96											50.54	3.54
Mandeville	27 06 96											61.6	6.2
Mandeville	10 07 96	2	20.5	213.00	0.94	5.42	18.34	1.05	4.57	6.47	18.90	66.69	4.4
Mandeville	23 07 96	2	21	194.46	1.77	22.58	1.81					92.34	9.09
Mandeville	23 07 96	2	21	194.46	1.77	34.39	6.35					92.34	9.09
Mandeville	13 08 96	2		168.87	1.06	60.15	8.22					11.35	0.47
Mandeville	13 08 96	2		168.87	1.06	22.60	1.38	15.80	1.85	38.39	2.31	11.35	0.47
Manitou	06 06 96											11.76	5.3
Manitou	19 06 96											12.01	1.17
Manitou	03 07 96	2	19.94	147.58		21.98						10.62	1.66
Manitou	16 07 96	2	20	147.45	0.40	14.58	8.15					12.4	1.92
Manitou	16 07 96	2	20	147.45	0.40	36.18	3.23					12.4	1.92
Manitou	25 07 96	2	20.6	153.62	1.89	13.88	21.50					15.7	0.97
Manitou	25 07 96	2	20.6	153.62	1.89	5.22	27.91	-2.01	1.88	3.21	27.98	15.7	0.97
Manitou	08 08 96	2		155.27	0.68	36.92	7.70					14.61	0.47
Manitou	08 08 96	2		155.27	0.68	14.37	4.22	-0.11	1.38	14.26	4.44	14.61	0.47
Manitou	03 07 96	4	18.5	149.51									
Manitou	03 07 96	8	9.13	173.62									
Mont.Noir	11 06 96											13.29	8.97
Mont.Noir	20 06 96											13.79	5.08
Mont.Noir	04 07 96	2	18.32	174.78		26.00						7.06	3.46
Mont.Noir	18 07 96	2		174.90	2.67	12.97	9.91					9.73	3.29
Mont.Noir	18 07 96	2		174.90	2.67	38.40	39.56					9.73	3.29
Mont.Noir	30 07 96	2		184.71	0.34	6.43	2.95	0.40	0.69	6.83	3.02	14.77	0.97
Mont.Noir	06 08 96	2		183.03	1.01	12.18	5.43					12.59	0.27
Mont.Noir	06 08 96	2		183.03	1.01	0.97	0.87	1.93	2.61	2.90	2.75	12.59	0.27
Noir	06 06 96											36.56	3.81
Noir	14 06 96											35.16	0.58
Noir	28 06 96											29.94	0.96
Noir	12 07 96											25.62	1.88
Noir	12 07 96	2	19.5	94.28	0.15	29.53	8.35					25.62	1.88
Noir	12 07 96	2	19.5	94.28	0.15	19.63	4.71					25.62	1.88
Noir	18 07 96	2	22.5	109.84	3.27	81.45	9.57					32.1	2.89
Noir	18 07 96	2	22.5	109.84	3.27	94.24	15.61					32.1	2.89
Noir	01 08 96	2		72.54	1.29	2.60	5.01	10.04	1.94	12.64	5.38	77.1	4.45
Noir	09 08 96	2		129.95	2.16	6.37	19.73	12.20	3.46	18.57	20.03	33.27	2.42
Raymond	06 06 96											45.07	1.92
Raymond	19 06 96											47.87	0.58
Raymond	03 07 96	2	20.15	383.35								50.54	1.88
Raymond	16 07 96	2	20.5	318.18		5.00	8.49					45.71	3.76
Raymond	16 07 96	2	20.5	318.18		11.29						45.71	3.76
Raymond	25 07 96	2	20.5	278.66	2.01		55.42					40.73	1.62
Raymond	25 07 96	2	20.5	278.66	2.01	11.91	44.76	1.83	2.12	13.74	44.81	40.73	1.62
Raymond	08 08 96	2		372.62	1.48	13.41	1.40	0.43	1.22	13.84	1.86	53.63	1.08

