DOMAINS OF SELECTION


I remember distinctly the first time George Williams’ writings had an impact on me: I was reading his distinguished Adaption and Natural Selection (1966) while on a train heading to Columbia University to attend graduate school. That book was widely read and discussed in graduate courses at the time, and deservedly so. It forcefully argued that if natural selection is to be invoked as a mechanism of evolutionary change, its locus of action should be sought first at the level of individual organisms, and only if that failed to explain the observations should higher-level selection be considered. A reader of this new book might well conclude that Williams has abandoned this line of thinking for one that sees selection operating, ubiquitously, above the level of individual organisms.

Natural Selection: Domains, Levels, and Challenges paints a much broader canvas than the earlier book, covering ideas of selection at different hierarchical levels, macroevolution, optimization, phylogenetic and developmental constraint, diversity, species concepts, morphological stasis, and numerous other topics. Because of this breadth, many evolutionary biologists should be attracted to it, and most undoubtedly will find much to think about. I think many readers will be frustrated, however, because relatively little space is devoted to any one topic, and rather than develop a line of argument in depth, the discussion often becomes a vehicle for the author’s opinions, frequently with little or no empirical support.

Like others before him, Williams wants a unified view of selection, and to this end he proposes two domains of selection: the codical domain, in which the units of selection (codices) are information, and the material domain, which includes the carriers (so-called vehicles or interactors of some authors) of that information. Individual selection is then the mechanism operating at the genic level via variance in fitness among individual organisms. Up to this point, most workers probably will not find this approach much different from the standard view, but Williams extends it to higher hierarchical levels. Here, gene pools or groups of related gene pools (what Williams calls clades) are the units within the codical domain, and phylads (the material groups having those gene pools) are the units in the material domain. He proposes that “all levels of genealogical inclusiveness from local gene pools to classes and phyla may be subject to selection” (p. 24), and although he identifies individual selection as the only force leading to adaptation, Williams also sees higher-level clade selection as demonstrably common.

In developing his discussion, there is surprisingly little critical analysis of the literature on levels of selection that has burgeoned over the last 10 or 14 years (indeed, key articles are not even cited). Along the way, moreover, Williams plays fast and loose with the terminology and conceptual ideas of that literature, which can only add confusion to our understanding of historical patterns of evolutionary change.

Thus, Williams effectively equates selection with “sorting”: if there is a change in diversity over time, that manifests selection. In contrast, numerous workers have argued that this approach will confound identifying the locus of causation for observed changes in diversity. It has been proposed, for example, that higher-level diversity patterns might be due to the statistical summation or “effects” (Vrba’s term) of within-population selection on individuals, to real higher-level selection for emergent properties of the group, or to other non-selective causes affecting speciation and extinction rates. To use selection as an umbrella term for all of these changes in diversity implies that the term is descriptive of a change in pattern (e.g., among phenotypes within populations or among species within higher taxa), rather than expressive of a potential cause of those changes.

Williams uses clade—as in his clade selection—in a way entirely at variance from the common use of that term in systematic and evolutionary biology, where it means a monophyletic group of species. Some key scientific issues are at stake here, and imprecision in language can obscure those issues. It has been conjectured, for example, that one monophyletic group (say a family or order) can replace another via competition, that predation can cause the decline and eventual extinction of a major group, and that the characteristics of some species can causally increase or decrease the speciation rate of those groups. Having a causal understanding of these phenomena resides not in calling all of these “clade selection,” with its specific causal implications, but in attempting to sort out causation acting at the different hierarchical levels.

These issues are complicated but, partially as a result of defining and viewing selection in the way he does, Williams in some sense sweeps away the complexities of causal analysis: “There can be no question of the reality of phylad selection and resulting clade selection at all taxonomic ranks” (p. 50). In fact, there is a major question as to the truth of this assertion, as numerous articles have debated (again, many of these are neither cited nor discussed). A reader unfamiliar with the literature will not be able to make heads or tails of this debate by reading this book. Therefore, its value in undergraduate and graduate courses is compromised.

There are many other parts of the book that will surely raise the hackles of various specialists. Williams takes shots at numerous icons of current thought, but unfortunately many of those attacks seem misplaced. His critique of the notions of punctuated equilibrium and morphological stasis over time, for example, are clouded by misunderstandings about the relevant philosophical arguments (over the “individuality” of species), species concepts (the problems that the biological species concept has for historical analysis), and systematic theory and methodology (how one identifies historical units or what types of historical patterns we might predict given certain evolutionary scenarios). All of these topics have been discussed extensively in the literature, but again this work is barely mentioned.

