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THEME SECTION

'Evolution' of fisheries science

Idea and coordination: Howard I. Browman

Application of evolutionary theory to fisheries science and stock assessment-management

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In addition to the often contradictory demands of industry, politicians, economists, and environmental/wildlife protection organizations, there are currently several sub-disciplines of marine science making persuasive cases for inclusion in the development of fisheries ecology, and in stock management practices. These include physical oceanography, reproductive biology, community ecology and — the focus of this Theme Section (TS) — evolutionary ecology. The essays (it is essential that they be viewed as such) that follow address several different aspects of this theme.

Jeffrey Hutchings' essay provides a somewhat historical perspective on the theme and represents a rationalization for the inclusion of evolutionary ecology in fish stock assessments and management practices. David Conover presents and discusses consequences of ignoring evolutionary ecology in the study and management of fishery resources. He focusses on evolutionary aspects of local adaptations in fish populations. Kevin Stokes and Richard Law consider commercial fishing as a massive, uncontrolled, experiment in evolutionary selection and discuss the effects of intense fishing pressure on several adaptive traits. Since Hutchings identifies the ecological models developed by Carl Walters and his colleagues (Pauly et al. 2000, Walters et al. 2000a, b) as potentially useful tools that will allow incorporation of evolutionary ecology into fishery science and fish stock assessment-management, the TS concludes with a contribution from Walters in which the conceptual basis for these models is presented, along with examples of their potential utility.

In all these essays it is argued that the application of theory from evolutionary ecology will improve the success of fishery resource management in the long term. While this may be true, assessment scientists can often not afford to think in terms of ecological time scales: the population dynamics of heavily exploited fish stocks change over proximate rather than ultimate time-scales. The challenge is to bridge time scales and to develop routine approaches and methods (sampling, data analysis, interpretative frameworks) for incorporating evolutionary theory more directly into fishery science and, thereby, support the sustainable management of the World's fish resources.

LITERATURE CITED

Pauly D, Christensen V, Walters C (2000) Ecopath, ecosim and ecospace as tools for evaluating ecosystem impacts on marine ecosystems. ICES J Mar Sci 57:697–706

Walters CJ, Pauly D, Christensen V, Kitchell JF (2000a) Representing density-dependent consequences of life history strategies in an ecosystem model: ECOSIM II. Ecosystems 3:70–83

Walters CJ, Pauly D, Christensen V (2000b) Ecospace: prediction of mesoscale spatial patterns in trophic relationships of exploited ecosystems, with emphasis on the impacts of marine protected areas. Ecosystems 2:539–554

Numerical assessment in the front seat, ecology and evolution in the back seat: time to change drivers in fisheries and aquatic sciences?

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Systems must be stressed before their strengths and weaknesses can be fully known. This seems true whether one is building a bridge or applying a set of analytical and research protocols in aid of the management of a natural resource. There can be little argument that the collapse of fish stocks worldwide has effected a level of stress sufficient to warrant critical examination of the palette of scientific contributions deemed adequate to paint robust caricatures of fish stock health. For example, many stock assessments have been predicated on the assumption that survey estimates of abundance, age-specific metrics of commercial catch, and a broad sense of the geographical limits of a commercially harvested fish population are all that one really requires to understand and predict the effects of fishing on fish populations. Yet, for many fisheries, we seem unable to predict either the susceptibility of fish stocks to collapse or their ability to recover therefrom. It is not unreasonable to argue that our generally depauperate knowledge of the ecology of targeted and non-targeted species, and of the natural and anthropogenic factors that influence their evolution by natural selection, has contributed significantly to this uncertainty (Frank & Leggett 1994).

The potential utility of an ecological and evolutionary framework in which to assess the effects of fishing was proffered as early as the 1880s, only to be swamped by the wake of technological development and scientific 'certainty' left by the paradigm of ocean inexhaustibility, the influence of which would persist for almost a century. For it was at the Great International Fisheries Exhibition in London in 1883 that Thomas Huxley posited

> …that the cod fishery, the herring fishery, the pilchard fishery, the mackerel fishery, and probably all the great sea-fisheries, are inexhaustible; that is to say that nothing we do seriously affects the number of fish.
>
> (Smith 1994).

Among other things, Huxley was impressed by the vast numbers of eggs that marine fish produce, suggesting to his audience that this great reproductive potential would prevent fishing from having any significant impact on fish stocks.

Periodically one hears a similar refrain today, albeit in a somewhat modified form. Because of their great fecundity, marine fish are somehow more resistant to over-exploitation and better able to recover from population collapse than fish with more modest egg productivity (see Hutchings 2001 for discussion). But, to an evolutionary ecologist, this refrain is fundamentally flawed because it obfuscates the importance of fecundity to fitness.

This was, in a sense, recognized at the same Fisheries Exhibition of 1883 by the English biologist Sir Ray Lankester, who argued, in effect, that the millions of young produced by marine fish are not superfluous. He outlined what was then a sophisticated theory that the fish in a specific area of the ocean are in equilibrium with their predators. He argued further that animal populations themselves are in equilibrium, such that 'those that survive to maturity in the struggle for existence merely replace those which have gone before' (Smith 1994).

Re-stated in today's terminology, when an animal population is at or near equilibrium, i.e., conditions under which selection is often assumed to have moulded life history traits such as fecundity, natural selection favours those individuals whose reproductive strategy allows them to produce enough offspring to replace themselves (Roff 1992).

But phylogenetic constraints coupled with the different challenges that different environments pose to organisms have conspired to produce a wide variety of reproductive strategies. For example, porbeagle sharks *Lamna nasus* produce 1 to 5 offspring every 1 to 2 yr for perhaps 10 or 15 yr (Scott & Scott 1988); this is the porbeagle's strategy for replacement. By contrast, Atlantic cod *Gadus morhua* produce several hundred thousand to a few million eggs every year for perhaps 5 to 10 yr (Chambers & Waiwood 1996); this is the cod's strategy for replacement. But, evolutionarily, the 2 strategies are equivalent in terms of their result—replacement at equilibrium. Clearly, survival from birth to maturity differs enormously between the 2 species. *That* and age at maturity, rather than fecundity, are the parameters of primary import to population growth and viability. Empirical support for this postulate lies in the observation that, among phylogenetically unrelated fishes, fecundity appears to have no effect on either maximum population growth rate, $r_{\max}$, (R. A. Myers & J.A.H. unpubl. data) or recruitment variability at low population sizes (Mertz & Myers 1996, Rickman et al. 2000).

One can, of course, legitimately argue that inclusion of ecology and evolution in fisheries science would not have significantly altered the recent history of over-exploitation. Nonetheless, it does seem unlikely that we could be worse off for having made the collection of basic ecologically relevant data on fishes, for at least the commercially targeted species, an integral and routine part of fisheries research. Interpreted within an ecological and evolutionary framework, comprehensive studies of life history, habitat selection, predator/prey interactions, and spawning/migratory behaviour would have provided a comprehensive knowledge base upon which to evaluate the influence of changes to age-specific fecundity and survival, habitat, community composition, and behaviour on population growth.

These ideas are neither novel nor new. The intellectual seeds of recognition that ecology and evolution may have a role in resource management were evident in the late 19th century (Smith 1994). Similarly, a cursory glance at the history of ecological and evolutionary research through the early- and mid-20th century reveals numerous attempts to identify the primary factors that affect population growth, e.g., interspecific interactions (Volterra 1926), density (Elton 1930), life history (Cole 1954), and habitat (MacArthur 1958). Indeed, Elton's (1930) prescient observation that,

> Changes in the population of one animal are really changes in the habitat of other animals

underscores the necessity of studying the effects of fishing on the community ecology of targeted and non-targeted species (Jennings & Kaiser 1998).

Few would disagree, of course, that the availability of more data, whatever the source, is always desirable. But given the sampling protocols and expertise required to comprehensively collect, analyse, and interpret biological data within an ecological and evolutionary framework, would the benefits of doing so outweigh the costs?

