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An Overview of Habitat Classification Systems, Ecological Models, and Geographic Information Systems Applied to Shallow Foreshore Marine Habitats

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APPLIED TO SHALLOW FORESHORE MARINE HABITATS

by

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ABSTRACT

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This document presents an overview of published systems and models that have been developed and used to assess the relationships between fish and habitats in shallow, foreshore marine areas. The following areas are reviewed: (1) Habitat classification systems offering a set of procedures to identify, delimit, and describe the habitats of foreshore fishes; and, (2) Ecological models describing relationships between habitat attributes (e.g., vegetation type) and fish properties (e.g., biomass). Ecological models can be divided into fish-habitat models, which can be divided on the basis of mathematical approaches (index, simple qualitative, complex qualitative, regression, and probability functions), and on the basis of structural approach (species-specific and habitat-specific). A second type of ecological model is the trophodynamic model, which describes feeding interactions among fish in foreshore habitats. There are two main types of trophodynamic models: predator-prey and food-chain models. A natural extension of the trophodynamic models are the energy/nutrient flow models. This third class of ecological model assesses the role of specific fishes in terms of energy transfer within a single foreshore habitat, or provides an holistic view of how various habitats interact. The document concludes with a brief discussion of the use and utility of geographical information systems (GIS), and how GIS offers a tool for developing models and systems for assessing the productive capacity of fish habitat in shallow foreshore marine areas.

RESUME

Robinson, C.L.K. and C.D Levings. 1995. An Overview of Habitat Classification Systems, Ecological Models, and Geographic Information Systems Applied to Shallow Foreshore Marine Habitats. Can. Manuscr. Rep. Fish. Aquat. Sci. 2322: 65 p.

Le présent document résume les systèmes et modèles, ayant fait l'objet d'une publication, qui ont été élaborés et utilisés pour évaluer les relations existant entre le poisson et l'habitat dans les zones peu profondes de l'avant-côte marin. Les domaines examinés sont: 1) les systèmes de classification des habitats offrant une série de procédures pour l'identification, la définition et la description des habitats des poissons de l'avant-côte et 2) les modèles écologiques décrivant les relations entre les attributs des habitats (types de végétation, etc.) et les caractéristiques des poissons (biomasse, etc.). Les modèles écologiques peuvent être répartis en modèles poissons-habitats, qui peuvent être divisés en fonction du traitement mathématique (indice, qualitatif simple, qualitatif complexe, régression et fonctions probabilistes) ou structural (spécifiques pour l'espèce ou l'habitat). Un deuxième type de modèle écologique est celui du modèle trophodynamique qui décrit les interactions alimentaires entre les poissons des habitats. Il existe deux grands types de modèles trophodynamiques: celui des prédateurs-proies et celui des chaînes alimentaires. Ce type de modèle donne naturellement naissance à celui des flux énergie-matières nutritives. Le troisième type de modèles écologiques porte sur l'évaluation du rôle de poissons donnés du point de vue du transfert d'énergie au sein d'un seul habitat ou donne un aperçu holistique des interactions entre divers habitats. Le document se termine par une courte discussion de l'utilisation et de la pertinence des systèmes d'information géographique (SIG) et de la façon dont ces systèmes peuvent servir à l'élaboration de modèles et de systèmes pour l'évaluation de la capacité productive des habitats du poisson dans les zones marines peu profondes de l'avant-côte.

INTRODUCTION

The Department of Fisheries and Ocean's (DFO) policy on fish habitat management is designed to achieve an overall net gain of fish habitat (DFO 1986). One of the three goals of this policy is to implement the principle of "no net loss" to maintain the current productive capacity of fish habitats. **Productive capacity** is defined as "The maximum natural capability of habitats to produce healthy fish, safe for human consumption, or to support or produce aquatic organisms upon which fish depend" (DFO 1986).

The challenge presented to fishery scientists and managers is to develop tools that can evaluate and predict productive capacity from biotic and abiotic attributes of the habitat. The majority of published work completed on this topic has focused on describing fish-habitat relationships, and developing mathematical models of these relationships, for freshwater systems and fisheries (e.g., Busch and Sly 1992; Korman et al. 1994). It is presently unclear as to what approaches exist or how they are used to understand fish-habitat relationships in coastal foreshore regions.

The main objective of this manuscript report is to review published ecological, trophodynamic, and habitat models that have been developed for intertidal and shallow marine zones. Studies reviewed include models that analyze energy flow between major habitat types, predict survival of juvenile fish, and interpret relationships between physical attributes at a variety of scales on fish survival and productivity. The approach taken was to divide the review into three major sections: habitat classification systems, ecological models, and geographical information systems. Initially some system or procedure is required to describe the types and distribution of coastal habitats that are utilized by, and are critical to, fish. Once critical fish habitat is delimited, ecological models could be used to evaluate habitat function. For example, models may use empirical data or mechanistic functions to describe relationships between habitat variables and fish properties, such as production or survival. A geographical information system offers a framework that organizes, presents, and analyses data regarding the distribution, type, and function of fish habitat. In summary, we discuss considerations for the development of a quantitative system incorporating these approaches for assessing the productive capacity of fish habitats in foreshore regions of the Strait of Georgia, British Columbia.

METHODS

A comprehensive literature search was conducted to locate primary and "grey" publications that describe techniques for assessing relationships between abiotic/biotic attributes and fishes living in shallow nearshore marine regions. The literature search included three tasks:

- 1) Seven primary research journals were searched manually for relevant studies conducted between 1983 and 1993:
 - Canadian Journal of Fisheries and Aquatic Sciences
 - North American Journal of Fisheries Management
 - Marine Biology
 - Transactions of the American Fisheries Society
 - Marine Ecology Progress Series
 - South African Journal of Marine Science
 - Fishery Bulletin
- 2) Three computer reference data bases were searched using the key words and phrases listed in Table 1 of Appendix 1. The data bases searched were:
 - WAVES
 - AQUAREF
 - ASFA (Aquatic Sciences and Fisheries Abstracts)
- 3) Over 40 North American researchers were contacted by phone to identify relevant research in progress, unpublished work, or low-circulation publications.

The manual and computer-based literature search identified over 300 studies relevant to the objectives and these are given in the "Literature Cited and Additional References". A listing of the citations is also available from the authors in electronic form. We then reviewed a subsample of the key studies identified in each of three major areas; namely,

- Habitat Classification Systems
- Ecological Models
- Geographic Information Systems

HABITAT CLASSIFICATION SYSTEMS

A habitat classification system (HCS) is a set of rules or procedures that are used to identify, delimit, and describe the habitats of naturally occurring biota. Habitat can be defined as the range of environments in which a species occurs (Whittaker et al. 1973). Combinations of physical or chemical variables are typically used to delimit the habitat of the most common or abundant biota, but habitats for animals may be defined botanically (Krebs 1989). Coastal habitat classification systems identified in the literature search (Table 1) are primarily used to:

- describe foreshore habitats that have similar physical and biophysical attributes
- inventory and map foreshore habitats and biodiversity
- provide a structured approach
- standardize concepts and terminology
- provide a system of linkages between a physical map of the coastline and biophysical surveys of habitat
- aid in decisions about resource management and conservation

- assess influence of human disturbance on natural systems
- describe the distribution and extent of habitats, communities and species

The majority of the coastal HCSs describe marine or estuarine habitats (Table 1), and almost all use a hierarchical approach to classifying foreshore habitats. The hierarchies progress from general levels such as systems (e.g., marine versus estuarine) to specific levels such as subclasses of habitats (e.g., sand versus mud). The various levels of habitats in a classification hierarchy are primarily determined using data on substratum, physical processes, and vegetation (Table 1). Because of this hierarchical approach HCSs have the advantage of being relatively open-ended and broad in scope. A wide range of coastal habitats can be classified, and new habitats can be readily incorporated without having to modify the HCS. Habitats can also be classified quickly using easily measured physical attributes of the system. Aircraft remote sensing, for example, has been used to collect physical and some biological data to classify foreshore habitats in the Queen Charlotte Islands (Harper et al. 1993). Most HCSs require data describing the abundance or presence/absence of common biota, collected from ground surveys. Typical biota include sessile plants and invertebrates, and fish are not usually considered. Habitat classification systems ultimately give a reasonable characterization of overall foreshore habitat diversity and distribution. An overview of the advantages and disadvantages of 11 HCSs, discussed in a recent review by Frith et al. (1993) is given in Appendix 2.

