

Understanding fish habitat ecology to achieve conservation*

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Habitat science can provide the unifying concepts to bring together ecological studies of physiological tolerances, predator avoidance, foraging and feeding, reproduction and life histories. Its unifying role is built on two assumptions, imported from terrestrial habitat science and not always stated explicitly: that competition is present interspecifically and intraspecifically under at least some conditions, and that habitat features have some persistence and predictability in space and time. Consistent with its central conceptual position in ecology, habitat science has contributed importantly to scientific advice on pollution, coastal zone management and many other areas of environmental quality, although it has been largely divorced from developments in fish populations dynamics done in support of fisheries management. Commitments by most management agencies to apply an integrated, ecosystem approach to management of human activities in marine systems, poses new challenges to marine science advisors to management. Integrated management and ecosystem approaches both inherently require spatial thinking and spatial tools, making habitat science a particularly relevant advisory framework, particularly because of the unifying role of habitat in ecology. The basic mechanisms behind ocean biological dynamics, productivity, concentration and retention, however, present much weaker opportunities for competition and less persistence and predictability, weakening the foundations of theory and concepts behind current habitat science. The paper highlights the new types of thinking about 'habitat' that will be required, if habitat science is to meet the advisory needs of the new approaches to management.

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INTRODUCTION

The new millennium has seen a proliferation of policy commitments to the 'ecosystem approach'. Examples include the Bergen Declaration (2001), Reykjavik Declaration (FAO, 2002a), WSSD (United Nations, 2002), Canada's Oceans Act (Government of Canada, 1997), U.S. Commission on Ocean Policy (2004), Government of Australia (2003), EC Marine Strategy (EC, 2004). These endorsements are being made even though the scientific community is far from sure what it means (Pikitch *et al.*, 2004), and those subject to management have serious concerns about what new restrictions may be implemented under the guise of being part of 'an ecosystem approach' (ICES, 2004a). Efforts are being made in many fora to explain that the 'ecosystem approach' is an evolution in management

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of human activities in the seas, and not a revolution (FAO, 2002*b*; EC, 2004). Whether constituting evolution or revolution, the move to an ecosystem approach does provide an incentive to review the role of many scientific lines of inquiry in supporting policy and decision-making about marine conservation and human uses of the sea.

This incentive is particularly strong for the role of habitat science in management. Regardless of the authority, an 'ecosystem approach' places habitat thinking in a central position (Table I). Habitat is relevant to how the environment affects the resources being used by humans, how the human uses change the ecosystem and to viewing management as an integrated task of planning and management rather than piecemeal activity-specific and jurisdiction-specific regulation. Both for fisheries conservation and management, and for protection of environmental quality from pollution and other forms of harm, this is a new opportunity. Adopting an ecosystem approach has removed the 'blinkers' that science advisors on fisheries can look only at fish population dynamics models, and science advisors to pollution regulators can only look at contaminant levels, loading rates and end-of-pipe sources for pollution. Each group of policy setters and managers have to place their work in the context of what else is present around the species or environmental feature for which they are responsible, and how the activities each regulates affect those ecosystem features and interact with the effects of both natural forcers and the other human activities in the area. It is habitat that provides this larger context. The dawning of a golden age in the role of habitat science should be seen forming a new and arguably central pillar of management, rather than just 'interfacing' with sectoral management (Langton *et al.*, 1996).

Habitat is central in integrated management because the cornerstone of integration is 'place', and place must be viewed on scales inherently amenable to habitat research. For traditional fisheries science, the spatial scale at which fish stocks were assessed and managed generally was too large for habitat research to have a central role, whereas for a lot of work on pollution and marine environmental quality the scales were quite local. Habitat science could work readily at these local scales, but the local scale of the research and often of the perturbation limited their generality. The scale of integrated management is not yet defined, but scales under consideration (CSAS, 2004; EC, 2004) are ones where habitat science tied to generalizable theory as well as large-scale monitoring is likely to fit very well.

In this paper the past value of habitat studies as a basis for scientific advice on management will be noted. This will necessarily include reviewing what functions habitat plays in the fitness and life history of species occupying it. These reviews are done to bring out how the role of habitat science in integrated management differs from its role in the more traditional management contexts. Once the role of marine habitat science in integrated management is delineated, the paper shifts focus to how well habitat science, as practiced in marine ecosystems, is prepared to fulfill that role.