As stated earlier, it is only when systems are stressed that their strengths and weaknesses are revealed. When fish stocks are healthy and catches high, the questions asked of fisheries science often centre upon means of estimating population size and monitoring commercial catches. But, as recent experience with Northwest Atlantic cod has revealed, when fish stocks collapse, the questions asked of fisheries science tend not to be restricted to those that were asked previously. For example, does the slow rate of recovery of Northwest Atlantic cod fall within the constraints imposed by environmental and demographic stochasticity or not (Hutchings 1999)? What influences rate of increase when a population is reduced to historically low levels and comparatively few age classes (Frank & Brickman 2000, Hutchings 2000)? How might fishing, and low population size, affect cod mating behaviour and reproductive success (Hutchings et al. 1999)? What are the effects of interspecific interactions (Swain & Sinclair 2000) and fishing-induced habitat disturbance (Dorsey & Pederson 1998) on the survival of cod to maturity? Has intense fishing changed cod from an evolutionary perspective, e.g., by altering life histories to such a degree that populations grow at different rates today than they did in the past (e.g., Law 2000)?

Regarding this last point, the potential for fishing to effect significant evolutionary change within a population is no different than that of any other form of predator-induced mortality that differentially affects the survival of individuals of different ages and sizes. As Rijnsdorp (1993) put it, fisheries are essentially large-scale experiments on life history evolution.

There should be no debate, then, as to whether fishing represents a selective pressure effecting evolutionary change in exploited populations — clearly it must. This leads to questions concerning the type of responses to exploitation, the reversibility of these responses, and their consequences to population growth rate and, thus, sustainable rates of fishing mortality.

Life history responses to fishing can be the product of phenotypically plastic changes, possibly along norms of reaction for life history traits such as age at maturity and fecundity (Hutchings 1993, Nelson 1993), or of genetic changes caused by selection against genotypes whose fitness is reduced in the presence of fishing mortality (Handford et al. 1977, Law & Grey 1989). Empirical evidence consistent with the hypothesis that fishing effects evolutionary change (Stokes et al. 1993, Rochet 1998), having been discussed at least since the 1950s (Miller 1957), is available for both age (e.g., Rijnsdorp 1993) and size at maturity (Handford et al. 1977, Ricker 1981), and possibly fecundity (Law 1979, Koslow et al. 1995).

Furthermore, one could argue that an exceedingly limited understanding of the factors affecting the ecology and evolution of marine organisms has permitted a further tightening of the viability ratchets on marine organisms. What, for example, are the biological consequences of harvesting previously unexploited deep-sea elasmobranchs and teleosts, about which we know little? What risks, if any, does our increased harvesting of northern shrimp *Pandalus borealis* off Labrador and northern Newfoundland pose to the population growth rates of numerically depressed Atlantic cod and Atlantic salmon *Salmo salar*? How might the survival and habitat quality of demersal vertebrates and invertebrates be affected by the dragging of bottom trawls (Dorsey & Pederson 1998), or by the combination of hot water and high-pressure vacuums used to extract surf clams *Spisula solidissima* from the soft-bottomed substrate of the Grand Banks? What are the key critical elements of oceanic ecosystems most important to the sustainability of aquatic resources? Models such as ECOPATH and EcoSim (Walters et al. 2000) have the potential to provide insight into this last question, but such models are ultimately limited by the quality of ecological data upon which the model's parameters are based.

The primary objectives of evolutionary ecology and fisheries stock assessment are in many respects complementary. Ecological and evolutionary theory can be used to predict how changes to abiotic and biotic environments, through effects on age-specific survival and fecundity, influence a genotype's, and ultimately a population's, rate of increase, the parameter that ultimately determines a population's ability to sustain various levels of fishing mortality and to recover from collapse. The ability of a population to recover from collapse, for example, can be expected to decline with increasing age at maturity, reductions in the age structure of spawners, declining $r_{\max}$, and substantive changes to the abundance of closely interacting competitors, predators, and prey. In another area of concern, research in ecology and evolution informs us that the consequences of genetic and ecological interactions between escaped farmed and native species are, in many instances unlikely to be either neutral or positive. Adaptation to local environments, genetic differences arising from altered selection pressures and rearing environments, outbreeding depression, and different disease/parasite profiles suggest that the frequency and intensity with which escaped salmonids enter rivers will negatively influence wild stocks, predictions that are increasingly borne out by empirical studies (e.g., McGinnity et al. 1997, Fleming et al. 2000).

Ecology and evolution are, in effect, 'joined at the hip'. Ecology is the study of how physical and biological environmental factors influence the distribution and abundance of organisms. Evolution is predicated by changes in gene frequencies resulting from interactions between genotypes and their environment. Thus, environmental changes (including fishing) in age-specific rates of survival and fecundity can be expected to influence both the ecology and evolution of affected genotypes.

The ultimate value of studying the ecology and evolution of exploited fishes lies in the hope of eventually being able to predict how short- and long-term anthropogenic, biological, and physical environmental perturbations influence life history, rates of population increase, population persistence, and community composition. Viewed in this light, it seems difficult to argue that comprehensive knowledge of ecology and evolution, and the integration of that knowledge into fisheries and aquatic sciences, should not be among the scientific accoutrements of stock assessment.

LITERATURE CITED

Chambers RC, Waiwood KG (1996) Maternal and seasonal differences in egg sizes and spawning characteristics of captive Atlantic cod, *Gadus morhua*. Can J Fish Aquat Sci 53:1986–2003

Cole LC (1954) The population consequences of life-history phenomena. Q Rev Biol 29:103–137

Dorsey EM, Pederson J (eds) (1998) Effects of fishing gear on the sea floor of New England. Conservation Law Foundation, Boston, MA

Elton C (1930) Animal ecology and evolution. Clarendon Press, London

Fleming IA, Hindar K, Mjølnerød IB, Jonsson B, Balstad T, Lamberg A (2000) Lifetime success and interactions of farm salmon invading a native population. Proc R Soc Lond B 267:1517–1523

Frank KT, Brickman D (2000) Allee effects and compensatory population dynamics within a stock complex. Can J Fish Aquat Sci 57:513–517

Frank KT, Leggett WC (1994) Fisheries ecology in the context of ecological and evolutionary theory. Annu Rev Ecol Syst 25:401–422

Handford P, Bell G, Reimchen T (1977) A gillnet fishery considered as an experiment in artificial selection. J Fish Res Board Can 34:954–961

Hutchings JA (1993) Reaction norms for reproductive traits in brook trout and their influence on life history evolution affected by size-selective harvesting. In: Stokes TK, McGlade JM, Law R (eds) The exploitation of evolving resources. Springer-Verlag, Berlin, p 107–125

Hutchings JA (1999) The influence of growth and survival costs of reproduction on Atlantic cod, *Gadus morhua*, population growth rate. Can J Fish Aquat Sci 56:1612–1623

Hutchings JA (2000) Collapse and recovery of marine fishes. Nature 406:882–885

Hutchings JA (2001) Conservation biology of marine fishes: perceptions and caveats regarding assignment of extinction risk. Can J Fish Aquat Sci (in press)

Hutchings JA, Bishop TD, McGregor-Shaw CR (1999) Spawning behaviour of Atlantic cod, *Gadus morhua*: evidence of mate competition and mate choice in a broadcast spawner. Can J Fish Aquat Sci 56:97–104

Jennings S, Kaiser MJ (1998) The effects of fishing on marine ecosystems. Adv Mar Biol 34:201–352

Koslow JA, Bell J, Virtue P, Smith DC (1995) Fecundity and its variability in orange roughy: effects of population density, condition, egg size, and senescence. J Fish Biol 47:1063–1080

Law R (1979) Optimal life histories under age-specific predation. Am Nat 114:399–417

Law R (2000) Fishing, selection, and phenotypic evolution. ICES J Mar Sci 57:659–668

Law R, Grey DR (1989) Evolution of yields from populations with age-specific cropping. Evol Ecol 3:343–359

MacArthur RH (1958) Population ecology of some warblers of northeastern coniferous forests. Ecology 39:599–619