One of the best examples of an approach commonly used in classifying foreshore marine habitats is that developed by the Washington State Department of Natural Resources (Dethier 1990). This system, developed for describing marine and estuarine habitats, builds on the National Wetland Inventory scheme of Cowardin et al. (1979). The Dethier HCS differs from Cowardin's approach in that it recognizes the importance of waves and currents in structuring coastal communities. The Dethier approach also removes the "aquatic bed" categories from all levels, making substratum by itself one of the highest levels in the hierarchy (Table 2). The Dethier system uses three major habitat classifiers: depth, substratum, and energy level. For each of the various combinations of classifiers, habitats are subsequently distinguished using "diagnostic" or dominant biota. The main premise of Dethier's approach is that a limited set of physical parameters (waves, currents, salinity, depth, substratum) strongly constrains the distributions and interactions of marine plants and animals. The hierarchy of physical factors, in turn, should "provide reasonable predictability of dominance types".

The Dethier system has been used by the Washington State Department of Natural Resources to classify about 60 habitats along the Washington coast. Several other state agencies have also used the Dethier

approach to classify nearshore marine and estuarine habitats (e.g., Oregon, Maine, and Alaska). The Oregon Department of Fish and Wildlife, for example, has combined the Dethier system with spatial scale as the central concept in defining coastal habitats (D. Fox, pers. comm. Oregon Dept. Fish and Wildlife, Astoria, OR). The Oregon HCS is arranged hierarchically on a spatial scale with seven levels from ecoregions (thousands of km) to microhabitats (< 2 m). The spatial level has ecological meaning because it defines an area occupied by a unique set of organisms or ecosystems. In addition, the spatial unit has resource management applications because it "can be assigned a unique set of management, use, or protection criteria tailored to the biota of the area" (Fox 1993). In turn, a specific HCS can be inserted at any given spatial level to describe ecosystem characteristics. For instance, a modified version of Dethier (1990) is used to describe the mesohabitat (along shore scale 2 m - 100 m) of the marine rocky intertidal system. The advantage of this HCS is that managers can evaluate ("enter") the ecosystem at different scales, and thus can ensure that outcomes are not "scale-driven".

Habitat classification systems have limitations because the definitions of some habitats and their boundaries are unclear. For example, although energy from waves, currents or wind are recognized as important in structuring biotic communities, methods for ascertaining differences among these as organizing forces of sessile invertebrate communities are not available (Brown 1993). Also, the areal extent of classified habitats is rarely known making their use in evaluating fish habitat capacity limited. More importantly, the majority of the HCSs are built on one assumption that makes their rigour as a classification system for fish habitats difficult: for each set of physical habitat parameters there is a unique set of biota with well defined distributional "edges" that can be discretely categorized. This assumption is unlikely to hold for sessile invertebrates, let alone highly mobile vertebrates. For example, it is well known that the distributions of many marine intertidal invertebrates are patchy even when the physical environment appears uniform and appropriate (Dethier 1990). For fish this assumption is even less valid because associations of fish with particular habitats do not necessarily imply utilization or dependence, and because temporal changes in habitat use due to seasonal or successional shifts in life history are common.

Describing the type and distribution of habitat based on physical features and/or dominant biota is thus not sufficient criteria for classifying fish habitat, but at present this method is used widely by habitat managers because there are few alternate methods. To successfully classify fish habitat for use in evaluating capacity or capability requires an understanding of functional relationships. Functional aspects of habitat that are important to fish include prey production, food-web structure, conditions that affect physiological condition, or habitat complexity as refugia.

It is apparent from the literature search that there are only a few attempts at classifying fish habitat on the basis of habitat type, distribution and function (Table 1). The best example of including habitat function (as well as type and distribution) in assessing fish habitat is the Estuarine Habitat Assessment Protocol for Puget Sound, WA (Simenstad et al. 1991). Although the protocol is not a true classification system *per se* it nevertheless provides insights into the potential function of habitat and how it may influence fish properties like survival, production, or biomass. The protocol utilizes information 1) delineating basic categories of estuarine habitat types (based on substratum), 2) describing habitat functions (reproduction, feeding, and refuge and physiology), and 3) representing species assemblage in each habitat. The three fish and wildlife habitat support functions are further subdivided (Table 3). One of the main advantages of the Puget Sound Assessment Protocol is that it can be accessed via habitat type, fish assemblage, or habitat attributes. Thus the system is extremely flexible, allowing the user to "define" habitat boundaries or assemblages.

An assessment protocol that considers habitat function was developed for DFO by Williams (1990) and this author recommended an approach for evaluating impacts of development on coastal fish-habitat productive capacity in B.C. Williams (1990) included summaries describing life cycle, coastal distribution, the biophysical characteristics of marine/estuarine habitats utilized by each of 20 commercially and ecologically important B.C. fishes, and a HCS with fish habitat requirements as a major consideration. The HCS was developed to "provide a comprehensive and ecological approach to describing marine and estuarine fish habitat". The HCS was developed primarily from existing coastal classification systems (e.g., Estuarine habitat mapping and classification system manual; Hunter et al. 1983), and incorporated functional relationships in the habitat descriptions that allow for evaluation of the productive capacity of fish habitats. Frith et al. (1993) suggest that one of the main limitations of the Williams HCS is that it is designed only to classify small areas of habitat. This highlights the perceived importance of scale in classifying habitats; HCSs are often developed for the convenience of the user and biologically meaningful scales are sometimes ignored.

An important biogeophysical classification of nearshore habitats in the Strait of Georgia is based on a data set of subtidal habitats and algal communities collected in the 1970s by R. Foreman of the Department of Botany, University of British Columbia, Vancouver, B.C. The subtidal data set consists of quantitative data obtained by destructive sampling, as well as by visual inspection on transects at selected sites accompanied by specimen collection. The data were analyzed to include algal-fauna community relationships, with each community being related to slope, substrate, depth, aspect, and disturbance history. Ten algal community types are recognized from these surveys in the Strait of Georgia (Levings et al. 1983).

Communities were quantified through calculation of biomass for particular community assemblages, and evaluated on particular substrate, and depth.

ECOLOGICAL MODELS

In the following section, we critically review selected ecological models used by fishery scientists to evaluate quantitative and qualitative relationships between habitat attributes and fish properties in foreshore coastal habitats. In this review, a model was assumed to be any mathematical function that was used to describe the relationship(s) between fish properties and habitat attributes.