HABITAT SCIENCE

WHY IT MATTERS

Habitat science has been one of the strongholds of descriptive ecology. Many papers report on the results of measuring features of the habitat and abundance

TABLE I. Pervasiveness of habitat-related issues in the current fisheries policy documents of five national or international jurisdictions and five non-governmental or independent agencies reviewing fisheries policy (see Rice, 2005*b*, for details of comparative analysis)

Australia: Looking to the Future: A Review of Commonwealth Fisheries Policy, (Government of Australia, 2004), Sections 1–3;
 Canada: Atlantic Fisheries Policy Review; Department of Fisheries and Oceans, (DFO, 2004), Table, Section 1.1–1.3; Table 2, Section 2;
 European Commission: EC - Green Paper on the Common Fisheries Policy, (EC, 2001), Table 1, Chapter 1);
 FAO: Code of Conduct Guidelines and Checklist for an Ecosystem Approach to Fisheries, (FAO, 2002*b*); Table 1, pages 1–6;
 U.S.: Magnusson-Stevens Act 1996, (NOAA, 1996) Tables 1 and 2; Section 2

Habitat factors explicit in government fisheries policies:
 Protect fish habitats: Australia, Canada, EU, FAO, U.S.A.
 Protect and enhance biodiversity: Australia, FAO
 Reduce ecosystem effects of fishing: Australia, Canada, EU, FAO, U.S.A.

Tools and approaches explicit in government fisheries policy:
 Apply ecosystem approach: Australia, Canada, EU, FAO, U.S.A.
 Apply precautionary approach: Australia, Canada, EU, FAO
 Reduce impacts of fishing gear on habitats: Australia, Canada, EU, FAO, U.S.A.
 Identify and protect fish habitat: Australia, Canada, U.S.A.
 Address ecosystem effects of fishing: Australia, Canada, EU, FAO, U.S.A.
 Use marine protected areas: Australia, Canada
 Greenpeace (Fishing in Troubled Waters & Principles, (Greenpeace, 2004),
 IUCN, Sea Change 1996, with WWF Co-sponsor (IUCN/WWF, 1996).
 Millennium Assessment, Millennium Ecosystem Assessment, 2004, Chapter 25, Marine Systems (MEA, 2004).
 Pew Ocean Commission, America's Living Ocean (POC, 2003)
 World Wildlife Fund, Ocean Rescue and Endangered Seas Programs (WWF, 2004).

Goals explicit in fisheries policy proposals from environmentalist agencies:
 Healthy ecosystems and biodiversity: Greenpeace, IUCN, MA, Pew, WWF
 Protect habitats and coastlines: Greenpeace, IUCN, MA, Pew, WWF
 Restoring populations and ecosystems: Greenpeace, IUCN, MA, Pew, WWF

Tools and approaches explicit in fisheries policy proposals from environmentalist agencies
 Marine protected areas: Greenpeace, IUCN, MA, Pew, WWF
 Apply ecosystem approach: IUCN, MA, Pew, WWF
 Apply precautionary approach: IUCN, MA, Pew, WWF
 Management objectives for ecosystem health, not fisheries yields: Greenpeace, IUCN, MA, Pew, WWF
 Implement marine zoning: MA, Pew
 Regulate gears which cause damage: Greenpeace, IUCN, MA, Pew, WWF
 Integrated management: : IUCN, MA, Pew, WWF

of animals, and then conducting some form of pattern analysis. Done well, this in itself is important work. Whether the immediate research goal is to support improved conservation and management of a species or to understand its ecology, evolution, and life history, progress on any of the goals has to build on

knowing where the species will be found. 'Knowing where' begins with descriptive habitat ecology, and subsequently quantifying the quality and quantity of those habitats can have a major role in accounting for fluctuations in a population's status.

Habitat has this central role in accounting for variation in both life history and population status because habitat selection integrates so many factors about a species' ecology. At the most fundamental level, selecting a habitat is selecting an area where individuals are likely to find conditions within their physiological tolerances, *e.g.* temperature, salinity and oxygen concentration. Selecting a habitat is also selecting the degree of exposure to predators, through the nature and quantity of shelter provided in the habitats. Selecting a habitat is selecting the food regime available, by the likelihood of occurrence of prey and competitors in or near the chosen habitats. Selecting a habitat is even making choices about reproductive potential, through both the likelihood that spawning partners will occur in the same habitat or the spawning products will be transported to places suitable for fertilization and development. There are, of course, 'chicken-and-egg' issues in all of these statements. Is an individual selecting a habitat to achieve some balance of all of these benefits, or is an individual making a series of function-specific choices with the result being what ecologists call 'habitat selection'? Such issues are fascinating to debate, and have important implications. For the purposes of this paper, however, what matters is that habitat science integrates all these choices.

The nature of the habitat does affect how large a role habitat plays in accounting for variations in life histories and abundances; as does, of course, the history of how human activities have affected the species. In the scientific literature, it is clear that ecologists have given habitat issues great emphasis for freshwater species, and often high emphasis for anadromous and estuarine species. For such species, papers on species-habitat associations are numerous and consider diverse types of 'habitat' variables. Many publications claim habitat explains a substantial portion of variation in the abundance and distribution of species (Table II). For fully marine species, papers are less numerous, the 'habitat variables' often simpler, and the papers generally attribute weaker explanatory power to habitat (Table III). Moreover, considering several marine species selected for their breadth of distribution in North Atlantic and long history of research and management, the majority of recent papers on habitat requirements were about habitat requirements of larval and juvenile stages rather than adults (Tables II and III). For reasons developed below, it is concluded that this focus reflects the greater affinity of these early life-history stages for benthic and estuarine habitats, compared with adults of the same species.