Raymond	08 08 96	2		372.62	1.48	12.73	8.86					53.63	1.08
Raymond	03 07 96	4	17.47	430.32									
Raymond	03 07 96	6	10.7	459.97									
Siesta	18 06 96											40.5	1.72
Siesta	26 06 96											42.79	0.22
Siesta	11 07 96	2	21	364.26	3.50	13.57	62.63	62.72	18.12	76.29	65.19	38.97	2.86
Siesta	24 07 96	2		402.62	0.88	20.38	1.83					53.32	2.6
Siesta	24 07 96	2		402.65	0.88	17.14	0.99					53.32	2.6
Siesta	07 08 96	2		429.97	9.23	36.75	46.40					42.59	3.26
Siesta	07 08 96	2		429.97	9.23	27.68	11.54	0.25	2.91	27.93	11.90	42.59	3.26
Siesta	15 08 96	2		459.55	1.54		19.71					121.56	5.64
Siesta	15 08 96	2		459.55	1.54	14.67	5.67	6.47	6.50	21.15	8.62	121.56	5.64
Thibault	06 06 96											45.71	30.14
Thibault	14 06 96											30.83	2.64
Thibault	24 06 96											26.26	1.14
Thibault	08 07 96	2		132.34	0.78	26.33	5.53					28.29	2.33
Thibault	08 07 96	2		132.34	0.78	19.01	10.33					28.29	2.33
Thibault	19 07 96	2	22.5	167.76	2.05	95.09	17.02					33.38	5.08
Thibault	02 08 96											55.18	10.51
Thibault	09 08 96	2		213.86	1.63	91.90	8.98	6.48	2.87	98.39	9.42	37.77	4.23
Triton	16 05 96	1	12.3	145.11	2.18								
Triton	10 06 96											16.21	4.08
Triton	21 06 96											17.99	1.59
Triton	05 07 96	2		108.57		1.88	43.64	12.51	4.67	14.39	43.89	18.44	0.27
Triton	05 07 96	2		108.57		7.90	4.86	20.11	9.32	28.01	10.51	18.44	0.27
Triton	17 07 96	2	20.9	99.73	0.84	8.38	0.80	3.68	0.69	12.06	1.05	16.97	1.92
Triton	19 07 96	2		99.73	0.60	7.80	3.93	5.72	1.14	13.52	4.09		
Triton	26 07 96											21.61	2.6
Triton	06 08 96	2		119.78	2.22	7.94	2.43	7.61	8.53	15.55	8.87	23.63	0.54
Triton	15 08 96	2		114.57	0.81	10.87	1.25	-5.90	2.19	4.97	2.52	31.25	2.1

[*] All rates are expressed as μg C / day. Pnet is net primary production, Pgross is gross primary production, Resp. is respiration, TP is total phosphorus concentrations ug /L. (SE) is the standard error. n=7 replicates for all metabolic measurements, n=3 for TP measurements.

Raw Size-Abundance data (size classes are in grams, assuming unit density; abundance is number of individuals per square metre):