The studies identified in the literature search used one of three main modelling approaches (Table 4): 1) The most common approach was to develop a model that described or evaluated empirical relationships between habitat attributes (e.g., vegetation type or density) and fish properties (e.g., biomass, production, survival, etc.). These fish-habitat models were developed to determine the fish-habitat relationships for individual species or for assemblages of fish species living in similar habitats. The models used relatively qualitative mathematical approaches like indices, correlation analysis, or multivariate techniques (e.g., ordination), or quantitative approaches such as regression, and nonparametric techniques such as probability density functions. 2) a second modelling approach identified and evaluated the importance of biological interactions, for example predation, on fishes living in a habitat. Thus models considering biological processes were included in this review because we assumed that physical or chemical habitat attributes not only directly influence fish, but also indirectly effect fish via the effects of predation or competition. 3) the third major modelling approach considered the flow of energy or nutrients among major components of a foreshore ecosystem. Ecosystem models include fish as only one of several major organisms found in one or more critical habitats that are linked in a food web. These models considered energy or nutrient flows among populations or entire food-webs, and thus considered simultaneously both the direct and indirect influences of habitat on fish, and the important interactions among habitats.

FISH-HABITAT MODELS

Fish-habitat models are models that describe relationships between habitat attributes (e.g., vegetation type or density) and fish properties (e.g., production, survival, biomass, abundance, etc.). The most important aspect of any fish-habitat model is the mathematical approach used to describe the relationship between the habitat attribute and the fish property. The approach used may be as simple as developing an index or a linear regression of one or more habitat attributes and fish properties, or as complex as developing a probability density function of the fish property as influenced by some key habitat attribute. Another important aspect of

evaluating any fish-habitat relationship is the structural approach taken to develop the model. Two major "structural" approaches to developing fish-habitat models were identified: 1) from the perspective of the "life-requisites" of an individual fish species, 2) from the perspective of the fish community or assemblage utilizing a specific habitat. Either structural approach can use any of the mathematical approaches discussed above to describe the fish-habitat relationship.

In the remainder of this section we discuss the mathematical and structural approaches used to develop fish-habitat models. We briefly introduce the approach, discuss several representative example studies, and point out major mathematical or biological limitations to the approach. At the end of each section we present a table of selected studies identified in the literature search. The tables do not include all studies, but rather provide background to selected mathematical or structural approaches.

Mathematical Approach

From the literature search, five major types of mathematical models were identified:

- Index Models (e.g., HSI)
- Simple Qualitative Models (e.g., correlations)
- Complex Qualitative Models (e.g., ordination)
- Regression Models
- Probability Density functions

Index models

The simplest approach used to evaluate functional relationships between habitat attributes and fish properties is to develop an index. For instance, Deegan et al. (1993) developed an estuarine biotic integrity index based on changes in the fish communities of eel grass ecosystems associated with anthropogenic stress. The authors found that the function of seagrass habitats as a habitat and nursery area for fish was severely compromised long before the beds were completely degraded. Generally, declines in total numbers of species, abundance and functional groups were correlated with eutrophication. From this information the authors developed an estuarine biotic integrity index. The index, in turn, correlated well with other measures of anthropogenic stress such as oxygen and increased chlorophyll concentrations, and can be used as a monitoring tool.

One of the most common indices used in the U.S. are the habitat suitability index models (HSI) developed for the habitat evaluation procedures of the U.S. Fish and Wildlife Service. The main premise of using HSIs is that there is a positive relationship between habitat condition and productive capacity, such that habitat quality is somehow related to critical fish properties. This relationship is typically described using an index which

represents the ratio of present habitat condition to an optimum or standard habitat. The standard represents the maximum potential production of an optimal habitat. HSI models offer a relatively simple method of quickly assessing the qualitative importance of habitat variables on fish life-requisites, like food or reproductive requirements. HSI models can be useful as qualitative descriptors of fish habitat based on life requisites, but they are generally not used for quantitative estimates of fish properties from habitat attributes.

Very few HSI models have been developed or validated for marine fishes in coastal habitats (Table 5). Most of the studies are for salmonids living in streams. However, a HSI model was applied to juvenile English sole (*Parophrys vetulus*) from estuaries and coastal areas of the Pacific northwest (Toole et al. 1987). The HSI model was based on the assumption that any environmental variable that impacts growth, survival, distribution or abundance of juvenile sole can be expected to impact the carrying capacity of the habitat. The English sole HSI model evaluated five habitat variables: hydrodynamic regime, dominant sediment type, bottom water temperature, bottom mean salinity, and dissolved oxygen concentration. The first two habitat variables combine to describe the food component of the HSI, while the latter three variables describe the effects of water quality. The two components (food and water quality) are combined to form the HSI. The authors stated that the HSI model "can be used to compare different habitats or the same habitat at different times. The habitat with the higher index value should be the area that could potentially support more juvenile sole".

As quantitative estimators of productive capacity from coastal habitat variables, HSI models are limited because the usual assumption of a positive, linear relationship between habitat and carrying capacity is unfounded. Factors other than habitat quality (e.g., density dependent factors) may reduce crop or production, thus resulting in a hyperbolic or sigmoidal relationship. HSI models are also inadequate because they do not require identification of specific equations to describe the functional relationship between habitat attributes and fish properties and are usually subjective. Attempts to derive empirical suitability index curves use techniques such as maximum performance, and thus ignore variance in the data. Even if index curve development is unbiased and objective, problems with the method used to combine curves (i.e., method of averaging), and the accumulation of errors in combining curves become problematic (White 1990). Moreover, Rice (1990) indicates that since index curves are not interval measures on a common scale they should not be combined. Another limitation of HSI models is that validation of their prediction is generally not successful (White 1990).

Simple Qualitative Models

One of the most frequently used approaches by researchers for evaluating fish-habitat relationships are relatively simple qualitative models, such as correlation or analysis of variance. When we wish to establish the degree of association between habitat attributes and fish properties then correlation analysis is appropriate. The degree of association refers to whether the two variables vary together (Sokal and Rohlf 1981). Thus correlation analysis can identify the potential direction of the fish-habitat relationship and describe it from empirical data.

The majority of fish-habitat models identified in the literature search used correlation analysis (Table 6). Bennett and Griffiths (1984) for example, examined correlations between aspects of fish community structure and physical descriptors of habitat in South African rock pools. Total number of fish and biomass per rock pool were highly correlated with the amount of rock cover in, and the surface area and volume of, the rock pools. The authors used the results from correlation (and regression) analysis to hypothesize that physical characteristics of rock pools were critical factors limiting the abundance and diversity of intertidal fish communities. Worthington et al. (1992) also used correlation analysis to assess the relationships between density of seagrass shoots and total (and individual species) abundance and diversity of fish and decapods. The null hypothesis was that there was no relationship between the two variables among separate seagrass beds distributed over a large spatial scale. The authors tested many correlations, which may have resulted in the detection of potentially spurious relationships. However, the authors did examine the probability of accepting the null hypothesis when in fact it is false (Type 2 error).

To circumvent the possibility of Type 2 errors and other parametric "problems", Moyle et al. (1986) used Spearman rank correlation coefficients to evaluate the patterns and abundance of fishes in a marsh in central California. The nonparametric approach was used because many of the variables did not conform to a normal distribution, and no single transformation could be applied to all environmental and fish variables. This approach provides a more conservative approach to describing fish-habitat relationships, but may be less rigorous statistically.

Another relatively simple descriptive approach commonly used is analysis of variance (Table 6). With this method, the investigator tests whether two or more means of fish properties are significantly different from each other in relation to habitat features. Bell and Westoby (1988), for instance, used a 3-way ANOVA to test for effects of height, density, and edge of seagrass leaves on numbers of species and individuals of fish and decapod fauna in a bay in New South Wales Australia. The authors found that the density of several fish and decapods were significantly affected by

changes in either height or density of sea grass leaves. The authors noted that further research is needed to determine the proximate causes of differences in abundance of species between areas of seagrass differing in leaf height and density.