THEORETICAL CONTEXT

Although the paper began with reference to descriptive ecology and pattern analysis, habitat science is not theory-poor. There have been several reviews of the theory of habitat use for marine species, probably most completely by MacCall (1990) and most recently by Shepherd & Litvak (2004). These reviews

TABLE II. Examples of the types of habitat features commonly used to explain habitat use by fresh water (F) and estuarine (E) fishes

Species	F/E	Habitat Attributes	Reference
Coho salmon <i>Oncorhynchus kisutch</i> (Walbaum)	F	Air Temperature Water temperature Water flow rate Water flow dates	Lawson <i>et al.</i> (2004)
	F/E	Land use features Water quality	Knowler <i>et al.</i> (2003)
Chinook salmon <i>Oncorhynchus tshawytscha</i> (Walbaum)	F	Geomorphological features Water flow rates Water temperature Patchiness of features	Hanrahan <i>et al.</i> (2004)
	F	Substratum type Grain size Water flow rates Cover and litter	Merz <i>et al.</i> (2004)
Atlantic salmon <i>Salmo salar</i> L.	F	Substratum type Water flow characteristics Patchiness of features	Coulombe-Pontbriand & LaPointe (2004)
	F	Substratum grain Substrate type Cover Water flow/seasonality Water temperature	Stanfield & Jones (2003)
Atlantic sturgeon <i>Acipenser oxyrinchus</i> Mitchell	E	Salinity Substratum type Bathymetry	Stein <i>et al.</i> (2004)
English sole <i>Parophrys vetulus</i> Gerard		Temperature Depth Substratum type Flow regime	Rooper <i>et al.</i> (2003)
Sole juveniles <i>Solea solea</i> (L.)	E	Temperature Fresh water inflow Substratum	LePape <i>et al.</i> (2003)
Small gadoids	E	Temperature Salinity Seasonality	Power <i>et al.</i> (2002)
Multispecies	E	Indices of integrity Emergent Vegetation	Hughes <i>et al.</i> (2002)
Multispecies	E	Vegetation Salinity Substratum Seasonality	Lazzari <i>et al.</i> (1999)

provide thought-provoking treatments of many contemporary issues in marine habitat science, particularly the dynamic interfaces of abundance of the species

TABLE III. Examples of the types of habitat features commonly used to explain habitat use by marine fishes

Species	Habitat Attributes	Reference
Atlantic cod <i>Gadus morhua</i> L.	Water temperature NAO Water temperature Salinity Oxygen	Sirabella <i>et al.</i> (2001) Neuenfeldt & Beyer (2003)
Atlantic cod juveniles	Depth Topographic relief Vegetation Depth Substratum features Water temperature Salinity Oxygen	Cote <i>et al.</i> (2004) Lindholm <i>et al.</i> (1998) Jarre-Teichmann <i>et al.</i> (2000)
Haddock juveniles <i>Melanogrammus aeglefinus</i> (L.)	Sediment type Temperature	Brickman (2003)
Whiting <i>Merlangius merlangus</i> (L.)	Bottom substrate Vegetation cover Sea Surface Temperature Depth	Atkinson <i>et al.</i> (2004) (Laboratory study) Zheng <i>et al.</i> (2001)
Plaice <i>Pleuronectes platessa</i> L. and dab <i>Limanda limanda</i> (L.)	Depth Substratum	Gibson & Robb (2000) (laboratory) Gibson <i>et al.</i> (2002)
Cod and plaice	Temperature Depth	Swain <i>et al.</i> (1998)
Atlantic Herring <i>Clupea harengus</i> L.	Temperature Salinity Seabed roughness Seabed hardness Zooplankton	Maravelias (2001)
Pacific Herring <i>Clupea pallasii</i> Valenciennes	Temperature Zooplankton	Norcross <i>et al.</i> (2001)
Pacific rockfish <i>Sebastes</i> sp.	Bottom substratum type	Yoklavich <i>et al.</i> (2002): juveniles Yoklavich <i>et al.</i> (2000): adults
Multispecies (deep-water)	Depth Topography Temperature Salinity	Uiblein <i>et al.</i> (2003)
Multispecies (shelf)	Temperature Depth	Perry & Smith (1994)
Multispecies (coastal)	Depth Latitude	Lloret <i>et al.</i> (2002)

NAO, North Atlantic Oscillation.

of interest with abiotic and biotic features of the environment, environmental change and abundances of the species' competitors. The point of importance for this paper, however, is that the concepts and theory used to explain these dynamic habitat-based interfaces come from terrestrial ecology. In terrestrial ecology, habitat science goes back to the earliest versions of niche theory (Gleason, 1926; Elton, 1927), and reinvigorated by MacArthur (1972) and Cody & Diamond (1975). These works have many variants of detail, but a common underlying foundation of competition and predictability (or 'persistence'), brought together in the concept of the 'ideal free distribution' (Fretwell & Lucas, 1969).