lake	date	mon.	year	1.33E -05	2.37E -05	4.22E -05	7.50E -05	1.33E -04	2.37E -04	4.22E -04	7.50E -04	1.33E -03	2.37E -03	4.22E -03	7.50E -03	1.33E -02	2.37E -02
achigan	16	06	1995	3906	2066	2586	2384	1716	1146	642	180	30	0	0	0	0	0
achigan	18	07	1995	6164	2920	4152	3456	1920	1000	760	384	76	16	0	0	0	0
achigan	10	08	1995	9110	4146	2442	1210	986	664	348	174	64	8	4	0	0	0
berthier	04	07	1995	17624	6910	3856	2154	1328	940	724	562	138	16	6	0	0	0
berthier	27	07	1995	10064	3240	1760	1148	1028	658	424	166	16	0	0	0	0	0
berthier	23	08	1995	2276	682	544	470	356	214	80	34	6	2	0	0	0	0
chertsey	15	06	1995	7178	4544	4684	3548	2886	2260	1454	738	516	120	38	12	0	2
chertsey	13	07	1995	3342	2528	3196	2038	1388	1040	536	242	158	54	4	0	0	0
chertsey	09	08	1995	5160	3440	4330	3122	2172	1236	502	140	52	12	2	0	0	0
coeur	21	07	1995	7720	2228	1192	612	286	202	202	156	74	32	2	0	0	0
coeur	11	08	1995	1330	408	132	48	20	8	4	6	2	0	0	0	0	0
connelly	20	06	1995	6996	4070	4388	3624	2828	1744	678	216	26	4	0	0	0	0
connelly	19	07	1995	4388	3370	3812	2974	2024	874	298	52	8	2	0	0	0	0
connelly	15	08	1995	1592	1492	2108	1654	1816	834	216	32	4	0	0	2	0	0
cristal	28	06	1995	3896	3262	4272	3596	2684	1968	1526	1258	758	144	22	4	0	0
cristal	25	07	1995	4456	2538	3558	2404	1242	694	412	310	122	12	0	0	2	0
cristal	22	08	1995	2978	2706	4170	2298	1266	508	268	126	30	4	0	0	0	0
croche	16	5	1995	4810	2535	3222	2780	1845	966	715	480	118	11	0	0	0	0
croche	16	5	1995	4961	2788	3593	3224	1978	1031	739	432	107	20	1	0	0	0
croche	16	5	1995	4302	2843	3840	3360	1992	973	743	420	106	15	0	0	0	0
croche	16	5	1995	5065	3172	4222	4038	3028	1711	1125	594	168	22	0	0	0	0
croche	16	5	1995	4289	2808	3719	3501	2333	1296	859	553	200	27	1	0	0	0
croche	16	5	1995	3306	1748	1948	2222	1836	1318	576	202	48	0	0	0	0	0
croche	16	05	1995	5390	3365	4471	4820	3786	2973	1519	827	128	29	0	0	7	0
croche	16	05	1995	6809	3765	4920	4578	3914	2624	1041	456	100	14	0	0	0	0
croche	25	5	1995	3450	2346	2831	2246	1745	954	521	305	73	7	0	0	0	0
croche	25	5	1995	5401	3701	4352	3417	2722	1615	778	402	100	9	0	0	0	0
croche	25	5	1995	4249	2936	3629	3082	2613	1665	1015	572	193	35	2	0	0	0
croche	25	5	1995	4992	3262	3370	2634	1942	1214	724	392	252	98	10	0	0	0
croche	25	05	1995	9875	6831	7672	6410	5533	4150	2938	1797	378	50	0	0	0	0
croche	25	05	1995	7422	4513	4521	2966	1676	891	250	185	21	7	0	0	0	0
croche	4	6	1995	7629	2816	2071	1036	689	352	91	9	2	0	0	0	0	0
croche	04	06	1995	6203	5283	5740	4278	3608	2930	2267	1504	635	314	50	0	0	0
croche	08	06	1995	4792	3500	4040	3290	2636	1514	642	268	54	2	0	0	0	0
croche	11	07	1995	2121	1793	1849	1475	1232	814	475	491	189	38	2	0	0	0
croche	04	08	1995	3836	1180	682	376	190	126	76	64	14	8	0	0	0	0
croche	21	09	1995	1034	463	428	143	135	71	43	14	0	0	7	0	0	0
cromwell	17	5	1995	2416	1186	1113	855	889	634	253	43	6	1	0	0	0	0
cromwell	17	5	1995	2277	1070	1028	862	920	652	217	49	6	0	0	0	0	0
cromwell	17	5	1995	2107	1016	996	795	916	678	209	51	6	0	0	0	0	0
cromwell	17	5	1995	2691	1502	1398	1028	951	593	220	47	7	3	0	0	0	0