Because this is a book written by George Williams, evolutionary biologists will want to consider it carefully.
Yet, its breadth of coverage may be its undoing. It does not make the case that a uniform view of selection can be applied across the different hierarchical levels, and its many unsupported assertions of rampant higher-level selection will surely not go unnoticed by those specialists in paleobiology and systematics whose research programs focus on the causal analysis of macroevolutionary patterns.

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CLIMATE CHANGE AND FISHERIES

This book’s title seems to offer an analytic basis for the policy decisions that must inevitably be made for fisheries in the eventuality of climate change. It contains 15 interesting case studies of fisheries’ ups and downs (mostly the latter). Each author’s contribution reviews the difficulties that management has faced and the many factors involved. Also, each author is acutely aware of the uncertainties of forecasting for fisheries, and each offers conclusions or lessons on the possible impacts of climate change.

Nevertheless, the editor’s introduction and summary (which might better have been combined) are unclear about the relationships among the book’s three titular subject elements. Nor do they provide a clear statement of the problems that fisheries may face. Rather, we are offered “forecasting by analogy,” which is “an attempt to respond to the consequences of yet-unknown environmental changes that might occur in the future, by looking at societal responses to recent environmental as well as societal (e.g., legal) changes” (emphasis added). The editor’s interests evidently lie in the sociopolitical aspects of fisheries, to the neglect of the biological and ecological, which are considered in some detail in the case studies. As a result, the book appears unfocused and may be of limited usefulness to policy makers.

It is abundantly clear that climate change could greatly complicate the predictive capacity for living resource management, especially within the coastal zone, where most fish and most fisheries occur and where climate change will first have major impacts in the form of sea-level rise, storm frequency alterations, and habitat change. The problems of forecasting for fisheries are abundant in the case studies and include: inadequate models (W. Wooster, king crab); alterations in industrial structures (E. Ueber and A. MacCall, California sardine); climatic events, such as El Niño (K. A. Muller and D. L. Fluharty, salmon); C. N. Caveides and T. J. Fik, Peru-Chile fisheries; habitat loss (R. Condrey and D. Fuller, shrimp); interrelationships among life history, industry, society, and ecological processes (L. E. Feingold, menhaden); sociopolitical factors (J. M. Acheson, Maine lobster; J. R. McGoodwin, Mexican fishery; M. H. Glantz, cod); predatory-parasitic species irruptions (H. A. Regier and J. L. Goodier, sea lamprey); climatic-oceanographic factors (R. S. Bailey and J. H. Steele, herring; A. S. Krovnin and S. N. Rodionov, herring; G. D. Sharp, Indian Ocean tuna); international fisheries politics and technology (Z. Russek, Poland-long-distance fisheries); and large-scale fluctuations in a coastal fishery (T. Kawasaki, sardine).

The summary by the editor and Feingold attempts to express insights, drawn from these case studies, about how future fisheries might respond to climate variability and change. Its conclusions include such vague statements as: “It is important to take societal changes into account,” “Climate change will likely have an uneven impact on the marine environment,” and “There is a strong need for an improvement in the scientific understanding of the interactions between societies, fish populations, and environmental changes.” Of course, but the real question is: How can decision makers and managers go beyond these basics to evolve specific procedures and potential solutions? Vague generalizations are not likely to be persuasive to the policy makers who will ultimately be responsible for altering how we handle fisheries and climate-change problems.

Subjects for fruitful scientific analyses are suggested by several of the authors, for example Caveides and Fik for the Peru-Chile fishery. They hypothesize that changing environmental conditions have produced marked changes in primary productivity and fish population levels in eastern boundary currents. Then they analyze long-term data series by means of a statistical model and posit that “the dampening effect of oceanic warming and reduced upwelling coupled with a sustained burden placed on the stock by overfishing, unleashed the dramatic decline of the anchovy fisheries in the southwestern Pacific.” This case offers an example of “the mixture of biological controls, the effects of climatic and oceanic variabilities and—perhaps more importantly—the national resource policies dictated by the economic imperatives imposed by international trade and world demand (p. 367).” The responsibility for fisheries declines is shown to be primarily overfishing; El Niño has become a scapegoat.

Knowledge of environmental effects on fish is not the same as forecasting for fisheries. Understanding fish involves natural history, biology, and ecology, which fishery models mostly ignore. Ecologically, the central point relates to the response of whole systems to climate change, what the rate and magnitude of change will be against the setting of natural variability, and whether these changes will be too fast and/or too great to sustain the fish—thus, the fishery. However, fishery science has long been plagued with a nonecological approach. Yield models, serving commerce, have mostly ignored the dynamics of the coastal-marine environment and of natural communities and have inevitably led almost everywhere to overexploitation. Recently, one of the case-study authors put the matter bluntly: “[F]ishery research was near the mainstream of ecology through the 20s, but the two disciplines have since been separated, with very little interchange of ideas or data in recent years. Ecologists are