In these various theoretical frameworks for understanding spatial habitat use, intraspecific and interspecific competition are central mechanisms. At the species level, as habitats become packed with individuals, density-dependent processes begin to function, changing the quality of a site relative to alternative sites. From this line of argumentation, patterns of distribution and productivity in space can be explained (MacCall, 1990; Rosenzweig, 1991; Shepherd & Litvak, 2004). At the community level, interspecific competition and density dependent habitat effects are the foundation for community ecology. Ecological and life-history strategies can diversify in response to increased structural complexity in a habitat (Kohn, 1997; Levin, 2000) because there are simply more ways to earn a living in a structurally complex habitat than in a structurally simple one. Increased productivity in a habitat also can foster diversification in the community. As more energy is entrained in the system, more complex and reticulate networks can be supported without any of the nodes or pathways finding themselves energy-deprived so often that there is a risk that the system will collapse (Tilman, 1999; Hebert *et al.*, 2004). When habitat is patchy in structure or productivity these systems can diversify further (Buttel *et al.*, 2002), by juxtaposing more species closely enough that they may interact despite adaptations to different habitat specialities. All these sources of complexity give the raw material for diversification in uses of space (niche space) and in resilience (resistance to invasion and recovery from perturbation).

Diversification at the community scale is not restricted to species packing. Many fishes and invertebrates have reacted to habitat complexity by evolving complex life histories, so that single species occupy many different habitats at different life-history stages (Jennings *et al.*, 2001). Theorists debate whether this makes populations and communities more or less stable (Tilman *et al.*, 1998; McCann, 2000), but it is an argument of nuance and definitions more than of fundamentally different concepts. By occupying different habitats at different life-history stages the species or population as a whole becomes much less vulnerable to being lost (*i.e.* extinction) because even the total loss of one stage due to a habitat-based catastrophe still leaves other stages able to carry on the population. Correspondingly, even if habitat conditions are ideal for one life-history stage, the population's growth may still be checked by the state of habitats of other stages. Hence model communities with such diversity within 'species' are less likely to collapse or explode (Pimm & Rice, 1987), and the species (or community) can be considered more stable because it is harder to lose altogether. On the other hand when habitat requirements vary across life-history stages there are more chances for the habitat status of some individual stage to have an extreme value. Hence the configuration of the community changes more

over time and can be called less stable (May, 1973). It is an interesting side-note that birds and mammals have largely lost this way of taking advantage of habitat diversity, but that may be a necessary cost of parental care. By definition, for parents to care for progeny both old and young have to be adapted to some degree to the same habitat.

Theory relating habitat to population dynamics has been developed to deal with heterogeneity in time as well as space. For theory imported from terrestrial ecology, variability in time is commonly expressed as seasonal habitat dynamics in terrestrial systems (Fretwell, 1972; Morris, 1996), but interannual variation in habitat features fits comfortably within the framework as well (Hofmann & Powell, 1998; Jonzen *et al.*, 2004). Interpreting the seasonal or interannual variation in habitat quantity and quality uses the competition-based thinking in almost all cases (Morris, 2003; Shepherd & Litvak, 2004). The combination of seasonal and interannual variation in habitat features, competition, and variance in the size of populations together produce graphic and algebraic models which, although simple, are quite powerful. In fact, the role of density dependence and competition need not be continuous processes for the models to retain their power. Depensation at low abundance is a major concern in marine fish population dynamics (Lierman & Hilborn, 2001; Hutchings & Reynolds, 2004), and would have the same consequences for how species are distributed among habitats and over time.

These interacting ecological processes have been pulled together several times with various weightings, and different thoughts on what causes what. Not all of the syntheses are structured explicitly around habitat science, but even when habitat is not featured it underlies the processes being discussed. MacCall (1990) built heavily on the ideal free distribution concept linked to interannual variation in population abundances for reasons other than habitat features. Shepherd & Litvak (2004) showed that the interactions among the processes need not assume an ideal free distribution in order to generate the observed patterns, but the additional patterns are still merely products of interactions among environmental variability, species interactions and population variation, played out in habitats with stable characteristics.

The theory developed by Huston (1994) differs somewhat more, featuring the disturbance of the habitat features or populations as the source of the dynamics. It is a small step to place the perturbation and disturbance aspects of habitat and community ecology at centre stage; the more often a set of species moving towards some equilibrium are perturbed before reaching it, the more diverse the array of life-history traits which can coexist. The further they are driven away, however, the smaller the number of life-history strategies which could recover consistently and rapidly. 'Habitat' is no longer a stable suite of properties, but it includes the external perturbations which make the community dynamic; the system is being continually perturbed away from some equilibrium in abundance-habitat relationships towards which it would otherwise move.

The arguments above place habitat science at the centre of marine ecology. The linkages could be described in different ways to give a paper a different slant, but the linkages themselves would all remain. What matters is that habitat gives a single vehicle in which thinking about populations and communities, distribution and abundance, response to environmental variation, and even life

histories and ecological scales can be unified. This makes marine habitat science a powerful construct, as has been recognized occasionally, for example by the Ecosystem Principles Advisory Panel (1999). In some areas of applied marine ecology that power has been used.