McGinnity P, Stone C, Taggart JB, Cooke D, Cotter D, Hynes R, McCamley C, Cross T, Ferguson A (1997) Genetic impact of escaped farmed Atlantic salmon (*Salmo salar* L.) on native populations: use of DNA profiling to assess freshwater performance of wild, farmed, and hybrid progeny in a natural river environment. ICES J Mar Sci 54:998–1008

Mertz G, Myers RA (1996) Influence of fecundity on recruitment variability of marine fish. Can J Fish Aquat Sci 53:1618–1625

Miller RM (1957) Have the genetic patterns of fishes been altered by introductions or by selective fishing? J Fish Res Board Can 14:797–806

Nelson K (1993) Individual variation in acquisition/allocation reaction norms. In: Stokes TK, McGlade JM, Law R (eds) The exploitation of evolving resources. Springer-Verlag, Berlin, p 91–106

Ricker WE (1981) Changes in the average size and average age of Pacific salmon. Can J Fish Aquat Sci 38:1636–1656

Rickman SJ, Dulvy NK, Jennings S, Reynolds JD (2000) Recruitment variation related to fecundity in marine fishes. Can J Fish Aquat Sci 57:116–124

Rijnsdorp AD (1993) Fisheries as a large-scale experiment on life-history evolution: disentangling phenotypic and genetic effects in changes in maturation and reproduction of North Sea plaice, *Pleuronectes platessa* L. Oecologia 96:391–401

Rochet MJ (1998) Short-term effects of fishing on life history traits of fishes. ICES J Mar Sci 55:371–391

Roff DA (1992) Evolution of life histories: theory and analysis. Chapman & Hall, New York

Scott WB, Scott MG (1988) Atlantic fishes of Canada. Univ Toronto Press, Toronto

Smith TD (1994) Scaling fisheries: the science of measuring the effects of fishing, 1855–1955. Cambridge Univ Press, Cambridge
Stokes TK, McGlade JM, Law R (eds) (1993) The exploitation of evolving resources. Springer-Verlag, Berlin
Swain DP, Sinclair AF (2000) Pelagic fishes and the cod recruitment dilemma in the Northwest Atlantic. Can J Fish Aquat Sci 57:1321–1325
Volterra V (1926) Fluctuations in the abundance of a species considered mathematically. Nature 118:558–560
Walters C, Pauly D, Christensen V, Kitchell HF (2000) Representing density dependent consequences of life history strategies in aquatic ecosystems: EcoSim II. Ecosystems 3: 70–83

Darwinian fishery science

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Humans actively and purposely increase the mortality rate of certain species in the wild, usually because they are considered either pests, pathogens, or food. A problem arises if survivors of such mortality represent genotypes that are less vulnerable to the force of mortality and then proliferate in subsequent generations. The importance of accounting for such Darwinian processes in the application or ‘management’ of human-induced mortality has been amply demonstrated by, for example, the evolution of resistance in pests and pathogens. Most of these cases involve species with short generation times where the goal is extermination. In fisheries, the objective is to continuously apply relatively moderate levels of mortality to longer-lived organisms in a manner that ensures a sustainable harvest in perpetuity. Beset with problems of predicting the ecological (immediate) response of stocks to fishing in the face of a continuously increasing harvest capacity, it is understandable that fisheries management theory has not yet dealt fully with the evolutionary consequences of exploitation (but see Stokes et al. 1993, Law 2000, Stokes & Law 2000 in this theme section).

Fisheries theory assumes that the ultimate causation of population productivity is energy flow, which determines the carrying capacity of the environment in terms of biomass. The productivity of a population is, hence, density dependent and responds positively to harvesting. It is assumed that a harvested population retains the capacity to grow back to its equilibrium state over a very short (i.e. ecological) time scale, and that repeated bouts of harvesting can go on indefinitely without changing the inherent dynamics of the population.

In this essay, I explore a few possible consequences of ignoring Darwinian principles in the study and management of fishery resources. I begin with a discussion of the prevalence and rapidity of the evolution of local adaptation. I then focus on 2 inter-related aspects of fishery science where I believe the application of natural selection theory will improve the success of resource management in the long term.

Importance of local adaptation. Much of the debate about the need to account for evolutionary changes in fish stocks (e.g. Stokes et al. 1993, Sheridan 1995, Policansky & Magnuson 1998, Law 2000) can be boiled down to 2 related questions. First, to what degree is the genetic component of traits that affect fitness (life history, morphology, physiology, behavior) finely tuned to the agents of selection found in a local environment? (Are local populations locally adapted?) Second, at what rate do such traits evolve when the environment changes? These questions are critical because, from the viewpoint of a fish population, human activity represents environmental change. The selective factors affecting a given species in a particular environment change whenever we start or stop harvesting that species and/or its competitors and predators, destroy or restore habitat, or modify climate. If adaptation occurs on local spatial scales and/or evolves quickly in response to a change in selection, then we must account for it in all aspects of population management including manipulations of harvest, habitat, stock enhancement via hatcheries or transplants, and climate.

Environmental change is not unnatural or uncommon. For example, most temperate species experience far greater differences in climate within their existing geographic ranges than are predicted to occur through global warming. We can measure the capacity for (and geographic scale of) local adaptation from studies of extant populations across spatially defined ecological gradients in climate, productivity, predator density, pollutant intensity, or harvest rate, etc. (methodology for detecting local adaptation across environments is described in Conover & Schultz 1995). Studies of local adaptation across environments reveal the traits that are sensitive to selection and the covariance among traits, and allow us to infer the likely agents of selection. For example, the existence of countergradient variation in growth among fish from different latitudes appears to result from a gradient in the severity of size-dependent winter mortality (Conover & Schultz 1995) and demonstrates clearly that growth rate is highly capable of evolving. If local adaptation is prevalent, we do not need to debate whether trait evolution in response to human-induced (or any other environmental) change will occur, but in what manner and with what impact on fitness.

Relatively few rigorous studies of local adaptation among fish populations exist. Those that do are restricted largely to a few mostly short-lived species in the Poecilliidae (Meffe & Snelson 1989), Gasterosteidae (Bell & Foster 1994), Atherinidae (Conover 1998) and somewhat more in the Salmonidae (Taylor 1991). In many of these cases, the geographic scale of adaptation is highly localized (e.g. within the same lake), the rate of evolution is quite rapid (a few generations; Reznick et al. 1997, Hendry et al. 1998, Thompson 1998), and local adaptive variation is extensive even in marine species that lack barriers to gene flow (Conover 1998). These lessons should be applied to longer-lived, harvested, marine fishes, which may be far more localized in population structure than currently appreciated (Hunt von Herbing et al. 1998, Swearer et al. 1999). Motivation for doing so is provided in the sections that follow.

Evolution in response to harvesting. Fishery management plans currently employ terms of reference reflecting human valuations that have little direct connection to evolution. Yield, for example, is not a currency that is crucial to fitness. From the fishes' point of view, the goal is maximizing the relative contribution of genes (*not* biomass) to succeeding generations. Fishery management plans, and the stock assessments on which they are based, are, therefore, non-Darwinian: they ignore the prey's co-evolutionary response to the effects of harvest.

A number of authors have addressed the potential for evolution in response to the selective force of fishing mortality in harvested stocks (e.g. Stokes et al. 1993, Miller & Kapuscinski 1994, Heino 1998). Many deal with the decline in yield that is expected to result from the selective harvest of faster growing individuals and/or the shift in the allocation of consumed energy from somatic to reproductive tissues at earlier ages, while others point out the expected loss in genetic diversity that results from directional selection or bottlenecks in population size. Law (2000) provides an excellent review of this literature. None of the empirical data is as yet sufficient to convince managers, stock assessment scientists, or harvesters that evolutionary dynamics need be taken seriously, especially in comparison with the always more immediate and ominous consequences of stock collapse. Despite this, I believe that a Darwinian perspective could at least bring new insights to our understanding of the causes of, and recovery from, stock collapse. First, recognize that life history variation within and among species likely represents an optimization of the age specific expectations of survival and reproductive success that evolved in response to natural agents of selection over thousands of years. The addition of fishing to natural mortality of an unfished stock will have 2 major effects: (1) it will reduce absolute fitness of the population, often dramatically; and (2) it will change the relative fitness of genotypes that code for different life histories within the population. As the stock adjusts to its new adaptive landscape, the evolutionary change in life history will partially ameliorate the reduction in fitness caused by fishing, but probably not without some loss of adaptation to the original agents of natural selection. How much so depends on the magnitude and selectivity of fishing.