cromwell	17	5	1995	2813	1552	1464	982	891	612	211	44	11	1	0	0	0	0
cromwell	17	5	1995	2425	1269	1242	979	877	599	167	26	4	0	0	1	0	0
cromwell	17	5	1995	3652	1781	1673	1171	1129	1009	447	109	14	1	0	0	0	0
cromwell	17	5	1995	3516	1731	1593	1191	1289	916	374	98	15	2	0	0	0	0
cromwell	17	5	1995	2860	1431	1322	1108	1238	948	412	106	12	0	0	0	0	0
cromwell	29	5	1995	4960	2808	2482	1440	934	596	250	56	0	2	2	0	0	0
cromwell	29	05	1995	7658	5469	5747	3251	2118	1070	499	78	7	0	0	0	0	0
cromwell	6	6	1995	6598	3424	3800	2560	1516	936	332	66	4	8	0	0	0	0
cromwell	06	06	1995	11052	9135	9091	4278	3075	1604	357	134	89	0	0	45	0	0
cromwell	06	06	1995	10963	8200	7576	3966	2718	1426	579	178	0	0	0	0	0	0
cromwell	06	06	1995	10829	6595	5392	2629	980	490	89	0	0	0	0	0	0	0
cromwell	06	06	1995	8763	7094	7715	5554	4685	2503	991	292	36	7	0	0	0	0
cromwell	06	06	1995	10545	7922	9590	6246	5419	3080	1070	207	43	21	0	7	0	0
cromwell	06	06	1995	9447	7572	8307	7023	4856	3166	1127	242	121	21	107	29	7	0
cromwell	06	06	1995	8357	7087	8421	6267	4948	3515	1483	314	121	57	78	43	21	0
cromwell	06	06	1995	8998	7166	8777	6645	5027	3672	1355	299	107	36	71	43	14	0
cromwell	06	06	1995	19029	12077	10740	5036	4144	1515	1070	267	312	89	45	0	0	0
cromwell	06	06	1995	11898	7041	7531	4501	2317	1337	713	134	45	0	89	45	0	0
cromwell	06	06	1995	9225	5615	5169	3342	2139	758	357	45	45	0	89	45	0	0
cromwell	21	06	1995	4699	3708	5091	3986	3351	2624	1077	321	36	7	7	0	0	0
cromwell	21	06	1995	5861	4613	6403	6004	5184	3658	1790	349	50	0	0	0	0	0
cromwell	18	07	1995	2052	778	960	836	494	258	96	18	10	2	0	0	0	0
cromwell	16	08	1995	786	246	176	150	158	54	30	4	4	0	2	0	0	0
cromwell	21	09	1995	4642	2232	1768	1169	1191	542	150	14	0	0	0	0	0	0
desiles	14	06	1995	4736	2326	2054	1884	1856	1410	748	430	312	106	10	0	0	0
desiles	14	07	1995	3274	2088	2016	1188	708	376	252	262	218	92	16	2	0	0
desiles	07	08	1995	4338	2238	2366	1392	926	480	314	220	152	74	10	0	0	0
desjardins	27	06	1995	3308	2220	2404	1970	1478	860	336	74	8	4	0	0	0	0
desjardins	26	07	1995	5428	2154	1428	708	358	166	28	0	0	0	0	0	0	0
desjardins	17	08	1995	3902	1740	1362	706	364	142	42	28	2	0	0	0	0	0
dufresne	13	06	1995	5754	3502	3860	2446	2072	1572	1076	442	86	24	0	0	0	0
dufresne	11	07	1995	4658	2748	2872	2198	2008	1170	532	180	32	4	2	0	0	0
dufresne	08	08	1995	2066	308	116	28	24	22	12	10	4	2	2	0	0	0
geai	29	05	1995	7736	4763	4820	3907	2588	2253	1882	1419	435	78	14	0	0	0
geai	29	05	1995	7351	4920	5355	4143	3308	2189	1077	1234	1112	342	78	71	14	14
geai	29	05	1995	6816	4656	5611	3943	3080	2039	1291	1433	1512	848	285	150	57	29
geai	21	06	1995	2572	2096	2484	1816	1304	818	296	132	58	38	24	30	16	4
geai	21	06	1995	4642	4299	5590	4228	3266	2417	1012	521	135	50	64	64	29	0
geai	18	07	1995	2552	1798	1720	1092	1064	588	342	84	34	58	58	18	6	2
long	26	06	1995	18454	6824	4550	2806	2076	1734	1460	968	224	44	0	2	2	0
long	24	07	1995	578	466	706	434	236	132	88	22	6	2	0	0	0	0
long	14	08	1995	1332	810	1046	642	286	116	34	12	10	8	0	0	0	0
mandeville	04	07	1995	3634	2248	2338	1594	1174	534	118	14	0	0	0	0	0	0
mandeville	27	07	1995	6910	3732	3218	1888	1158	352	58	2	0	0	0	0	0	0
mandeville	23	08	1995	6386	2158	1892	1022	456	176	44	16	2	0	0	0	0	0
manitou	19	06	1995	5468	3528	3686	3202	3100	2786	1862	1164	356	40	4	0	0	0
manitou	20	07	1995	15068	5900	4166	2380	1606	1294	898	854	352	82	6	0	0	0
manitou	10	08	1995	26896	13896	7680	2618	1250	956	744	364	74	12	0	0	0	0