In another study, Mgaya (1992) used ANOVA to determine if significant differences existed in production of a tidepool fish among different tidal zones in British Columbia. The author found that none of the physical variables examined (depth, perimeter, width, length, tide zone) significantly affected production. The author concluded that a lack of significant variations in growth among tidal zones as indicated by ANOVA may have resulted because there were no consistent differences in elevations among the pools.

Simple qualitative approaches, like correlation analysis or ANOVA, only identify the degree and possible direction of the fish-habitat relationship. For example, the numbers of fish were found to be significantly and positively correlated with mean macrophyte biomass (Stoner 1983). Similarly, Sogard and Able (1991) found significantly more fish in *Zostera* than *Ulva* beds. The possible direction or significance of the relationship does not however indicate that the abiotic factor is the cause of the fish property (Sokal and Rohlf 1981). It is likely that a fish-habitat correlation results from both direct influence and interactions between common causes. It is also noteworthy that biological correlations typically breakdown over time (e.g., Mann 1992); supporting the concept that relationships between the physical environment and fish populations are very complex and nonlinear. Simple qualitative approaches are also limited as fish-habitat models because they are at best descriptive, and do not provide predictive ability.

Complex Qualitative Models

Complex qualitative fish-habitat models utilize multivariate techniques to identify general patterns in fish-habitat relationships. Multivariate analyses measure similarities or differences among many variables such as fish species abundance and environmental characteristics simultaneously. Two multivariate approaches that are frequently used in the coastal fish-habitat literature are ordination and classification (Table 7). Ordination techniques reduce a matrix of distances or similarities among abiotic and biotic attributes to one or a few dimensions. Classification analyses join or lump "objects" together (e.g., species or habitats), into hierarchical categories using a matrix of how similar or dissimilar the "objects" are (James and McCulloch 1990). Multivariate analyses reduce large complex abiotic and biotic data sets into a few correlative dimensions so that relationships can be identified and evaluated.

Most studies use complex qualitative approaches to relate the diversity and numerical distributions of fish species to habitat attributes, such as

salinity, depth, or vegetation. For example Gibson et al. (1993) evaluated the seasonal and annual variations in abundance and diversity of fishes on a Scottish sandy beach. The authors used detrended correspondence analysis, an ordination technique that assumes no systematic relationship between the ordination axes, and a classification technique that classifies fish species according to their ecological preferences. The authors found that a few common species dominated numbers and biomass, and that these species exhibited seasonal cycles that closely paralleled those of temperature and salinity. However, the authors concluded that the temporal cycles in fish properties were ultimately caused by variability in recruitment of young to the foreshore habitat, and not to characteristics of the habitat.

Weinstein and Brooks (1983) used clustering and ordination analyses to evaluate the relative fisheries value of tidal creek habitat to adjacent seagrass meadows in Virginia. The authors found that seagrass meadows were characterized by significantly greater richness, diversity and abundance of constituent taxa. The multivariate analyses also clearly demonstrated several habitat associations of individual species with either *Zostera* or *Ruppia* beds. For example, abundance distributions and length frequency analyses indicated that marsh is the "preferred" habitat for the sciaenid *Leiostomus xanthurus*.

The main limitations of numerous multivariate techniques are summarized in James and McCulloch (1990). Only a few salient points will be discussed here. Complex qualitative approaches like clustering techniques are limited because the results depend on the distance measure (similarity/dissimilarity) and on the algorithm chosen for forming clusters in the classification method. From the literature review, there does not seem to be a common choice of methodology (Table 7). The limitations of ordination techniques vary depending upon the technique used. The most common limitation of these techniques are that they are unsuitable for nonlinear data sets (i.e., will not discover nonlinear relationships), and that results vary depending upon the technique used (James and McCulloch 1990).

Regression Models

Regression models have been frequently used to describe fish-habitat relationships in numerous foreshore coastal studies (Table 8). The main use of a regression model is to determine the dependency of a dependent variable (Y) on an independent variable (X; Sokal and Rohlf 1981), with dependency determined to:

- lend support to hypotheses regarding possible causation of changes in Y by changes in X
- predict Y in terms of X
- explain some of the variation in Y by X, by using the latter as a statistical control

It is clear from reviewing the coastal fish literature that regression techniques are primarily used for the latter goal, although the data are seldom obtained under controlled or experimental conditions (Table 8). Many of the fish-habitat studies that use regression techniques rarely publish parameter values of the regression equations. Most studies simply describe the significance of the linear relationship or how much variation is accounted for. From the studies examined, regression analysis is also frequently misused by:

- extrapolating beyond the limits of the independent data
- using the regression equation for similar habitats for which no data are available, and for which no verification has been carried out (see Shirvell 1989)
- conducting exploratory analysis on a large number of variables and then reporting or discussing only the significant relationships
- stating that a significant correlation was observed but not reporting the sample size, or correlation coefficient
- concluding, or implying, that correlations are due to causality.

Fish-habitat relationships quantified for freshwater systems also frequently rely on regression models. Korman et al. (1994) compared the predictability of 119 empirical regression models that have been developed to describe habitat capability for freshwater sportfish in North America. An interesting result of the quantitative comparison was that both lentic and lotic habitats models with the highest proportion of explained variance in the dependent variable had the smallest sample size. This is opposite of what would be expected. Estimates of model prediction variance are sensitive to linear regression assumptions. Non-parametric methods approaches can provide confidence limits which are not based on these assumptions. Jackknife methods, for example, estimate model coefficients after deleting each record sequentially and replacing them with a random record. This method is repeated for all records in the data set and it thus provides a measure of the variance as reflected by the distribution of the data. The authors also made several comments concerning regression models that are worth noting: 1) the application of models developed outside the geographical area where they were developed often gave poor results (see also Shirvell 1989), and 2) users should but do not typically assess the predictive ability of the regression using nonparametric methods.

The main limitation of using regression models to evaluate fish-habitat relationships is that the two major underlying data assumptions are seldom met: 1) sample data are normally distributed, and 2) residual error is centred on the regression line. It is also unlikely that biologically important (dependent) variables are determined by a strictly linear relationship. Rice (1990) points out that there is little theoretical framework for developing parametric models of fish-habitat relationships, and most studies use linear regression by default. The ecological associations between habitat and

biological properties are generally more complex than can be described by simple linear models. Multiple regression analysis by the same token is often used to identify groups of independent variables that may be functionally associated, and to reduce the unexplained variance in the dependent variable. James and McCulloch (1990) point out that only when a "well-defined" population has been identified and randomly sampled can multiple regression provide statistically reliable results. These conditions are rarely met in fish-habitat studies (Rice 1993).

Regression analyses typically showed weak predictive ability (i.e., low coefficients of variation) because the assumed functional relationship between fish and the habitat variable may be too simplistic or wrong. Frequently extrapolation is made from statistically significant relationships to causality. For example, egg survival may be shown to be significantly correlated with predator abundance, but reducing the number of predators may not increase egg survival. Predator abundance may have increased with the water temperature, while oxygen concentration decreased. The latter variable may have been ultimately responsible for the negative correlation with egg survival.

The improper use of regression analysis also can lead to spurious conclusions that have no fundamental or theoretical foundation. Typically there are often enough data collected from a fish-habitat study to run a series of simple linear regressions. However, at a 95% confidence level one significant but untrue relationship will be discovered in every 20 attempts with data that have no relationship at all. Such "discoveries" can be extremely misleading.