Although any change in total mortality rate may affect life history evolution, the change in optimal life history and absolute fitness caused by fishing may be most severe when the age or size-specific trajectory of fishing mortality represents a radical departure from that caused by natural mortality. Suppose that in a given stock natural mortality tends to diminish with increasing size and age, which is generally true at least for the early ages. Fishing mortality that targets larger/older fish produces an age-specific schedule of survivorship that is different from that to which the stock originally evolved. In the case of bet-hedging life histories, for example, long reproductive life spans lead to large quantities of biomass stockpiled in the adult stages that become targeted by the fishery. Truncation of the age distribution of the stock reduces reproductive life span and may nullify bet-hedging as a viable life history strategy compared with what existed in the absence of fishing. In any case, the survivors of the harvesting process are likely to be genotypes with traits that confer relatively high fitness under fishing selection (e.g. slower growth, earlier age at maturity) but may be less than optimal with respect to natural selection. Hence, when fishing mortality is relaxed, the surviving genotypes in the stock may be those with reduced fitness with respect to natural selective forces, leading to slow recovery times. Because the cessation of fishing does not automatically produce an equal selection intensity in the opposite direction, the time required for the adaptive genetic traits of stock to return to their original condition may be quite long.

The problem for a Darwinian fishery manager then is to determine what manner of fishing will cause the least reduction in fitness while still producing a reasonable yield. To do so, we first need to understand how the life history strategy (reproduction, migration, demography, behavior, etc.) of any particular species is adapted to the agents of natural selection in the absence of fishing. Then we ask how the addition of any particular age- or size-specific trajectory of fishing mortality changes the optimal life history. Next, we calculate the change in fitness caused by fishing under the newly evolved optimal life history. Finally, we calculate the yield under the new conditions. Many such iterations would constitute an analysis of the trade-off between fitness reduction and yield.

Inclusion of the change in absolute fitness and optimal life history of a stock under different patterns of fishing mortality in the stock assessment process would enable fishery managers to consider the evolutionary consequences of fishing. There are, of course, many potential complications to this approach. For example, we need to know the means and variances of age-specific natural mortality and reproductive success in unfished stocks. The current approach of merely assuming natural mortality to be a constant driven by unknown sources is not likely to be very informative. Studies of unfished populations inside reserves could begin to fill this gap. Another complication is that harvesting may have numerous other effects on ecosystems that change the selective forces of natural mortality. In freshwater lakes or other closed systems, it may be possible to set up long-term fishing experiments to test for evolutionary and ecosystem responses to selective harvest, as MacAllister et al. (1992) have outlined for anadromous fishes. In marine systems, no-harvest reserves could be established for the same purpose, as well as to provide a sanctuary for maintenance of genetic diversity in adaptive traits (Trexler & Travis 2000).

Stock structure, local adaptation, and spatial scale of fishery management. Stock structure is typically evaluated by either phenotypic approaches involving morphological or behavioral (migration) differences, or molecular genetic variation in markers that are presumed to be neutral to selection. As explained below, neither of these approaches, either alone or together, provide direct measures of the geographic structure of, or diversity in, adaptive genetic variation (see Conover 1998).

Phenotypic variation as observed in nature is confounded by environmental influences during development, genotype × environment interaction, and the covariance between genotypes and environments. Because the covariance term may be either positive or negative, thereby either inflating (cogradient variation) or reducing (countergradient) phenotypic variation, the magnitude and pattern of phenotypic change among environments can be a poor measure of the magnitude and pattern of genetic differences (Conover & Schultz 1995). Common garden experiments can disentangle the web of genetic and environmental influences on phenotypic trait variation.

Failure to understand the geography of adaptive genetic variation can have serious consequences. For example, the stocking of Florida largemouth bass throughout much of North America was conducted under an assumption that the fast growth of the southern subspecies in warm climates might have a cogradient genetic basis. It didn't. Largemouth bass actually display countergradient variation: Florida genotypes grow more slowly than those from the north (Philipp & Whitt 1991). Countergradient variation in growth appears to be widespread in various fish taxa (e.g. Schultz et al. 1996, Conover et al. 1997, Arendt & Wilson 1999, Jonassen et al. 2000) and provides an illustration of the pitfalls of transplanting stocks.

Molecular genetic surveys of variation in non-coding DNA do not suffer the problems of environmental variance or effects of selection. They depend on the existence of random genetic variation that arises due to founder events (genetic drift) or the accumulation of variation that arises by chance over thousands of generations, and is maintained by the virtual absence of gene flow. If knowledge of ancestral relationships (phylogeny) or long-established patterns of gene flow is the goal, variation in genetic markers that are neutral to selection is the right tool. But not if your interest is in the diversity or geographic structure of genes that influence fitness. However, molecular trait variation can be used to study the geography of adaptive variation if specific genes (or markers linked to such genes) that are known to affect trait expression can be identified (e.g. anti-freeze genes in cod, Goddard et al. 1999).

Traits that affect fitness are influenced strongly by differences in selection among environments; hence their spatial structure may differ dramatically from what would be predicted from estimates of gene flow alone. Such traits are capable of evolving far more rapidly, despite much higher levels of gene flow, and on much finer spatial scales than can be detected by neutral genetic markers. New techniques of stock identification, such as otolith microchemistry, are beginning to suggest that marine fish populations are more localized that previously believed (Hunt von Herbing et al. 1998, Secor 1999, Swearer et al. 1999). In Atlantic silversides *Menidia menidia*, a multitude of adaptive traits vary dramatically with latitude (in both cogradient and countergradient patterns) despite the opportunity for (and evidence of) substantial gene flow (Conover 1998).

In the design of fishery management plans, it is the spatial scale of genetic variation in adaptive traits that we most need to understand. In stock enhancement, for example, it is the similarity of donor and wild stocks for genes that affect fitness with which we ought to be concerned. With respect to creating marine reserves or managing harvest, it is the loss of adaptive genetic diversity that concerns us when stocks go extinct, bottlenecks in effective population size arise, or directional selection due to fishing causes genetic change.

Even in open marine populations with dispersive larvae, gene pools of adaptive variation may exist on much finer spatial scales than is now appreciated. The current debate over the connectivity versus local retention of spatially discrete coral reef fish populations is a prime example. Molecular genetic studies suggest that many populations of marine species with dispersive larvae are spatially well mixed over large areas. Swearer et al. (1999) and Cowen et al. (2000) have argued, however, that local populations of such species must be maintained by physical mechanisms of local retention, in part because high rates of diffusion and mortality rule out the probability of substantial connectivity with downstream sites. If so, specific larval behaviors that increase the probability of local retention are likely to evolve rapidly as long as variation in larval behavior is heritable. The behaviors that successfully enhance recruitment are likely unique to each locality due to local topographic steering of currents. Hence, isolated spawning populations may evolve unique early life history behaviors that enhance local retention. Yet, due to occasional migrants from other systems, such adaptive variation may be invisible to the usual molecular surveys of non-coding genes or those that code for other traits. Without a Darwinian perspective of the recruitment process, spatially-structured adaptive genetic variation that is crucial to management of the resource may remain hidden from our view.

Summary. Examples of the rapidity of evolution in human-manipulated wild populations are increasing (Reznick et al. 1997, Hendry et al. 1998, Thompson 1998, Huey et al. 2000). Our knowledge of the prevalence of local adaptation in traits such as growth rate and age at maturity (and their potential for evolution) is also increasing. While many of these cases are from short-lived fishes and other organisms, evolutionary change in longer-lived organisms is simply a matter of time. If a goal of fishery management is to ensure a long-term sustainable harvest, then evolutionary effects of fishing and stock enhancement practices may need to be incorporated into our thinking. Unfortunately, stock assessment scientists and managers are typically under so much pressure to respond to the short-term fluctuations in stocks that addressing such long-term issues would seem a luxury. Yet ultimately the success of fishery management may be judged not by the catch achieved in any given year or decade, but by whether it was sustained across future generations.