marois	16	06	1995	4452	2442	3494	4260	3690	3156	2340	1616	958	450	114	18	0	0
marois	19	07	1995	11000	5360	7172	9072	8512	5660	3004	1768	796	244	84	4	0	0
marois	15	08	1995	1916	800	1264	1932	2638	1446	544	146	38	16	6	2	0	0
matambin	04	07	1995	18344	9164	9292	6372	4092	2096	668	120	20	0	0	4	0	0
matambin	01	08	1995	4470	1764	1834	1044	694	368	190	60	22	26	0	0	0	0
matambin	23	08	1995	7348	2880	2726	1512	690	188	36	6	4	0	0	0	0	0
montagne noir	13	06	1995	4788	3420	3268	2654	2074	1478	938	838	576	184	36	6	2	0
montagne noir	11	07	1995	5066	3658	3586	2820	2168	1248	524	360	118	40	4	2	0	4
montagne noir	08	08	1995	3770	2778	2548	1446	926	544	296	132	56	2	2	0	0	0
noir	03	07	1995	2356	1300	2364	2068	924	360	80	8	0	0	0	0	0	0
noir	31	07	1995	842	200	110	76	62	30	16	8	6	0	0	0	0	0
noir	18	08	1995	466	108	28	24	4	4	0	0	0	0	0	0	0	0
olgivy	27	06	1995	5316	3748	3970	2978	2406	1678	1012	728	368	96	10	0	0	0
olgivy	26	07	1995	7076	3138	3088	1866	1060	586	268	174	136	40	12	0	0	0
olgivy	17	08	1995	3952	2048	1840	1216	794	554	204	144	128	24	6	0	0	0
patrick	06	07	1995	2928	2058	1998	1194	756	492	458	436	82	8	0	0	0	0
patrick	02	08	1995	7032	2062	2008	1252	748	468	248	142	70	20	2	0	0	0
patrick	25	08	1995	6470	2410	1930	1222	564	346	210	94	72	30	2	0	0	0
pontbriand	15	06	1995	82	36	30	23	12	4	2	1	0	0	0	0	0	0
pontbriand	13	07	1995	174	78	48	20	24	4	10	2	0	6	4	0	0	0
pontbriand	09	08	1995	122	78	68	34	12	8	0	2	0	0	0	0	0	0
quatre	29	06	1995	6430	2936	2050	724	326	140	68	14	12	4	0	0	0	0
quatre	28	07	1995	1068	272	140	38	20	18	6	2	0	0	0	0	0	0
quatre	16	08	1995	794	180	64	58	40	26	4	0	0	0	0	0	0	0
rawdon	07	07	1995	4478	2650	2940	1606	650	192	32	4	2	0	0	0	0	0
rawdon	01	08	1995	3082	1654	1534	906	418	210	50	2	0	0	0	0	0	0
rawdon	21	08	1995	1828	652	430	130	46	12	8	0	0	0	0	2	0	0
raymond	06	07	1995	4168	2038	1876	1226	1064	736	260	52	4	0	0	0	0	0
raymond	02	08	1995	2138	1480	1910	1614	1266	842	328	112	18	4	2	4	0	0
raymond	24	08	1995	982	530	470	318	218	146	62	12	2	4	0	0	0	0
siesta	28	06	1995	9074	3980	3254	1950	954	362	78	8	0	0	0	0	0	0
siesta	25	07	1995	4784	2912	2498	1256	568	172	22	4	0	0	0	0	0	0
siesta	22	08	1995	4872	2588	2580	1802	886	248	30	2	0	0	0	0	0	0
thibault	10	07	1995	902	268	198	112	56	18	2	6	2	0	2	0	0	0
thibault	03	08	1995	2910	538	272	82	20	4	0	0	2	0	0	0	0	0
thibault	25	08	1995	7616	2624	1026	236	66	26	4	6	2	0	0	0	0	0
triton	16	5	1995	2624	1413	1249	825	362	124	29	4	0	0	0	0	0	0
triton	16	5	1995	2575	1396	1236	746	318	97	18	3	0	0	0	0	0	0
triton	16	5	1995	2507	1389	1258	669	352	94	13	3	0	0	0	0	0	0
triton	16	5	1995	2854	1599	1481	867	443	141	30	5	0	0	0	0	0	0
triton	16	5	1995	2868	1580	1526	894	369	72	11	1	0	0	0	0	0	0
triton	16	5	1995	2631	1443	1335	761	336	110	16	0	0	1	0	0	0	0
triton	16	5	1995	2308	1048	1002	486	221	81	14	8	1	1	0	0	0	0
triton	16	5	1995	2324	1069	878	482	181	32	5	0	1	0	0	0	0	0
triton	16	5	1995	2178	1020	803	442	176	34	1	2	1	0	0	0	0	0
triton	26	5	1995	2841	1952	1929	1246	716	340	60	12	0	0	0	0	0	0
triton	26	5	1995	5867	3290	3148	1642	701	186	31	5	0	0	0	0	0	0