Shirvell (1989) has stated that fisheries scientists expect that habitat models will identify important habitat variables, describe how ecosystems work, and predict positive or negative relationships between fish populations and habitat parameters. However, the author examined 33 habitat variables used in 6 different models and concluded that no single habitat variable universally regulated fish production, and that different populations were regulated by different characteristics of the environment. Shirvell (1989) also indicated that models are only valid for the geographical region where they were developed, and that regressions can not be extrapolated to new situations without recalibrating the model.

Because fish interact with their habitat in complex ways it is unlikely that simple regression-based habitat models will result in successful predictive or assessment tools for fish habitat managers. Regression analyses may have some use as exploratory tools that describe potential relationships between habitat features and fish properties, but non-parametric approaches with less stringent data assumptions should also be utilized.

Probability Density Functions

An alternative mathematical approach to quantifying habitat-fish relationships is the use of nonparametric density estimation techniques (Rice 1990, 1993). With this method, there are no *a priori* assumptions about the associations between fish properties and habitat attributes, or the distributions of either variable. The assumption is made that for a range of any habitat attribute there is a probability density function describing fish properties. The observations of fish properties are thus random samples from the full range of possible values of fish properties; hence a probability density function (pdf).

The pdf of fish properties, given specific habitat attributes, can be estimated using a nonparametric probability density technique, called kernel estimators. Rice (1993) describes a "modified" kernel estimator algorithm. If the abundance of an animal at a site of interest (test site) is considered to be a pdf, then the problem is: Given a set of observations of abundances and habitat attributes from past sampling (reference data), and measurements of habitat attributes at the test site, estimate the corresponding abundance pdf. The modified kernel estimator used by Rice (1993) estimates the pdf by weighting each observed abundance in the reference data set according to the similarity of the habitat attributes of that reference site to the habitat attributes at the test site. The kernel estimator rigorously quantifies similarity and schedules how influence falls off with decreasing similarity.

The end product is a full pdf for a test site, not a single expected value. The output is a plot of probability (on the y-axis) plotted against the fish property (on x-axis) for each value of a habitat feature. A useful approach is to accumulate the probabilities of a fish property over the range of the habitat feature and scale from 0 to 1. A plot of the cumulative pdfs is called an ogive. Generally, if the ogive plot is steep (i.e., rises rapidly to 1) then only a narrow range of abundance is likely given the location along the gradient of habitat variable. Conversely, if the slope of the ogive is shallow then individual abundance estimates are likely to have large scatter. In this case, individual samples are not reliable indicators of what to expect from samples at similar sites.

Nonparametric pdfs are a potentially useful alternative approach to developing "standard" functional models for evaluating quantitative relationships between habitat functions and fish properties. Interestingly however, the use of pdfs to estimate fish properties from habitat attributes is rare. Rice (1993) described the estimation of pdfs for several species of fish in relation to habitat attributes including Atlantic salmon and brook trout biomass, capelin density, and Atlantic cod catch. In each case the ogives were compared to data scatter plots evaluated using regression techniques. The influence of cover on brook trout abundance for a series of hypothetical

sites is shown in Fig. 1. The author provided the following interpretation. "The ogive is very steep for 5% cover, with less than a 0.1 probability of biomass greater than 1.0. For 35% cover, there is still a 20% chance of a very low biomass, but the shallow and even slope between biomasses of 0.5 and 4 suggests that biomasses anywhere in this range have a similar likelihood of being observed. For very high cover, the ogive is steep above 4.0, but there is nearly a 40% chance of observing biomasses from 0.5 to 4.0".

The main limitation of using the pdf approach is the difficulty of deciding on an appropriate kernel estimator. It is also apparent that while a few outliers do not bias the predictions from the density estimation methods, a large number of samples is needed to provide completely unbiased estimates (Rice 1993). PDF methods also yield much more information than is obtained from other model analyses and more interpretation by the user is required. Another consideration also worth noting. If the "true model" can be specified accurately and variance in the data is small relative to the signal from the mathematical function, or if estimates of model parameters are needed, then other methods with more demanding assumptions should be used (Rice 1993).

Structural Approach

It is apparent from the literature review that there are two general model "structures" used to describe the relationships between fish properties, such as biomass, and physical or chemical habitat features. One set of models considers individual fish species and/or stages (e.g., juveniles) and their relationships with habitat features in different habitats. A second general set of models is structured to consider communities or assemblages of fish and their associations within particular habitats, such as sea grass beds. Any of the five mathematical approaches discussed above can be used in either of the two structural approaches.

Species-Specific Models

Species-specific models describe the relationships between habitat attributes and the properties of various life stages of individual fish species. For instance, the majority of the published species-specific models identified use relatively simple qualitative models such as correlation analysis, rather than predictive relationships, to evaluate the habitat properties that affect number, biomass, or survival of stages living in foreshore habitats. Most published studies focus on life requirements of juvenile stages occurring in foreshore habitats. Several studies, for example, evaluated the rearing habitat requirements of juvenile Pacific salmon (Table 9).

Rockfish appear to be a group whose habitat requirements are fairly well understood because of their strong association with certain substrates

and their tendency to reside within the same area. Norris (1991) published an annotated bibliography and review of juvenile rockfish habitat associations in Washington, U.S. Many of the publications cited are relevant to habitat utilization in deep water habitats but there were few studies of nearshore shallow habitats. Useful methodologies for shallow studies can, however, be extrapolated from some of the deep water studies. O'Connell and Carlile (1993), for example, computed probability density functions for the frequency of yellowtail rockfish (*Sebastes ruberrimus*) observed over boulder habitat in deep water using a submersible. They used probability density functions to calculate density estimates that they suggested would be useful for fisheries management. Their objective was to develop a quantitative predictive model to estimate density of rockfish species based on one or more parameters reflective of structural habitat complexity. Matthews (1989) indicated that rockfish densities are directly proportional to habitat quality and that this forms the basis of many current habitat models in rockfish resource management. However, the author suggested that for rockfish, true measures of habitat quality should include factors other than densities, such as availability of essential resources, stability over time, survival, reproductive output, growth, and the animal's "preference" for the habitat.

Salmon, herring and other "pelagics" differ from rockfish and flatfishes in that they typically utilize a specific identifiable habitat for only a short period. The pelagic species also utilize a wide variety of habitats as their life stages develop. For example, Healey (1980) indicated that ocean-type chinook salmon fry spend about 25 days growing rapidly (up to 6% weight per day), before leaving estuarine areas for coastal rearing habitats. Movement among habitat types, associated with ontogenic development, makes it difficult to develop one species-specific model that characterizes the habitat requirements for an individual species.

Changes in habitat use with ontogenic development are also complicated by temporal shifts in habitat quality. For instance, river discharge and estuarine winter temperatures were strongly correlated with growth and survival of young-of-the-year gulf menhaden, but these features changed seasonally (Deegan 1990). Reduced mortality and rapid growth is often suggested as the main reason why small pelagics utilize a wide variety of habitats during their development in nursery areas of estuaries (Ahrenholtz 1981; Nelson and Ahrenholtz 1986). Another good example of changes in habitat use as a result of ontogenic changes is the work by Holtby and Scrivener (1989). The authors presented correlative models that quantify relationships between survival and growth of various life stages of coho and chum salmon with climatic, hydrological and physical variables of Carnation Creek, B.C. The authors indicated that the overall variability in salmon abundance tends to increase in response to land-use activities, particularly when accompanied by high levels of exploitation and adverse environmental conditions.