ADVICE ON MANAGEMENT OF HUMAN ACTIVITIES IN THE SEA

How has habitat science been used in past scientific advice on management? For anadromous and estuarine species it has been an important research area, and important for advice on human activities which may alter habitat quality (Table IV). Nevertheless, despite its potential relevance habitat science has been almost completely disarticulated from fisheries resource management teams (Langton *et al.*, 1996). Stock assessments of anadromous species rarely had any habitat quantification. Habitat scientists in Canada advised a completely different group of managers than fisheries scientists did; the two groups largely attended different meetings and used different tools. In ICES advice on both North Atlantic and Baltic salmon *Salmo salar* L., scientific advice on fisheries devotes more than 95% of the text to classic population dynamics data and models, with extremely limited treatment of habitat quality, quantity and change (ICES, 2004b). Estimates of productive potential and, therefore, reference points of the managed *S. salar* stocks have their roots in habitat studies, but these roots are not reflected in the annual business of the advisory groups. Both the habitat scientists and the stock assessment scientists are trying to conserve stocks and promote productivity, but there is very little on-going cross-fertilization of ideas and expertise at the advisory level.

TABLE IV. Numbers of research publications since 1995 found by a Cambridge Scientific Index reference search, when various types of potential perturbations are entered along with 'fish' and 'habitat'. Although there are some false hits in these collections, the numbers give a general idea of the importance of the various types of perturbations affecting the quality of fish habitat

Type of perturbation	Habitats affected	Number of papers
Logging and forestry	Fresh water, estuaries	448
Urbanization, municipal development, sewage	Fresh water, estuaries	725
Mining	Fresh water	293
Hydroelectric power and dams	Fresh water	844
Acid rain, acid precipitation	Fresh water	2287
Contaminant	All	328
Global warming/climate change	All	218
Trawling	Marine, estuaries	479
Dredging	Marine, estuaries	350
Eutrophication	All	423
Pollution	All	4020

Habitat science has played an important role in fresh water and coastal pollution studies, but usually in an inverse context. Change in diversity of benthic communities or abundance of specific species has long been taken as indication of change in habitat quality, rather than using the change in habitat characteristics to predict changes in community composition or abundance of individual species (Hart & Fuller, 1979; Table IV). This approach is well grounded in ecological theory linking both habitat quality and community structure to disturbance regimes. The links to fish or invertebrate population dynamics theory are much more weakly developed. Again there are no inherent contradictions between population dynamics theory and how pollution is linked to habitat quality in advisory contexts; there is just little visible cross-fertilization.

Is the linkage of habitat science to population dynamics any better in the open marine systems than for anadromous or estuarine species and management problems? In fully marine contexts, the debates on how fishing gear affects habitat quality and the consequences of marine protected areas are the main management issues in which fisheries management and habitat science have met (Jennings & Kaiser, 1998; Collie *et al.*, 2000; ICES, 2000; Roberts *et al.*, 2002; Hilborn *et al.*, 2004). The fishing gear issue focuses on direct damage to the three-dimensional structural complexity of the substratum and the productivity, diversity and richness of the benthic community. Debates certainly extended to indirect effects of these direct ones (Jennings & Kaiser, 1998; Greenstreet *et al.*, 1999), but the mechanisms causing both direct and indirect effects were ones consistent with how terrestrial ecology thinks about habitat quality. Even the language of the debate was couched in terrestrial ecology with analogies to 'clearcutting' of the epifauna and macroalgae by mobile gears (Watling & Norse, 1998).

The arguments have been more sophisticated in debate about the benefits of marine protected areas (Hilborn *et al.*, 2004). Nonetheless, the role of habitat in these debates is the direct inverse of its role in the arguments regarding mobile gear impacts. With various nuances it is argued that if the physical features of habitats are protected from structural harm, and communities are protected from being set back in successional time, then a rich, diverse community will develop. Interpreting results of closed areas has been made complex by confounding reductions in fishing mortality (on target species and bycatch) with protection of habitat features and successional communities. There is enough evidence, however, to show that within closed areas it is possible to get many of the reactions predicted by the theory of how animals use habitats of increasing complexity and decreasing disturbance (Murawski *et al.*, 2001). It is not a coincidence, though, that the evidence is strongest for the benthos itself, and for portions of fish communities tied directly to the benthos by their life histories. The thinking about habitat science borrowed from terrestrial ecology applies most readily to these situations.

THE NEW MANAGEMENT CHALLENGES

The new initiatives of applying an ecosystem approach and integrated management in marine ecosystems are promoted widely as evolutionary rather than

revolutionary (FAO, 2002*b*; EC, 2004; Rice, 2005*a*). Can the new initiatives succeed, however, if science advisors and managers continue to use terrestrially-derived concepts of habitat science as the basis for advice and management in these expanded frameworks? Some extrapolations are being made directly, such as the call for protecting comparable percentages (variously 10 to 20%) of terrestrial and marine areas in wholly protected reserves (IUCN/WWF, 1996; Greenpeace, 2004). Even in the case of marine reserves, though, the arguments are usually through analogy with terrestrial systems rather than built on analyses which have independently suggested that the same percentages of habitat provide the same benefits at the ecosystem and landscape (or seascape) scale. More importantly, protected areas are simply one tool in the broad initiatives of the ecosystem approach and integrated marine management.