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LITERATURE CITED

Arendt JD, Wilson DS (1999) Countergradient selection for rapid growth in pumpkinseed sunfish: disentangling ecological and evolutionary effects. Ecology 80:2793–2798

Bell M, Foster SA (eds) (1994) The evolutionary biology of the threespine stickleback. Oxford University Press, Oxford

Conover DO (1998) Local adaptation in marine fishes: evidence and implications or stock enhancement. Bull Mar Sci 62:305–311

Conover DO, Schultz ET (1995) Phenotypic similarity and the evolutionary significance of countergradient variation. Trends Ecol Evol 10:248–252

Conover DO, Brown JJ, Ehtisham A (1997) Countergradient variation in growth of young striped bass (*Morone saxatilis*) from different latitudes. Can J Fish Aquat Sci 54: 2401–2409

Cowen RK, Kwiza KMM, Sponaugle S, Paris CB, Olson DB (2000) Connectivity of marine populations: open or closed? Science 287:857–859

Goddard SV, Kao MH, Fletcher GL (1999) Population differences in antifreeze production cycles of juvenile Atlantic cod (*Gadus morhua*) reflect adaptations to overwintering environment. Can J Fish Aquat Sci 56:1991–1999

Heino M (1998) Management of evolving fish stocks. Can J Fish Aquat Sci 55:1971–1982

Hendry AP, Hensleigh JE, Reisenbichler RR (1998) Incubation temperature, developmental biology, and the divergence of sockeye salmon (*Oncorhynchus nerka*) within Lake Washington. Can J Fish Aquat Sci 55:1387–1394

Huey RB, Gilchrist GW, Carlson ML, Berrigan D, Serra L (2000) Rapid evolution of a geographic cline in size in an introduced fly. Science 287:308–309

Hunt von Herbing I, Kornfield I, Tupper M, Wilson J (1998) The implications of localized fishery stocks. Natural Resource, Agriculture & Engineering Service, Ithaca, NY

Jonassen TM, Imsland AK, Fitzgerald R, Bonga SW, Ham EV, Naevdal G, Stefansson MO, Stefansson SO (2000) Geographic variation in growth and food conversion efficiency of juvenile Atlantic halibut related to latitude. J Fish Biol 56:279–294

Law R (2000) Fishing, selection, and phenotypic evolution. ICES J Mar Sci 57:659–668

McAllister MK, Peterman RM, Gillis DM (1992) Statistical evaluation of a large-scale fishing experiment designed to test for a genetic effect of size-selective fishing on British Columbia pink salmon (*Oncorhynchus gorbuscha*). Can J Fish Aquat Sci 49:1294–1304

Meffe GK, Snelson FF Jr (eds) (1989) Ecology and evolution of livebearing fishes (Poeciliidae). Prentice Hall, Englewood Cliffs, NJ

Miller L, Kapuscinski A (1994) Estimation of selection differentials from fish scales: a step towards evaluating genetic alteration of fish size in exploited populations. Can J Fish Aquat Sci 51:774–783

Philipp DP, Whitt GS (1991) Survival and growth of northern, Florida, and reciprocal F1 hybrid largemouth bass in central Illinois. Trans Am Fish Soc 120:58–64

Policansky D, Magnuson JJ (1998) Genetics, metapopulations, and the ecosystem management of fisheries. Ecol Appl 8:119–123

Reznick DN, Shaw FH, Rodd FH, Shaw RG (1997) Evaluation of the rate of evolution in natural populations of guppies (*Poecilia reticulata*). Science 275:1934–1937

Schultz ET, Reynolds KE, Conover DO (1996) Countergradient variation in growth among newly-hatched *Fundulus*

heteroclitus: geographic differences revealed by common-environment experiments. Funct Ecol 10:366–374
Secor DH (1999) Specifying divergent migrations in the concept of stock: the contingent hypothesis. Fish Res 43:13–34
Sheridan AK (1995) The genetic impacts of human activities on wild fish populations. Rev Fish Sci 3:91–108
Stokes K, Law R (2000) Fishing as an evolutionary force. Mar Ecol Prog Ser 208:307–309
Stokes TK, McGlade JM, Law R (1993) The exploitation of evolving resources. Springer-Verlag, Berlin
Swearer SE, Caselle JE, Lea DW, Warner RR (1999) Larval retention and recruitment in an island population of a coral-reef fish. Nature 402:799–802
Taylor EB (1991) A review of local adaptation in Salmonidae, with particular reference to Pacific and Atlantic salmon. Aquaculture 98:185–207
Thompson JN (1998) Rapid evolution as an ecological process. Trends Ecol Evol 13:329–332
Trexler JC, Travis J (2000) Can marine protected areas restore and conserve stock attributes of reef fishes? Bull Mar Sci 66:853–873

Fishing as an evolutionary force

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To an evolutionary biologist, fishing is a massive uncontrolled experiment in evolutionary selection. There are 3 sets of participants: fishery managers, who set patterns of selection through regulations such as mesh size and catch quotas; fishers, who apply the selective mortality; and the fish stocks, which evolve due to directional selection. Curiously, fisheries institutes around the world have shown little interest in this selection experiment. Some years ago, when we were working on the subject with Cathy Rowell, we found a real reluctance among fisheries biologists to consider the evolutionary consequences of fishing. Perhaps it was felt that fisheries management is complicated enough in the short term, without worrying about issues perceived to be the stuff of centuries. Whatever the reason, we know of only 1 fisheries research institute investigating the strength of fishing-generated selection on fish stocks (Sinclair et al. 1999). Moreover, the genetic architectures of traits such as growth and maturation, crucial for productivity of fisheries, are essentially unknown in the wild, and it is barely possible to even guess the rate at which these traits are evolving as a result of fishing. There is, however, increasing evidence that evolutionary effects of fishing need to be on the research agenda.

First, there is the issue of whether there is genetic variation for traits selected by fishing. It has sometimes been argued that the phenotypic variation observed among fish is due to their different environments rather than their different genes, in which case the amount of selective fishing is immaterial: there is no evolution. But this argument is becoming increasingly untenable in the light of selective breeding for aquaculture. The heritabilities (i.e. the proportion of phenotypic variation due to the additive effects of genes) of traits selected for aquaculture are typically non-zero, and very much in the range that applies to life history traits of other kinds of animals. The relevance of heritabilities from carefully controlled aquaculture experiments to conditions in the wild could still be questioned. Phenotypic variation includes an environmental component, which depends on where the fish are living; in the wild, the environmental variation might be expected to be much greater than in controlled experiments. The only study we know of in which heritability has been estimated in the wild was on Atlantic salmon parr of known parentage, tagged and released from sites in Iceland (Jónasson et al. 1997). Remarkably, the heritability of body weight for these fishes when they returned after 1 winter at sea (0.36) was similar to that estimated in salmon farms. Surprising though this result is, it is in keeping with other comparisons of heritabilities on organisms in the laboratory and in the wild (Weigensberg & Roff 1996). There is much to learn about heritabilities of production-related traits of fish in the wild, but the evidence available argues against any blanket assumption that the heritabilties are zero, and suggests that they are likely to be in the range of 0.2 to 0.3. This is enough to lead to observable evolution over tens of years in the presence of the selection differentials generated by fishing.

Second, there is the issue of how strong the selection caused by fishing is. Fishing gears are usually designed to remove larger individuals and would be expected to generate selection on body size. Of course, a measurable selection differential on body size needs more than just selectivity of the gear: if fishing removes only a small proportion of the population, the average body size of the survivors would be little changed. However, exploitation of major fish stocks is intense, with fishing mortality often exceeding natural mortality by a factor of 2 to 3. For many of the world's fisheries, removals of fish after recruitment to the fisheries often run as high as 50% each year. Arguably then, selection differentials on body size should be substan-

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tial and measurable. We know of only 2 attempts to estimate selection differentials on body size caused by commercial fishing. The first was on North Sea cod under the levels of exploitation that applied in the 1980s, and gave a selection differential acting on a cohort as it entered the fishery of approximately –1 cm (Law & Rowell 1993). Roughly, this means that the fish surviving after entry into the fishery were, on average 1 cm smaller than they would have been in the absence of fishing. The second estimate was on cod in the Gulf of St Lawrence, and gave selection differentials around –0.5 cm yr^{-1} from the mid-1970s, up to closure of the fishery in 1993 (Sinclair et al. 1999). Bearing in mind the fact that such selection applies year after year, and the likelihood that heritabilities of body size are not negligible, an evolutionary decline in body size would be expected, at least on a decadal time scale.