triton	26	5	1995	2405	1562	1483	918	503	172	44	10	4	0	0	0	0	0
triton	09	06	1995	7772	4692	4898	2938	1291	513	150	93	21	21	7	0	0	0
triton	12	07	1995	7547	3090	2984	2228	1779	1143	487	97	4	2	1	0	0	0
triton	03	08	1995	716	250	156	68	16	6	6	4	0	0	0	0	0	0
triton	21	09	1995	324	86	56	34	38	10	4	4	2	0	0	0	0	0
achigan	04	06	1996	14750	9581	9269	7932	4679	1961	668	89	134	45	0	0	0	0
achigan	12	06	1996	18984	12701	12389	9002	5838	3209	1471	936	446	0	0	0	0	0
achigan	25	06	1996	14305	10695	8155	5882	3743	2406	1515	936	134	0	0	0	0	0
achigan	09	07	1996	11765	4857	4456	2986	1292	1025	223	223	0	45	0	0	0	0
achigan	17	07	1996	12790	7932	7130	6952	4234	2139	1114	1292	223	0	0	0	0	0
achigan	31	07	1996	8467	4590	4724	3565	2496	1248	401	357	312	45	45	0	45	0
achigan	14	08	1996	9135	4991	5615	6194	7620	4857	2763	1515	713	89	0	0	0	0
berthier	13	06	1996	24020	18093	17068	11230	7175	3565	891	357	45	0	45	0	0	0
berthier	27	06	1996	22861	14572	14349	11542	6506	3699	1560	579	134	0	0	0	0	0
berthier	10	07	1996	20455	12879	12790	8066	4545	1783	847	1381	357	45	45	0	0	0
berthier	23	07	1996	3119	1916	2629	1515	713	312	89	45	45	0	0	0	0	0
berthier	13	08	1996	4501	2629	4055	2362	2362	2228	802	401	89	45	0	0	0	0
chertsey	12	06	1996	26203	14394	12611	6506	4545	3209	1426	802	802	267	0	0	0	0
chertsey	17	06	1996	9849	6996	8824	4947	2897	1649	713	535	579	490	134	45	0	0
chertsey	25	06	1996	17513	10428	8690	4635	2094	1159	891	357	312	45	134	0	0	0
chertsey	09	07	1996	19118	14572	13057	8244	5080	4234	1916	1649	847	579	45	89	45	0
chertsey	31	07	1996	11809	8155	11007	5838	3298	2005	1159	1114	1025	668	45	0	0	0
chertsey	14	08	1996	8601	6863	8512	4189	2406	1203	1025	624	802	178	0	0	0	0
connelly	18	06	1996	14750	10383	13636	11141	9046	5258	2941	847	45	0	0	0	0	0
connelly	26	06	1996	13770	9269	8868	8957	6105	3610	1560	535	45	134	45	0	0	0
connelly	11	07	1996	15731	11408	9358	7709	3521	2317	668	134	223	0	45	0	0	0
connelly	24	07	1996	20143	12968	13235	10027	7264	3521	758	45	0	0	0	0	0	0
connelly	07	08	1996	24688	16800	18761	12077	8200	3922	1604	267	45	0	0	0	0	0
connelly	15	08	1996	10829	8690	11765	9759	7442	3476	936	223	0	0	0	0	0	0
croche	12	08	1996	9135	9225	12255	7709	6150	4545	1649	1025	490	178	0	0	0	0
croche	12	05	1996	5169	1693	1426	1025	1426	579	312	89	0	0	0	0	0	0
croche	20	05	1996	3877	1916	3075	1604	1515	1025	89	223	0	0	0	0	0	0
croche	04	06	1996	9492	8467	9269	7308	6016	5526	2184	579	624	89	0	0	0	0
croche	05	06	1996	9492	9314	10918	8645	6640	5481	2005	668	267	223	0	0	0	0
croche	17	06	1996	12032	12611	13414	9269	9314	8422	5125	3030	1025	535	0	0	0	0
croche	02	07	1996	12389	11096	15419	10829	10517	5704	3565	2585	891	267	0	45	45	0
croche	22	07	1996	6150	4590	6150	2406	1783	847	267	312	134	89	0	0	0	0
croche	29	07	1996	11631	7531	7888	4367	1961	713	713	312	312	45	0	0	0	0
croche	12	08	1996	13146	8467	11453	8378	5392	2585	1961	1070	223	0	45	0	0	0
croche	10	09	1996	15330	8610	10220	6790	4060	2030	1960	3220	6720	3290	280	0	0	0
croche	10	09	1996	22960	11200	14070	12460	4550	1820	910	3220	8820	4130	770	70	0	0
croche	10	09	1996	18060	9240	10010	6160	1540	1260	700	700	910	420	0	0	0	0
croche	10	09	1996	74690	45500	41860	23030	9660	2660	210	0	0	0	0	0	0	0
croche	10	09	1996	73990	46480	41370	21280	7770	1400	140	140	0	0	0	0	0	0
croche	10	09	1996	65380	39900	30450	14280	3990	910	140	70	0	0	0	0	0	0
cromwell	12	05	1996	4768	1872	2050	1693	1070	847	267	0	0	0	0	0	0	0
cromwell	17	06	1996	11230	5615	4501	3387	2585	1471	401	134	0	0	0	0	0	0
cromwell	02	07	1996	12121	5927	3610	1292	1471	357	89	0	0	0	0	0	0	0