In the broader context science advisors will have to integrate the terrestrially-derived theoretical approach to habitat science with fish and invertebrate population dynamics analyses, which are derived from a separate set of theoretical and empirical models. Such integration may not be easy, but after a long period when the fields could develop largely independently, the integration is now necessary. The new suite of policies and flood of management challenges and commitments arising from the Convention on Biological Diversity, the ecosystem approach to fisheries, integrated management in marine strategies, and the panoply of related programmes share in common a spatial focus. For the tools needed for all the new policies and initiatives to work in harmony rather than to conflict, they have to be integrated on a meaningful spatial basis. As argued above it is habitat science more readily than any other starting point which brings the spatial dimension to understanding the dynamics of systems and advising on their sustainable use. This moves habitat science up off the seafloor, and out of the estuaries and coastal areas, into the water column. In this new and much broader setting can the terrestrially derived concepts and theory provide as sound a basis for understanding and advice as their have shown they can in the previous applications?

There are major challenges to making this transition successfully. In developing the preceding arguments, predictability and competition were highlighted as the two cornerstones of theory about habitat use. It was noted that the various theories of habitat use could deal with variation in space (patchiness) and time (seasonal and interannual change in productivity). Patches, however, are assumed to have a fundamental stability, and theory about use of patchy environments has animals distributing themselves according to probabilistic rules (Hughes & Grand, 2000; Frank, 2004). There is lawfulness to seasonality that habitat theory can also accommodate readily (Fretwell, 1972). Interannual variability may or may not be lawful. Where evidence is accumulating that species' life histories may reflect the selective pressures of decadal-scale variation in *e.g.* the Pacific Decadal Oscillation (PDO) and North Atlantic Oscillation (NAO) (McKinnel *et al.*, 2001; Reid *et al.*, 2001; Conners *et al.*, 2002), there is no evidence, at least not yet, that animals plan for when the regime shifts will occur. For mobile species like many fishes and invertebrates, however, adaptation may emphasize strategies to find a particular habitat type at a given time within the region rather than accommodating how habitat features may change at a specific place. Given that classic theoretical treatments of habitat use assume at least

probabilistic predictability for habitat features, can that assumption be extended to all of these situations?

The first cause for pessimism may be that when Longhurst (1996) asked biogeographic questions of marine ecosystems, he found that classic theory was not adequate for the task. This is important because it can be argued that biogeography is only a step beyond descriptive habitat ecology. It is multispecies pattern analysis with some explanatory theory for emergent and recurring patterns. It may not be easy, but it is less ambitious a step than integrating habitat ecology with population and community dynamics. Moreover, it is not necessary to endorse Longhurst's (1996) marine biogeographic zones to accept his arguments for why classic biogeographic theory was inadequate for ocean-wide marine applications. Longhurst (1996) stresses the inadequacy of transferring the theoretical basis for biogeography from land to sea. His reasons include weaker morphological differentiation of taxa in the sea, weaker evidence for self-sustainability of populations below the species level, very few analyses showing species abundance relationships with habitat features on spatial scales large enough to be meaningful to biogeography, and lack of evidence for concordant distributional boundaries of multiple species. Longhurst (1996) notes that some or all of these shortcomings may arise simply from the inadequate database to quantify patterns. Even if that were the only cause, it is a limitation that scientists and science advisors will face when applying ecosystem approaches and integrated management in the seas. There are even more fundamental reasons, however, why the ability to apply terrestrially-derived theories of habitat use to open marine ecosystems will be severely limited. Those reasons have important implications for the ability of habitat science to support ecosystem approaches to integrated management.

THE NATURE OF OPEN MARINE HABITATS

One cause for concern about the transferability of the 'terrestrial' concept of habitat to marine systems is the basic nature of the demersal and especially the pelagic portions of the seas. The preceding discussion highlights that terrestrial habitat theory assumes habitat features are tied at least probabilistically to place and can accumulate three-dimensional complexity. This description applies to freshwater habitats, estuaries and to the seafloor and its benthos. It does not apply readily to the water column of the open seas.

Bakun (1996) characterized the fundamental processes than underlie marine ecosystem dynamics as productivity, concentration and retention. The variance in ocean features caused by these three processes really comprises the habitat diversity of the water column. Importantly, the distribution of these features is neither stable in space nor reliable in time, although neither is their distribution wholly random. Spatial predictability usually occurs on scales of at most tens to hundreds of km with regard to where major fronts and upwelling sites will be. Temporal predictability of new features may be on scales of several days to weeks with regard to when features may occur in a specific locality, and once a feature occurs it may persist for no more than hours to a few days. Predictability usually does not occur on the scale of 10s of m to a few km, which better characterizes the spatial scale of predictability of terrestrial habitat features.