Selection differentials on age and size at sexual maturation are also important, and yet they are easily overlooked because maturation is not the direct target of selective gear. It is intuitive that fishing causes selection on maturation. Think for instance of a North Sea cod that matures at 2 yr of age, and another individual that matures at age 8; under the intense fishing mortality that currently applies, the late maturing individual is most likely to be caught before it reproduces; other things being equal, the earlier maturing individual leaves a greater contribution of offspring to future generations. Rowell's (1993) calculations suggested that this contribution could differ by a factor of 10 under the levels of fishing that applied in the 1980s. The selection differential fishing generates on maturation can evidently be large.

The third issue is that large phenotypic changes are taking place in major fish stocks (e.g. Trippel 1995). This includes, for instance, a reduction in length and age at maturation in many of the gadoid stocks in the North Atlantic, North Sea, Baltic Sea and Barents Sea, and similar changes in some flatfish stocks. Directional change in size-at-age has been observed, for instance, in Atlantic and Pacific salmon species and in North Sea sole. These changes are large enough to affect the productivity of the fisheries and their causes need to be understood.

The role of genetic and non-genetic factors in bringing about these phenotypic changes is a matter of debate. Exploitation reduces abundance of the stock and may leave more food available for survivors, affecting the rate of growth and maturation. This has been suggested as an explanation for changes in maturation of NE Arctic cod and Baltic Sea cod. Exploitation can also have direct effects on the environment. It is thought that the increased growth of North Sea sole in the 1960s came about from greater disturbance of the sea bed by heavy beam trawlers. Properties of the physical environment, such as water temperature, may change, altering the growth of fish. At present, it is hard to disentangle these non-genetic causes of change from directional genetic change due to fishing. The only study that has done so was on North Sea plaice, where it was shown that, after removing the effects of non-genetic factors, a substantial decline in maturation over the 20th century still remained, consistent with genetic change caused by exploitation (Rijnsdorp 1993).

Any doubt about the capacity of size-specific mortality to bring about genetic change in maturation should be dispelled by the work of Reznick and his colleagues on guppies in Trinidadian streams (Reznick et al. 1990, 1997). This work made use of differences in size-specific mortality caused by 2 natural predators, the pike cichlid that mostly catches large mature guppies, and a killifish that mostly catches small immature ones. Reznick and his co-workers moved guppies from sites with the cichlids to sites with the killifish, thereby changing the pattern of size-specific mortality. After some years, there were genetic differences in maturation between guppies in the original and introduced sites. Male and female guppies both matured later, and at larger sizes, when living with the killifish than with the cichlid.

The messages from the evidence are: (1) there is likely to be genetic variation for traits selected by fishing; (2) selection differentials due to fishing are substantial in major exploited stocks; and (3) large phenotypic changes are taking place in fish stocks, although the causes of these changes are hard to determine unambiguously. Placing these observations in the context of a precautionary approach to management, there is a compelling case for developing an evolutionary perspective to fisheries management.

The precautionary approach to management, as it has developed over the past decade, is essentially a call to consider wider and longer-term consequences of actions. In particular, it is a mechanism intended to ensure that irreversible changes do not occur and that future generations of humankind are afforded the same opportunities for fishing as this generation. In this context, it is important to understand that genetic change caused by fishing is not readily reversed: the genetic structure of exploited fish stocks will not revert rapidly to some earlier state simply by altering the patterns of exploitation. We run the risk of leaving to future generations a marine realm in which the surviving exploited species are small-sized prolific reproducers, and for which no quick way exists of returning the stocks to their earlier more productive state. A longer-term, decadal perspective, that takes account of the selection pressures generated by fishing and the genetic changes that might result, is needed.

LITERATURE CITED

Jónasson J, Gjerde B, Gjedrem T (1997) Genetic parameters for return rate and body weight of sea-ranched salmon. Aquaculture 154:219–231

Law R, Rowell CA (1993) Cohort-structured populations, selection responses, and exploitation of the North Sea cod. In: Stokes TK, McGlade JM, Law R (eds) The exploitation of evolving resources. Lecture Notes in Biomathematics 99. Springer-Verlag, Berlin, p 155–173

Reznick DN, Bryga H, Endler JA (1990) Experimentally induced life-history evolution in a natural population. Nature 346:357–359

Reznick DN, Shaw FH, Rodd FH, Shaw RG (1997) Evaluation of the rate of evolution in natural populations of guppies (*Poecilia reticulata*). Science 275:1934–1937

Rijnsdorp AD (1993) Fisheries as a large-scale experiment on life-history evolution: disentangling phenotypic and genetic effects in changes in maturation and reproduction of North Sea plaice, *Pleuronectes platessa* L. Oecologia 96:391–401

Rowell CA (1993) The effects of fishing on the timing of maturity in North Sea cod (*Gadus morhua* L.). In: Stokes TK, McGlade JM, Law R (eds) The exploitation of evolving resources. Lecture Notes in Biomathematics 99. Springer-Verlag, Berlin, p 44–61

Sinclair AF, Hanson JM, Swain DP, Currie L (1999) Size selective mortality of cod in the southern Gulf of St Lawrence. Canadian Stock Assessment Proceedings, Series 99/05:43-48. Fisheries and Oceans, Ottawa

Trippel EA (1995) Age at maturity as a stress indicator in fisheries. BioScience 45:759–771

Weigensberg I, Roff DA (1996) Natural heritabilities: can they be reliably estimated in the laboratory? Evolution 50: 2149–2157

Natural selection for predation avoidance tactics: implications for marine population and community dynamics

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Introduction. The evolutionary fitness of any marine organism depends partly upon how it balances 2 potentially conflicting needs: acquisition of resources (food, cover, etc.), and avoidance of being something else's resource (predation). This conflict arises because activities involved in resource acquisition most often also expose organisms to risk of predation (and parasitism and disease). You cannot feed if you spend all of your time hiding motionless under a rock, or in the midst of a dense school of conspecific competitors, or in the pelagic deeps where both phytoplankton and visual predators are scarce, or with your shell tightly closed. Many of the morphological and behavioral adaptations that we see in marine organisms, from development of spines and shells to schooling behavior, appear to be quite costly and would very likely not have evolved if resource acquisition (efficient foraging, feeding niche specialization) were a much more important problem than predation risk.

This paper briefly reviews a few key predictions (based upon evolutionary models) about how organisms ought to behave so as to maximize fitness in relation to the food acquisition/predation risk tradeoff. Then it explores some of the implications of these behaviors for aspects of population and community dynamics that are particularly important in fisheries management (e.g. stock-recruitment relationships; compensatory mortality patterns). My basic argument is that many of the most striking and puzzling features of how marine ecosystems respond to fisheries arise very directly from risk-sensitive foraging behaviors.

Models for balancing foraging and predation risk. There is relatively well-developed theory about how organisms ought to allocate time and select where to live so as to maximize fitness when food acquisition is risky (Werner & Gilliam 1984, Stephens & Krebs 1986, Mangel & Clark 1988, Walters & Juanes 1993, Anholt & Werner 1998). When factors such as past feeding success (as reflected in current body size) are considered, the predictions that follow from this theory can be quite complex. However, they basically reduce to the argument that fitness is the product of 2 terms, growth × survival rate. If growth is proportional to time spent foraging, and survival decreases exponentially with foraging time due to predation risk, then fitness should be maximized by 'choosing' a foraging time $T_{\text{opt}} = T_{\text{o}} + 1/R$, where T_{o} is a foraging time needed to obtain maintenance ration and R is predation risk per time. That is, organisms ought to take some minimal risk, plus additional risk ($1/R$), that decreases with increasing predation risk. Similar reasoning applies when we think about allocation of time among habitat 'patches' or types with which are associated differing feeding opportunity and predation risk.