cromwell	22	07	1996	17558	10918	8111	4144	2184	713	45	45	0	0	0	0	0	0
cromwell	29	07	1996	13013	5838	5303	3966	2273	802	178	89	0	0	0	0	0	0
cromwell	12	08	1996	4679	1381	1426	1292	713	178	0	89	134	0	0	0	0	0
cromwell	10	09	1996	20090	6650	7350	6300	4410	630	210	0	0	0	70	0	0	0
cromwell	10	09	1996	13580	4130	4410	5040	2660	630	140	0	0	0	0	0	0	0
cromwell	10	09	1996	14630	4340	7280	7210	5320	1330	350	70	0	0	0	0	0	0
geai	11	06	1996	12745	6952	6774	4902	4189	3476	2941	1025	223	45	0	45	45	0
geai	20	06	1996	10116	6373	6640	6952	3164	2317	1827	802	267	134	0	0	89	45
geai	04	07	1996	6952	4635	6729	3966	2763	1471	802	267	134	45	178	45	0	45
geai	18	07	1996	8021	3966	5303	3387	1961	1025	535	668	89	0	0	134	223	89
geai	30	07	1996	1649	802	980	535	579	357	267	134	0	0	223	45	89	0
geai	06	08	1996	7442	3832	4635	2807	1292	1114	1515	446	223	89	134	89	89	134
geai	10	09	1996	10570	8750	8190	5530	10080	6090	4130	1400	70	140	0	0	0	0
geai	10	09	1996	7420	5040	5880	3920	7280	3570	2590	420	70	70	0	0	0	0
geai	10	09	1996	7700	5880	4970	4690	6860	4690	3500	1190	0	0	0	0	0	0
mandeville	13	06	1996	16711	11586	11854	7041	4724	3164	713	134	0	0	0	0	0	0
mandeville	27	06	1996	21257	13547	10918	7308	5214	2005	624	45	0	0	0	0	0	0
mandeville	10	07	1996	18360	11720	8601	2986	758	401	0	0	0	0	0	45	0	0
mandeville	23	07	1996	20365	13324	8556	5214	4100	1783	312	45	0	0	0	0	0	0
mandeville	13	08	1996	67291	26426	18405	9447	4590	1159	312	0	0	0	0	0	0	0
manitou	06	06	1996	12611	9225	7620	3387	2451	980	579	312	134	45	45	0	0	0
manitou	19	06	1996	18449	16488	19251	14661	12299	9180	5214	2273	401	357	0	0	0	0
manitou	03	07	1996	13102	10517	11720	6774	6239	6328	3075	1426	535	0	0	0	0	0
manitou	16	07	1996	15642	11586	11765	7799	5526	3521	2273	1248	758	223	0	0	0	0
manitou	25	07	1996	16221	11364	12077	5838	4189	3387	1961	1381	535	89	0	0	0	0
manitou	08	08	1996	23218	17335	18093	10071	5125	3209	2540	1604	1203	178	0	0	0	0
montagne noir	11	06	1996	19920	10918	11230	7264	5526	3699	1203	401	223	45	0	0	0	0
montagne noir	20	06	1996	7175	3654	3521	3209	2941	1693	1070	312	45	0	0	0	0	0
montagne noir	04	07	1996	10383	5971	5971	3922	5036	3164	1248	891	89	134	45	0	0	0
montagne noir	18	07	1996	11586	6150	7264	4144	3298	2406	936	624	267	89	0	0	0	0
montagne noir	30	07	1996	27184	16399	17736	9715	7308	4456	2941	1426	1070	178	89	0	0	0
montagne noir	06	08	1996	30660	21524	20499	13458	9091	5080	3431	1604	1070	267	45	0	0	0
noir	07	06	1996	14439	7709	6016	2451	713	401	45	45	0	0	0	0	0	0
noir	14	06	1996	16444	9537	7932	3654	1025	134	0	0	0	0	0	0	0	0
noir	28	06	1996	10606	4456	3743	936	802	134	45	0	0	0	0	0	0	0
noir	12	07	1996	11988	6239	4501	1783	490	223	45	0	0	0	0	0	0	0
noir	18	07	1996	4234	2362	2451	1604	891	178	45	0	0	0	0	0	0	0
noir	01	08	1996	3832	1693	1604	1471	535	134	45	45	0	0	0	0	0	0
noir	09	08	1996	2941	1159	1337	1471	624	178	178	0	0	0	0	0	0	0
raymond	06	06	1996	23173	11141	7398	2139	446	89	89	0	0	0	0	0	0	0
raymond	19	06	1996	8244	3654	2718	713	178	0	0	0	0	0	0	0	0	0
raymond	03	07	1996	11096	6105	4011	2718	1604	891	267	89	0	0	0	0	0	0
raymond	25	07	1996	7888	4144	3743	2540	1560	1114	490	223	0	0	0	0	0	0
siesta	18	06	1996	20722	16711	17201	13235	7398	3387	758	89	0	0	0	0	0	0
siesta	26	06	1996	14305	8289	9893	5214	2317	668	223	0	0	0	0	0	0	0
siesta	11	07	1996	18137	10071	11141	5615	2451	579	0	0	0	0	0	0	0	0