Nor is persistence of ocean features reliable on time scales of weeks to months characteristic of terrestrial habitat features. It is exactly the stability on these finer space scales and persistence on longer time scales that is the foundation for the majority of theory and thinking about terrestrial habitat, whether considering just patterns of habitat selection or its consequences for niche diversification and structural and functional properties of communities. In fact, even in terrestrial systems the basic theories require augmentation when terrestrial habitat loses this predictability, for example when short-lived blooms of annual flowers are an important habitat feature.

How does this different space and time scale of predictability of habitat features affect marine ecology and population and community dynamics? Consider each of the functions which habitat serves. Areas which meet physiological tolerances generally are only measured in temperature, salinity and depth, which are the common covariates of habitat-abundance studies of marine species (Table III). Such studies sometimes find moderately strong patterns of association, but have all the usual problems of linking pattern to cause and the relationships rarely are useful in formulating management advice. The three-dimensional habitat structure cannot offer shelter as terrestrial and benthic structure can, so protection from predators ceases to be a habitat function in the open sea. Rather, behavioural mechanisms such as schooling for predator avoidance come into play (Ryer & Olla, 1998). The implications of the different nature of habitat for foraging are particularly interesting. Because the three-dimensional niche diversification is not available either structurally or in terms of temporal predictability, competitors cannot evolve increased distance from each other in foraging space. Individuals can only predict probabilistically when and where the right 'habitat' for foraging will be, and this limits the degree to which predators can specialize on different prey. It is this aspect of habitat which may be the root cause of marine trophic relationships being better explained in size-based models than in species-based trophodynamic models (Rice, 1995; Pope *et al.*, 2003). The different spatial and temporal scales of predictability of marine habitat features even affects reproductive strategies by making it impossible to predict where the proper spawning habitat will be in the water column. This means a species either becomes an obligate bottom spawner where conditions are stable on the scales typical of terrestrial systems (for example herring *Clupea harengus* L.), or becomes a "bet-hedger", typically a broadcast spawner with multiple learned spawning aggregations on much finer scales (Rickman *et al.*, 2000; Einum & Fleming, 2004). The broadcast spawning and unpredictability of suitable habitat in space and time then unfold as diverse life-history strategies as growth increases the capacity of individuals to control movement in the water column. This in turn allows life-histories strategies that are less passive, and allow better risk management 'choices' by the individuals.

In summary, then, the key processes in open marine ecosystems: productivity, concentration and retention, give habitat features different properties of predictability and persistence than terrestrial habitat features. The features of marine habitat still offer a unifying way to look at physiology and energetics, predator avoidance, foraging and reproductive behaviour, and life-history diversification. The unifying view is just a very different one. What does this new view mean for the concept of 'habitat' in marine ecosystems? It means that theories and

concepts derived from terrestrial ecosystems cannot be as readily imported for species and community in the water column as they can be for benthic, estuarine and freshwater species and communities. It is the reliability of habitat features in space and time which allows competition to be a consistent directional pressure in terrestrial community ecology. Lacking that fine-scale reliability of habitat features in the water column, competition must function in different ways, and generally more weakly in marine systems (Rice & Kronlund, 1997; Rose, 2000). Having weakened both pillars of terrestrial habitat theory, how far the comprehensive theory of habitat use borrowed from terrestrial ecology really applies to habitat features as they exist in the sea must be questioned. Likewise how borrowed theories are applied to build from marine habitat features to the other ecological processes must be scrutinized carefully.

IMPLICATIONS OF 'MARINE HABITAT' FOR ECOSYSTEM BASED INTEGRATED MANAGEMENT

If future movement is towards integrated management, an ecosystem approach, multispecies area-based fisheries management, and regional planning, then the theories and concepts that will form the basis for scientific advice on these new approaches to management of human activities in the seas must be considered. First, understanding and theories of how marine populations, species, and communities will respond to perturbation (fishery or otherwise) are needed. A theory linking marine 'habitat' features, population dynamics and environmental variation that is based on the probabilistic nature of productivity, convergence and retention rather than on stability of habitat features in space and time leading to strong intra- and interspecific competition is also needed. There are many reasons to question the extent to which the theories and concepts derived from terrestrial habitat science will apply to open marine systems. The limitations of the borrowed theories and concepts have to be seriously explored and, where necessary, adapt them for marine applications.

Unfortunately there are some severe impediments to testing and adapting the habitat-based theories and concepts. First of all, it is never easy to modify theories and concepts when specific ways of thinking about problems are deeply entrenched. More importantly, though, for most of the marine ecosystems many of the key populations are severely depleted. Whether it is traditional fisheries management or any of the new more comprehensive approaches, recovery of these depleted stocks dominates management planning (EC, 2003), and will be the focus of the discussion.