Many organisms are likely capable of detecting maintenance foraging time and current predation risk, and adjusting their behavior accordingly so as to follow an optimum foraging 'trajectory' over time. If this is so, they may exhibit surprising responses to changes in foraging opportunity and risk. Increases in maintenance foraging time caused by resource shortage (e.g. due to intraspecific competition) may result in changes in mortality rates rather than the more obvious changes that we might intuitively expect in food intake and growth rates. Increases in predation risk may result in changes in growth rate rather than mortality rates, again the opposite of what we might intuitively expect.

During the 1970s, we largely overlooked one of the most striking types of evidence that some marine animals do indeed spend relatively little time foraging. During this period, there was much enthusiastic and optimistic work on developing marine ecosystem models to aid in management (e.g. Walters et al. 1978). At that time, we knew that 'rates of effective search' (Holling 1959), or volumes swept per time feeding, had to be estimated as part of the prediction of feeding and predation rates. Two types of data were available to us: (1) estimates of actual feeding rates at particular prey densities, from field sampling and enclosure experiments; and (2) direct estimates of search volumes from measurements of movement (swimming, advection) speeds and observations of reaction distances to prey (volume/time = speed × reactive area). Generally, we saw huge discrepancies in the search volume estimates generated from these 2 data sources, with the behavioral data predicting search volumes 10 to 100 times what we would back-calculate from actual feeding rates and prey densities. Instead of treating such discrepancies as evidence that effective foraging times T are often very low, we instead interpreted them as meaning that for some reason predators 'see' (or successfully pursue) only a very small proportion of the prey that they should encounter based on how much they move and how far they can react to prey. What we should have realized is that search efficiencies are indeed very high, because there has been very harsh selection for such capability in order to minimize time spent actually searching.

We also failed to think carefully about the extreme small-scale patchiness that characterizes the spatial distribution of most organisms. We treated this patchiness as 'noise' in the calculation of larger-scale ecosystem properties (such as predation rates), rather than as a result of active 'management' of foraging opportunities and risks by organisms. In particular, we failed to recognize how natural selection might drive risk management behaviors so as to severely limit interaction rates and 'trophic flows'.

Another common observation that we should have taken more seriously is the low incidence of full stomachs in most field diet sampling, even in situations where prey appear to be very abundant. That is, fishes at least generally appear to eat much less than we might expect if natural selection were operating mainly to maximize resource acquisition rates. Comparing bioenergetics model estimates of ration for a variety of fishes, D. Schindler (pers. comm.) argues that mean ration from published studies averages only 30 to 40% of the maximum we would expect from laboratory and culture studies.

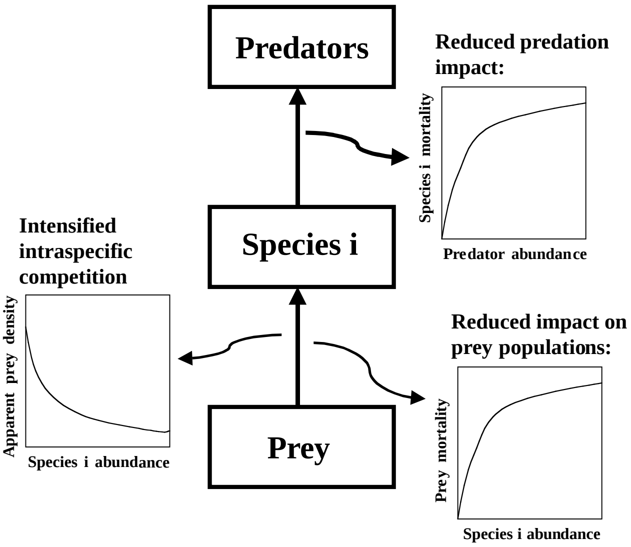

Fig. 1. Selection for spatial and temporal restriction of foraging activity to reduce predation risk by any species '*i*' in a food web has consequences both up and down the food chain. Restricted activity places a limit on the 'flow' of species *i* to its predators, but also limits the flow from prey to species *i*. Intraspecific competition for prey is intensified in those locations or 'foraging arenas' where species *i* does feed. Another effect not shown in this diagram is food niche formation: when the impact of species *i* on its prey is reduced, other species that feed on the same prey may be able to coexist with it

Spatial effects. When selection drives an organism to adopt spatial refuging and time management behaviors in response to predation risk, there can be at least 4 immediate consequences for the organization and limitation of competition/predation interactions (Fig. 1). All of these consequences should tend to promote temporal stability and diversity in marine communities, and hence are critical to the development of sustainable harvesting regimes.

First, spatial aggregation in relatively safe locations (e.g. reefs; fish schools) creates an apparent 'bottom-up' effect on food availability: if the predator does not occupy most of the volume or area where its food is produced, that food is at least partially 'protected' from predation. Further, the food supply rate to the particular places ('foraging arenas') where the predator does feed may be dominated by physical transport processes and dispersal behaviors of the food organisms, rather than by search efficiency of the predator itself. The foraging arenas available to these organisms may be correspondingly small, particularly for smaller individuals that have a limited ability to move away from refuge sites in search of food.

Second, concentrating of feeding in foraging arenas that have limited food supply rates should lead to more intense intraspecific competition. That is, the predator may exhibit symptoms of food 'shortage' (increased feeding time or reduced growth rates with increased population density) which we would not expect on the basis of crude or large-scale sampling of total food abundance. We have argued that this is likely why many marine fishes show flat stock-recruitment relationships, with maximum recruitment rates that are not predictable from broad calculations of potential food supply (Walters & Juanes 1993, Walters & Korman 1999). The argument is simply that, when initial juvenile density is high (high parental stock size), juveniles either must spend more time foraging in order to maintain growth, or must grow more slowly and hence remain at smaller sizes (with higher predation risk per time spent feeding) for longer. Under either response, the net effect is a higher mortality rate when juveniles are more abundant, and this higher mortality rate will tend to remove 'surplus' individuals so as to create the appearance of a very limited juvenile 'carrying capacity'. An important example of this effect may be the Pacific northwest salmon fishery, where stocking programs have been associated with declining marine survival rates indicative of a possible limit on the carrying capacity of the species' marine habitat; simple models of food availibility to salmon in the oceans had not predicted such a limit.

Third, space-time risk management behaviors should directly reduce potential predation rates, again creating a 'bottom-up' rate limiting effect, but this time on the supply rate of the prey to its predators. But if most predation occurs in the same foraging arenas where the organism competes with conspecifics for food, predators may learn to target such arenas (where the prey organism is relatively concentrated) so as to substantially reduce the population-scale 'benefit' (in terms of reduced predation mortality rate) of the risk management behavior. Most fisheries stock assessment methods assume stable natural mortality rates (ignoring effects of changing natural predation regimes on mortality rate), and it may well be that this modeling tactic has not caused many really obvious assessment errors because there is indeed strong bottom-up, stabilizing control of mortality rates.

Fourth, restriction of foraging to space-time sites near refuges can allow coexistence of species that apparently 'compete' for the same foods. Simple competition theory tells us that 2 species cannot coexist if they eat exactly the same food organisms at the same time and place, since one should be able to drive the density of these food organisms low enough to cause the other to decline toward extinction. This argument fails if neither species is capable of significantly impacting the overall abundance of food organisms, because each is restricted to taking the food organisms in its own distinct foraging arena. Examples of this effect may be the diversity of opportunistic, planktivorous fishes that occupy coral reefs, and the diversity of demersal fish species that feed mainly on Euphausids.