siesta	24	07	1996	14260	7487	5125	2852	980	267	0	0	0	0	0	0	0	0
siesta	07	08	1996	23084	15463	13770	7888	3209	936	134	0	45	0	0	0	0	0
siesta	15	08	1996	23396	16444	18271	10963	5704	980	89	0	0	0	0	0	0	0
thibault	07	06	1996	22906	13636	13770	6907	4234	2005	2005	936	579	0	89	0	0	0
thibault	14	06	1996	14127	7888	6952	4991	2273	1426	312	0	0	0	0	0	0	0
thibault	24	06	1996	15686	8289	5437	2228	802	178	134	134	0	0	0	0	0	0
thibault	08	07	1996	2228	1783	2585	2674	2451	936	134	0	0	0	0	0	0	0
thibault	19	07	1996	5927	2763	1560	1114	579	223	45	89	0	0	0	0	0	0
thibault	02	08	1996	3743	1961	2184	802	357	89	0	0	0	0	0	0	0	0
thibault	09	08	1996	12344	7130	7799	5036	2451	312	45	0	0	0	0	0	0	0
triton	05	06	1996	6996	2496	1738	535	401	89	45	0	0	0	0	0	0	0
triton	21	06	1996	11007	4501	3565	1872	579	178	89	0	0	0	0	0	0	0
triton	05	07	1996	12522	8289	7888	5437	2362	713	89	0	0	0	0	0	0	0
triton	10	07	1996	3654	1025	713	223	89	45	0	0	0	0	0	0	0	0
triton	15	07	1996	8467	5036	5660	3521	1025	357	267	0	0	0	0	0	0	0
triton	26	07	1996	15686	11408	15775	11988	5793	2094	401	178	0	0	45	0	0	0
triton	05	08	1996	1649	1203	3342	1693	980	223	45	45	0	0	0	0	0	0
triton	16	08	1996	3966	1693	3521	2807	1025	446	45	0	0	0	0	0	0	0

— *Appendix 10* —

CALCULATION OF WATER COLUMN STABILITY

Water column stability is defined as the amount of work required to mix an entire lake to uniform density.

If we define Q as the depth where the mass of water above equals the mass of water below, then:

Stability

$= $ the work required to lift the water column from $Q_{\text{stratified}}$ to Q_{mixed}

$= $ (mass of water) * (gravitational acceleration) * $(Z - Q_{\text{mixed}})$ / (lake surface area)

$= g / \text{Area}_{Z=0}\ \text{I}\ (\rho_Z - \rho_{\text{mixed}})\ \text{Area}_Z\ (Z - Q_{\text{mixed}})\ dZ$

where g is the gravitational acceleration, 9.8 m s^{-2} and ρ_Z is the density of water at a given depth Z. Thus, any density changes due to thermal, chemical or turbidity influences increases Z and thus the work required to completely mix the water column (Cole 1979:182).