As noted above the habitat use of larvae and juveniles of the major commercial stocks are much better studied than the habitat use patterns of adults, and results are more consistent with the borrowed concepts. Whether the depleted stock of concern is cod *Gadus morhua* L., haddock *melanogrammus aeglefinus* L., or flatfishes, it is hard to argue that habitats for the early life-history stages are limited. The structural complexity of near-coastal and benthic areas is important for younger ages of many demersal species. At least in the north-west Atlantic, however, the historic distribution of trawl effort which could alter these habitats overlaps very little with the historical distribution of juvenile cod and other demersal species (Rice, 2005b). Moreover, at least for cod in the north-west

Atlantic both the recruits produced per spawner and the spawners produced per recruit are neither markedly better nor worse than historic values (CSAS, 2003). Hence it is simply that both juveniles and adults have been depleted far below levels which would saturate available habitat. Both these lines of evidence suggest that however important juvenile (and adult) habitat quantity and quality may be, its consideration has a marginal role at best in the scientific dialogue about recovery. With current knowledge it is even harder to see a major role for habitat science in recovery planning for the spawning component of the stocks.

Such a conclusion is premature, of course, because the arguments are circumstantial. Nonetheless, although identification of important habitat is a legal requirement for recovery planning of depleted stocks (Canada: <http://www.laws.justice.gc.ca/en/s-15.3/text.html>; U.S.: <http://www.fws.gov/endangered/esa.html>), the depleted state of the stocks mitigates against doing applied research on the species, habitat relationships, even in the more classic contexts. First of all, many spawning components are believed to have been lost from the depleted stocks (Smedbol & Wroblewski, 2002), and transport mechanisms have a strong effect on the distribution of eggs and larval of these demersal species (Heath & Gallego, 1998; Bradbury *et al.*, 2003). Combining these two observations, the distribution of spawning products from the residual population will give quite biased information about the patterns of distribution of larval and juveniles across habitats that existed when stocks were healthy and productive. If fisheries targeted and selectively depleted the larger and more productive stock components, some of the best quality habitats now may be receiving few recruits whereas some poorer quality habitats may be receiving disproportionately more. Hence the classic methods of relating abundance to habitat features may produce very misleading indications of what is 'preferred' habitat and what is 'secondary'.

More detailed process-based research on growth and fitness across habitats can overcome this problem, but only with a much greater investment of research effort. Unfortunately, there is a second problem that limits the ability to conduct meaningful process-based research as part of recovery planning for depleted stocks. At low abundances evidence for competition will not be apparent in distributional data even if competition is moderate to strong when abundances are higher. Hence, if it is merely conceded that habitat is unlikely to have been depleted to the extent that populations of many over-exploited stocks have been, data on species habitat use collected under present conditions will be uninformative about what will happen on local to regional scales once recovery is actually underway. For the older life-history stages this is unlikely to be a major complication. It has already been noted that the unreliable location and timing of marine habitat features resulting from Bakun's (1996) three processes means that classic views of competition may apply weakly or not at all, regardless of abundance. If some key early life-history stages are linked tightly to benthic or coastal substratum features, however, studies under current conditions are likely to fail to provide information about potential competition-based bottlenecks along the path to recovery. This problem may be most serious for early life-history stages in intermediate positions on the recovery trajectories of populations, when availability of habitats which have more terrestrial-like characteristics may become limited.

Protected species legislation also requires recovery planning to identify appropriate recovery targets for the depleted species. This also may be problematic when ocean temperature and salinity features of habitats are changing on scales of hundreds to thousands of km. Concerns about fish community impacts of warming of the southern North Sea (Edwards & Richardson, 2004) and regime shifts in the North Pacific and North Atlantic (Frank *et al.*, 2005) are growing. To this point, these discussions have played some role in science advice on management, such as estimates of thermal habitat for Atlantic salmon in the North Atlantic (ICES advice 1993 unpubl.) and survivorship of Pacific salmon *Oncorhynchus* spp. (Mueter *et al.*, 2002). There is some speculation, usually weakly thought through, about what these environmental changes mean for fisheries management reference points (ICES, 2002). The true test of whether habitat science has a central role in the new ecosystem-based integrated management of marine regions may be in how these speculative discussions mature into new, quantitative ‘habitat’ science in the demersal and pelagic parts of the oceans.

Although habitat science was often not prominent in science advice on management of living marine resources, it can be viewed as the central construct around which the other applied science concepts are structured. It has had important roles in some advisory contexts to management, particularly with regard to shoreline and coastal issues. In these roles, theory and concepts taken from terrestrial habitat science have served adequately, but they have served adequately because the management issues have addressed the ‘skin’ of the ocean. The new wave of management challenges from applying an ecosystem approach and integrated management, and recovery of depleted species, have a central spatial focus. Now habitat science may emerge as the central structuring construct for understanding and scientific advice on these management issues. It is necessary, however, to move thinking about habitat to the entire marine water column. Up in the water column the question ‘what is habitat?’ has very different answers than when posed about areas around the ocean’s skin. Some new and imaginative thinking about what habitat is in dynamic oceans and what that concept means for integrated, regionally based management is needed. This new thinking is particularly important, but particularly difficult when management must focus on recovery of all the populations that have been depleted.

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