Community diversity, stability, and cascade effects: Ecosim. Most models for exploring the trophic organization of marine ecosystems have used the simplifying assumption that interaction (predation, biomass/energy flow) rates can be predicted by treating organisms as though they were chemicals in well-mixed reaction vats, encountering one another at mass action rates proportional to the product of predator and prey densities. When we have tried to represent meso-scale spatial effects of processes like advection, we have generally used the mass action assumption for interaction rates within spatial grid cells that are still quite large (ca 100+ m) compared to the spatial scales at which heterogeneity in distributions and encounter patterns can be created by risk-sensitive behaviors. Whether or not meso-scale spatial patterns are represented explicitly, such models commonly make at least 3 types of long-term predictions that we suspect are qualitatively incorrect: (1) cyclic behaviors of predator-prey interactions, where predators with realistic search efficiencies (estimated from behavioral or laboratory observations) drive prey to low levels, then crash and allow prey to increase, then expand again; (2) loss of diversity, where models that include many species tend to lose most of them through competitive interactions and/or high predation rates supported by the few most productive prey species; (3) strong trophic cascade effects, where perturbations in primary productivity or apex predator abundance lead to large changes in abundance at alternating trophic levels.

Seeing such effects manifested in even simple models has tended to discourage fisheries scientists from even trying to move beyond single-species assessment methods. Occasionally we can account for weakness in these effects (at least for smaller pelagic organisms) through meso-scale spatial displacement effects, such as the 'downstream' trophic organizations that can form as upwelling water moves offshore. But unrealistic predictions then reappear when we try to include a variety of larger, more mobile organisms in the calculations. We have postulated a variety of rather vague mechanisms like 'predator switching' and 'bottom-up control' that might prevent such pathological predictions, but it has been difficult to see precisely why and how to include such mechanisms in the models. The 4 impacts of risk management behaviors identified in the previous section appear to offer a more parsimonious way to explain all of the pathologies, if we can show that their effects are indeed large enough when included in models for large-scale ecosystem behavior.

In developing the Ecosim/Ecospace modeling system for aiding in the design of marine ecosystem management strategies (Walters et al. 1997, 2000a,b, Walters 2000, Walters & Kitchell 2000), we decided right from the outset to incorporate effects of microscale patchiness and risk-sensitive foraging behavior as a key feature of model structure. We treat each biomass or numbers 'flow' rate from prey to predator as being proportional to a vulnerable biomass of the prey (rather than total biomass), and we assume that the vulnerable biomasses are maintained through behavioral exchange of organisms between invulnerable and vulnerable states. Assuming behavioral exchange rates are fast compared to rates of overall biomass change, this results in a model where the overall predation (flow) rates can vary between simply 'donor controlled' (limited by how fast prey become vulnerable) to purely 'predator controlled' (when prey exchange between safe and vulnerable states very rapidly or spend little time in safe states). We know from studies of simple predator-prey models that use of such a 'ratio dependent' formulation can have strong stabilizing effects on the dynamics of the system (reviewed in Abrams & Walters 1996). It is obviously an oversimplification to think of organisms as having only 2 possible behavioral (or positional, or size, or whatever) states with respect to vulnerability to predation; the 2-state exchange model is meant to provide only a first approximation to what in nature is likely to be a complex, time-varying distribution of behavioral states.

Ecosim models have now been developed for a wide variety of marine ecosystems, using initial state and parameter estimates provided through Ecopath mass-balance and trophic flow rate assessments (Christensen & Pauly 1992, 1993). We have 'exercised' these models by varying the vulnerability flow rate parameters, and in most cases we find that unreasonable ecosystem behaviors (violent cycles, loss of species) are predicted for high exchange or mass-action assumptions. Generally, we start to see unreasonable behaviors and poor fits to historical population trend data when we include potential predation mortality rates that are greater than twice the baseline rates (when predator abundances are high). On the other hand, we are generally unable to obtain good fits to time series data for harvested fish populations if we assume the vulnerabilities to be very low; compensatory growth and mortality responses to harvesting are overestimated under such conditions.

Evolutionary arguments have been helpful in providing independent starting estimates of the vulnerability parameters that are so critical in Ecosim predictions about responses to harvesting (and will likely be critical in any future ecosystem modeling that recognizes how risk-sensitive behavior may influence trophic relationships). If we assume that organisms generally increase both their food intake rates and their vulnerabilities to predators by spending more time foraging, we can think of foraging time as a leading predictor of predation interaction parameters. If we then use per capita biomass rates of change as simple evolutionary fitness measures, recognizing that biomass change is a sum of food intake minus predation rates, we can explicitly represent how fitnesses for all types of organisms should vary with foraging time. For a natural ecosystem that has been subject to a long evolutionary history, we expect to see foraging time (and associated rate parameters) set so that no organism in the 'natural' system should be able to improve its fitness much by moving toward a higher average foraging time. We have calculated such 'balancing' foraging times for a variety of Ecopath models. These times are generally balanced for all organisms simultaneously only when most model species have rate parameters near those that correspond with general ecosystem observations about stability and diversity, and with time series data on response to harvesting.

It appears that models like Ecosim are going to be important in the formulation and screening of future 'ecosystem management' policies and practices such as marine protected areas (Walters 2000, Walters & Kitchell 2000). We simply cannot continue to ignore trophic interactions in the formulation of models for exploited marine fishes, particularly in evaluation of policies like protected areas that are almost certain to have a variety of whole-ecosystem effects. Obviously, we are a long way from providing reliable quantitative estimates of vulnerability parameters for Ecosim; e.g., those representing behavioral tactics that may limit or shape trophic interaction effects. Ultimately, we will have to learn what these parameters are through hard empirical experience, by seeing how population rate processes like feeding, growth, and recruitment respond to changes in trophic conditions. Nonetheless, evolutionary arguments can provide reasonable starting points for this learning process and can, thereby, speed the disciplines development considerably and hence reduce some of the costs of 'learning the hard way' about the importance of trophic interactions.

LITERATURE CITED

Abrams PA, Walters C (1996) Invulnerable prey and the paradox of enrichment. Ecology 77:1125–1133

Anholt BR, Werner EE (1998) Predictable changes in predation mortality as a consequence of changes in food availability and predation risk. Evol Ecol 12:729–738

Christensen V, Pauly D (1992) ECOPATH II — a software for balancing steady-state models and calculating network characteristics. Ecol Model 61:169–185

Christensen V, Pauly D (eds) (1993) Trophic models of aquatic ecosystems. ICLARM Conf Proc 26, Manila

Holling CS (1959) Some characteristics of simple types of predation and parasitism. Can Entomol 91:385–398

Mangel M, Clark CW (1988) Dynamic modeling in behavioral ecology. Princeton University Press, Princeton, NJ

Stephens DW, Krebs JR (1986) Foraging theory. Princeton University Press, Princeton, NJ

Walters C (2000) Impacts of dispersal, ecological interactions, and fishing effort dynamics on efficacy of marine protected areas: how large should protected areas be? Mote Symposium Issue, Bull Mar Sci 66:745–757

Walters CJ, Juanes F (1993) Recruitment limitation as a consequence of natural selection for use of restricted feeding habitats and predation risk taking by juvenile fishes. Can J Fish Aquat Sci 50:2058–2070

Walters C, Kitchell J (2000) Cultivation/depensation effects on juvenile survival and recruitment: implications for the theory of fishing. Can J Fish Aquat Sci 57:(in press)

Walters CJ, Korman J (1999) Linking recruitment to trophic factors: revisiting the Beverton-Holt recruitment model from a life history and multispecies perspective. Rev Fish Biol Fish 9:187–202

Walters CJ, Hilborn R, Peterman RM, Staley MJ (1978) Model for examining early ocean limitation of Pacific salmon production. J Fish Res Board Can 35:1303–1315

Walters CJ, Christensen V, Pauly D (1997) Structuring dynamic models of exploited ecosytems from trophic mass-balance assessments. Rev Fish Biol Fish 7:1–34

Walters CJ, Pauly D, Christensen V, Kitchell JF (2000a) Representing density-dependent consequences of life history strategies in an ecosystem model: ECOSIM II. Ecosystems 3:70–83

Walters CJ, Pauly D, Christensen V (2000b) Ecospace: prediction of mesoscale spatial patterns in trophic relationships of exploited ecosystems, with emphasis on the impacts of marine protected areas. Ecosystems 2:539–554

Werner EE, Gilliam JF (1984) The ontogenetic niche and species interactions in size-structured populations. Annu Rev Ecol Syst 15:393–425

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