Species-specific models will have greater utility if habitat requirements of critical stages are more accurately defined. Species-specific model assumptions are often too simplistic and do not account for an animal's ability to make use of less suitable habitats. Habitats are rarely quantified to the detailed level required to make accurate predictions about species-specific habitat preferences over large areas, and fish are often assumed not to have the ability to adapt to stresses, such as shortage of suitable habitat. Although effort may have been expended describing the availability of high quality habitat, there is usually less effort expended on "marginal" habitats. It is likely that fish choose preferred habitat using more criteria or different ones than those that are typically measured.

Many species-specific models also assume that the association or non-association of a fish species with a particular habitat shows dependence. However, a species may not occupy a "preferred" habitat for reasons other than the abiotic factors evaluated in the model. For example, choice of habitat resulting from behavioural changes of fish from biological factors such as predation and/or competition are usually ignored in species-specific habitat models. In addition, preference for a certain habitat and hence occurrence in it may ultimately be proportional to the availability of that habitat, and not to measured habitat attributes. These two factors, extrinsic quality and quantity of habitat, must eventually be incorporated if species-specific structured models are to advance our understanding and their predictive value for management.

Habitat-Specific Models

Habitat-specific models differ from species-specific models in that they describe relationships between assemblages or groups of fishes and relatively large scale habitat attributes that vary temporally and spatially. The fish considered are usually not attributed to functional groups (e.g., feeding guilds) but rather to co-occurring assemblages. Most habitat-specific studies, by design, are very qualitative or descriptive. These studies measure properties such as diversity, abundance, biomass, recruitment success, or survival for several fish species simultaneously, and thus offer a "community-habitat" approach. Mathematical approaches typically used to relate fish assemblage properties to habitat attributes include multivariate techniques like ordination or classification, and simple qualitative approaches like ANOVA or correlation analysis.

The habitat modelling approach can identify external factors that influence properties of local species assemblages that are not necessarily linked to local habitat attributes. Worthington et al. (1992), for example, indicated that a habitat may be functionally suitable, but the supply of larvae could be low due to regional water current patterns. Fish larvae may also settle to the first habitat (e.g., eelgrass bed) they encounter regardless of

the detailed structure (e.g., leaf density) it provides. The larvae may reside in this refuge for the next few months.

Table 10 gives selected examples of the habitat-specific studies for co-occurring fish species identified in the literature search. A few of the habitat-specific studies describe temporal or spatial relationships between fish properties and habitat attributes. For example, the temporal variability in the abundance of fish larvae in three regions of an estuary in Australia was studied by Neira et al. (1992). The authors related the times and locations of larval capture to the distribution and breeding periods of the adults of the various species. Allen and Horn (1975) related the number and abundance of 23 species in a small California Bay to seasonal changes in water temperatures.

Additional studies evaluated differences in fish assemblage properties among various foreshore habitats. Ferrell and Bell (1991) examined whether seagrass habitats support greater diversity and abundance of fishes than bare sand over a large spatial scale. The authors used analysis of variance to test the null hypothesis that there was no difference in the fish assemblages associated with *Zostera*, in adjacent and distant sand habitats among locations within estuaries, or among estuaries. The authors found that the relationship depended on the fish assemblage property used (e.g. number of species versus number of individuals) and the distance from the seagrass habitat. The authors concluded that *Zostera* beds support more species and individuals than sand, provided the sand habitat was > 100 m away from the seagrass habitat. This study illustrates the potential utility of the generic habitat modelling approach, in that generalized mechanistic relationships may be identified. These relationships could be better quantified, and thus become more predictive and useful to management, if approaches like probability density functions were incorporated into data analyses.

A few habitat-specific studies identified important questions about relationships between fish community properties and habitat attributes from sampling at different spatial and temporal scales. Bell et al. (1992) for instance investigated the differences in fish abundance and composition associated with shallow and deep seagrass beds in Australia. The authors compared results of sampling at two depths in a small-scale survey (one large bed) versus large-scale survey results (three large beds). The authors found that sampling habitats on a small-scale identified a relatively strong relationship between fish abundance/composition and seagrass bed depth, but these relationships could not be confirmed in the larger-scale survey. This study demonstrated how the results and conclusions of small-scale surveys, a feature of many environmental impact assessments, can be misleading when applied to larger spatial and temporal scales, even within the same bay.

The main limitation of the habitat-specific modelling approach is that it is very descriptive or qualitative and, thus has little predictive power. This limitation is partly due to the biases associated with spatial and temporal sampling variability, and to the natural variation in abundance of biota. These limitations may be reduced by sampling critical life history stages (as juveniles) and by using more quantitative mathematical approaches. Another limitation is that habitat-specific models do not deal explicitly with commercially important species, and all fish are lumped into assemblages. This approach may be suitable for regions with many fish species, but it is of limited use in temperate regions where only a few fish species dominate community biomass or numbers, and one of these species is usually of commercial importance.

TROPHODYNAMIC MODELS

The previous section discussed modelling approaches used for describing relationships between physical or chemical attributes of habitat and fish properties. As mentioned, biotic factors such as predation are ignored when developing these kinds of fish-habitat models. The impact of fish predators on resident fish can be significant and is typically related to habitat factors. For example the relative structural complexity of vegetation (e.g., density) in a habitat can determine the quantity and quality of prey refugia, and/or the number and type of piscivores present. Thus, it is important to consider the indirect effects, or condition, of habitat on biotic interactions, and how these relationships are characterized or modelled. Models that describe the feeding interactions or trophodynamics among fish in foreshore habitats can be described as predator-prey models, or food-chain models. Table 11 summarizes some of the trophodynamic models identified in the literature search.

Predator-Prey Models

Predator-prey models usually describe feeding interactions between one predator and one prey fish species occurring in a similar habitat. This modelling approach can be useful to habitat managers because it 1) focuses attention on important temporal and spatial predator-prey interactions, 2) offers a means of organizing and extracting information from current understanding of predation in a habitat, and 3) highlights potential habitat attributes that may be manipulated to enhance prey survival or production.

Very few studies have developed predator-prey models for foreshore habitats. The majority of the studies that have used relatively simple predator-prey models that are qualitative in their approach and rely on first-order estimates of predator consumption and production. Evans (1983) for example, calculated the impact of predation on juvenile plaice, sand goby, and shrimp on the macro and meiofauna of shallow water habitats in a Swedish fjord. Predation impact was calculated using estimates of gross

production efficiency and production rates, and then compared to prey production estimated using P/B ratios and biomass estimates. Evans concluded that shallow soft bottoms provide an abundant food supply that will not limit growth, although epibenthic predator diets overlapped, and that the abundance of epibenthic feeders was controlled by their predators.

A more quantitative predator-prey model is that of Beamesderfer et al. (1990). This model was developed for a reservoir on the Columbia River, but it explicitly considered the effects of northern squawfish preying on juvenile salmon. The model described salmon survival as a function of the number and distribution of northern squawfish, number and timing of salmon entering the system, salmon residence time, water temperature, and flow rate. The model predicted salmon survival rates similar to independent estimates and approximated differences among areas and months. The simulation results indicated that the best approach to reduce predation was to reduce the number of predators, pass the juveniles through the reservoir earlier in the year, or maintain or increase size of the juvenile salmon run.

The predator-prey modelling approach has limited application to habitat problems because it is too simplistic. The models usually only consider predation by one or a few predators in a habitat, and parameter values used are typically selected to represent average conditions, while large uncertainties exist about the form of the predator consumption functions (e.g., Holling type II versus type III). It is typically assumed that the sensitivity of predator-prey models to adjustments of parameters by some percentage (e.g., 10%) can identify important or critical natural responses. This assumption is dubious given that most biological parameters show wide variability, and many important habitat attributes and biotic feedbacks are difficult to incorporate in the models.

Food-Chain Models

Several foreshore modelling studies have considered feeding interactions among several fish species and their prey in the same habitat. We describe these models as food-chain models. Food-chain models generally require large data sets describing temporal, spatial, and ontogenetic variability in diet composition, species biomass, and feeding rates. Food-chain models evaluate trophic requirements of various stages or species of fish and relate them to habitat attributes, and as well provide estimates or assessments of secondary and tertiary production for the species in that habitat. This approach can provide clearer understanding of how possible feeding interactions affect key fish species either via predation or prey production limitations. Food-chain models also offer insights into possible biotic interactions and responses to habitat conditions on a variety of spatial and temporal scales. However, because of the multitude of biotic assumptions and simplifications required, this modelling approach lacks the quantitative predictive rigor required of a habitat management tool.

The simplest food-chain models compare and evaluate fish community trophic ecology in a single habitat using descriptive mathematical approaches, such as classification analysis. Smith et al. (1984), for example, used "normal" and "inverse" classification methods and determined that six dominant fish species in a shallow marsh in Virginia were trophic opportunists feeding on a variety of prey. The results of the multivariate analysis reflected the possible surfeit of food and associated low competition in these habitats. Other important aspects of the fish communities in a habitat that can be identified using qualitative food-chain models include: size selective feeding distributions reflecting ontogenetic shifts, and morphological differences among predators.

An example of a more quantitative food-chain modelling approach is offered in the study by Livingston (1982) in which cluster analysis was initially used to evaluate temporal changes in food preference by different size classes of 14 fish species in a seagrass system. Livingston was able to identify a progression of predators through time by treating each developing stage of trophic preference as an individual entity ("ontogenetic trophic unit"). The author then used multivariate linear regression to analyze for relationships between key habitat attributes and the trophic response of the ontogenetic unit. The main conclusion was that no single feature of the seagrass system controlled the relative abundance of a given ontogenetic trophic unit or species. In addition, various species appeared to have changing habitat needs with time.

The complex food-chain model of Peters and Schaaf (1991) quantified the relationships between primary production and fishery yield for tidal marshes, estuaries, and coastal waters on the east coast of the U.S. The approach demonstrated energy flow through the food-chain using an empirically based, top-down approach. That is, the authors calculated food demands from fish yield and determined production required at each level based on trophic relations and with no attempt to balance material or energy flows. This approach "conservatively" estimated production and trophic requirements of the 17 species food-chain. The authors concluded that to relate coastal fishery production to total ecosystem function, better data are needed describing natural mortality (especially for forage fish and pre-recruits), species composition and diets of forage fish, and detritus production.

Food-chain models are limited because they only offer a "snap-shot" view of either the structure or dynamics of the predator-prey interactions in the habitat. In addition, the description of local habitats cannot be easily extrapolated to ecosystem-wide considerations. Food-chain models also typically ignore energy flows to non-commercial fish species or to omnivorous fishes and flows from prey to fish. Average food conversion efficiencies and diets are often utilized and thus accumulate errors in estimates of fish production and other results.

ENERGY/NUTRIENT FLOW MODELS

Energy/nutrient flow models are extensions of trophodynamic models. Flow models differ from trophodynamic models as they can: 1) incorporate additional ecological processes occurring in a foreshore habitat, such as primary production or nutrient recycling, 2) include both resource and predator limitations in the habitat, and 3) use energy budgets to quantify important processes occurring in the habitat. Energy flow models are considered in this review because they illustrate the important linkages between additional properties of foreshore habitats (e.g., primary production) that can significantly influence properties of fish, such as production or survival. From studies identified in the literature (Table 12), there are two general types of energy/nutrient flow models: population models and ecosystem models.

Population Models

Population energy models can assess the role of specific fishes or groups of fishes in energy transfer within a single foreshore habitat. These models can develop an energy budget for the dominant fishes and thus provide a quantitative basis for evaluating the role of each species within the habitat. Population energy flow models assess the energy budgets of individual fishes or groups of fishes by assuming that the general partitioning of energy is: energy consumed = energy lost to faeces + nitrogenous waste excretion + activity + standard metabolism + specific dynamic action + growth or reproductive products.

Du Preez et al. (1990), for example, examined the energy budgets of six major ichthyofauna groups in surf-zone habitats in eastern Cape beaches, South Africa. The study showed that most energy consumed was used in metabolism and growth. The study also determined that in surf-zone habitats fishes were important predators, with piscivores consuming 30% of the available fish production from other species. In addition, the surf zone generated adequate food for other fish assemblages, partly because the fishes recycled energy as excretory products. The fish were also found to export energy across the outer boundary of the surf-zone habitat, indicating important connections with other nearby foreshore habitats. Another example of a population energy budget is that established for the carnivorous fish *Clinus supercilliosus*, a resident of tide pools in rocky intertidal habitats of South Africa (Bennett 1984). Using laboratory data, the author estimated population consumption and production for *C. supercilliosus*. The results showed this carnivorous fish exerted considerable pressure on available intertidal prey such as small crustaceans, molluscs, and polychaetes.

Population energy flow models are usually limited as predictors of fish properties such as production because they only consider fish energy

requirements over the short term (weeks) and small spatial scales, while seasonal variability in habitat use by different stages or species of fish is not usually considered. Parameter values of budget processes (e.g., excretion) are also often estimated from laboratory work or from the literature, and then extrapolated to field conditions. It is difficult to account for the temporal variability in various budget components or parameters, and therefore most studies only consider average values, often derived from laboratory studies.

Ecosystem Models

Ecosystem models are important to consider when discussing foreshore habitat management because they provide a large scale or holistic view of how various habitats interact. For example, an estuary may consist of several distinct habitats, each being important to juvenile fish (e.g., tidal marsh, tidal channels, and mud flats). Together the three habitats form an estuarine ecosystem with subtle linkages or interconnections that are important to survival and growth of temporary resident fish, such as juvenile salmon. Ecosystem-level studies attempt to incorporate sufficient functional attributes of key component habitats to mimic some, but not necessarily all, aspects of the ecosystem's behaviour. Ecosystem models are useful because they can evaluate the function of several habitats simultaneously, synthesize available data and knowledge, identify sensitive processes and data gaps, examine the relative influence of physical and biological factors on habitat functioning and energy/nutrient flows, and help formulate testable hypotheses about an ecosystem's structure and function (Wetzel and Hopkins 1990).

Ecosystem models also provide a quantitative framework that tests our understanding of how various habitats are interconnected, and provide a broad perspective from which more objective analyses of important processes can be derived. Ecosystem models are also useful because they evaluate the influence of habitat and biotic feedback interactions on communities of organisms. In contrast, population models primarily describe responses of organisms under limited conditions of a single habitat type. These responses may differ in larger context where organisms are affected by a variety of unforeseen interactions. Ecosystem models are usually constructed with the following 3 approaches:

- 1) **Function:** The two major functional approaches used in ecosystem modelling are dynamic simulation and steady-state models. Dynamic simulation models consider changes in the ecosystem step-by-step over time (usually daily) and/or space. Most of these ecosystem simulation models synthesize large amounts of information about individual components over time and space, and thus can be used to objectively explore inter-component relationships. Steady-state ecosystem models on the other hand, evaluate average or "equilibrium" energy flows over time. That is, these models assume that mortality is balanced with

survival, so that there is no change in biomass over time. The steady-state approach allows for a snap-shot evaluation of energy/nutrient flows and recycling of the average or equilibrium biomass. Since adequate data on standing stocks and feeding estimates are usually available, steady-state models are frequently used. To evaluate how ecosystems function at steady-state, most studies have used network analysis. Network analysis can quantify the direct and indirect dependence between major components and subsystems, helps define the key pathways of organic matter cycling, as well as the dominant structure of trophic exchanges or the number of pathways of exchange among biotic components (Asmus and McKellar 1989).

- 2) **Aggregation:** Aggregation describes how many biological data are used to characterize biota and interactions among biotic components in the various habitats. Highly simplified or aggregated models use generalized functions to describe interactions between trophic levels or guilds of species, and thus require relatively few data for parameterization. Highly aggregated ecosystem models are substantially more complex, and require detailed data/parameters describing age or size structure of numerous biota in each of the critical habitats. The most common method of building ecosystem models is by aggregating the characteristics of biota among habitats.
- 3) **Forcing-function:** The steady-state approach assumes a static situation, and does not evaluate temporal or spatial variability in processes that may affect energy/nutrient flows among habitats or biota. Dynamic simulation ecosystem models on the other hand, evaluate the ecosystems response over time and/or space. These models typically operate on only one temporal or space scale at a time. The majority of ecosystem models evaluate conditions within single habitats, during a single season (Table 12). However, some simulation models are also "forced" by seasonal variability in key environmental functions, such as water temperature.

Relatively few ecosystem models were identified in the literature that were developed for foreshore habitats. This is in contrast to the plethora of ecosystem models developed for the coastal pelagic ecosystem (e.g., Franz et al. 1991). It is also apparent from the literature review that the majority of foreshore ecosystem models use the steady-state functional approach (Table 12). Baird and Ulanowicz (1993) for example, presented results from highly aggregated steady-state models constructed for each of four tidal estuaries. The authors gave specific attention to the trophic structure, and to the structure and magnitude of cycling in each estuary. Fish were aggregated into feeding guilds, represented as benthic, planktivorous, or carnivorous fish. The trophic and cycling structures were analyzed using network analysis (see Asmus and McKellar 1989). The authors found that although trophic structure was similar among the estuaries, there were differences in the rates of primary production and its utilization, in the system's trophic efficiencies, and in the detritivory:herbivory ratios.

One of the few examples of a dynamic simulation model describing foreshore fish-habitat relationships is that developed by Valiela and Kistritz (1980). These authors described two simulation models describing the utilization of Fraser River estuarine habitat by juvenile salmon. One model evaluated salmon growth, survival and use of the Fraser River estuarine ecosystem, while the other model evaluated detritus production and availability of detritus to the salmon food-web. The authors concluded that data used to parameterize, calibrate, and validate the first model were not adequate to evaluate the importance of the estuary to salmon. However, construction and conceptualization of the models did serve to identify data gaps, and several important questions for further study. The authors suggest that this result was in itself a desirable end product of constructing a simulation model.

Another ecosystem model dealing with foreshore habitats was developed by Keizer et al. (1987) for the Cumberland basin (an estuary composed of intertidal mudflats and saltmarshes) in the upper reaches of the Bay of Fundy, Nova Scotia. A one-dimensional linear box-model was used to synthesize available data, identify important environmental processes, uncover serious data gaps and indicate preferred directions of future research. The model simulated carbon flow between major ecological "units" including phytoplankton, planktonic bacteria, herbivores, detritivores, and carnivores, and resident and migratory larval and adult fish. These authors also concluded that the modelling process was the prime benefit providing insight into further research.

The dynamic simulation model of Kemp et al. (1983) is one of the few that have been developed for foreshore fish habitats. An alternative to building one extremely large and complex simulation model is to develop a series of sub-models describing different biological and physical processes. These sub-models are in turn linked together. Kemp et al. (1983) developed such a "nested ecosystem model" consisting of five principle sub-models: autotrophs; epibiota; plankton and water; benthos and sediments; and, nekton. Output from one sub-model serves as input to one or more of the other sub-models. An advantage of this approach is that the modeller becomes part of the interactive process by controlling output and connectivity among sub-models.

The major limitation for developing or using ecosystem models is the difficulty of evaluating the whole system from "piecing" together independent observations of various biota for component habitats. The predictive ability of ecosystem models has also so far shown to be limited, because of a lack of qualitative and quantitative data for parameterization, calibration, corroboration, and validation. Extensive data requirements and unavailability of key data can limit the construction and realism of ecosystem models. Data describing diet composition and consumption, physiological rates of excretion or respiration, biomass, biotic feedbacks

(e.g., predation), and temporal and spatial relationships to abiotic attributes are often required. Ecosystem models can often become so complex that their output may be difficult to relate to "real-world" observations, or worse yet, the model becomes mathematically or conceptually intractable.

GEOGRAPHIC INFORMATION SYSTEMS

One of the newest modelling techniques that will help habitat managers understand and/or predict fish-habitat relationships are Geographic Information Systems (GIS). GISs have evolved over the last decade from inflexible mainframe software to versatile products that are commonly used on work stations or personal computers. There are three classes of GIS products available: work station ('high-end') systems, PC-based systems that have lower, but often adequate, analytical power, and desktop mapping products ('low-end') that have low or no capability to do map layer analysis. Part of the reason for the surge in popularity of GIS is that newer personal computers can handle large software products and data sets, and therefore both work station and PC-based systems are easier to use.

The main advantage of a GIS to the habitat manager is its ability to input, store, manipulate, and display large amounts of geographically referenced (geo-referenced), as well as non-spatial data. This is especially useful if the manager has to regularly make decisions based on changes in large spatial data sets. A GIS however, is not 'just another' software package, and cannot be run casually like a word processor or spreadsheet application (Legault 1992). For instance, creating a GIS database and gathering new data to update it can be costly, while management of the data requires a highly structured administrative approach. A GIS is also more than just mapping software. Its real value is in its ability to answer queries about location and area, and to perform mathematical operations on geo-referenced data from more than one attribute map or layer. An attribute layer refers to any geo-referenced biophysical data. For example, using attribute maps of bathymetry, 1993 herring spawn location, hypothetical herring habitat type 'A' locations, and point sources of pollution for the Strait of Georgia, it would be a simple matter to answer any of the following queries using the mapping and analysis functions of a GIS:

- What is the total spawning area of the southern Strait of Georgia that coincides with herring habitat 'A' at depths between 1 and 5 m? Overlay this information and plot on the bathymetric map.
- Calculate the total spawning area by eliminating any area that is within 500 metres of a pollution source. Print out a table of pollution sources within the 500 metre buffer that includes the type of pollution and estimated volume of pollution if known.
- If a 300 metre buffer were placed around all 1993 herring spawning areas excluding herring habitat type 'A', and only those areas <10 m were included, map the area?

In practice, many attribute layers can be used to investigate questions about geo-referenced information in the region of interest. The more attribute maps that are added to the data base, the greater the possible combination of questions that can be asked of the GIS. GIS also has a high potential for habitat managers as an analysis tool. Once the GIS database has been created analytical models (e.g., regression models or probability density functions) can be developed, but this is an area of research that is poorly known.

GEOGRAPHIC INFORMATION SYSTEMS AND FISHERIES SCIENCE

Ecological processes operate at a variety of spatial scales in space, but fish habitat managers usually focus on changes over relatively small geographical areas. Habitat managers often have to deal with habitats $< 1000\text{m}^2$ in area, such as wetlands in the Fraser River estuary (Levings 1991). During the past two decades, ecologists have also incorporated spatial detail into models, and have applied these models to larger geographical areas (Hunsaker et al. 1991). Spatial modelling in terrestrial and freshwater ecosystems is more advanced than in marine systems, although the latter are well suited for the application of GIS (Hunsaker et al. 1991). It is interesting to note that ecologists rarely combine geometric, statistical, or mechanistic approaches with spatial attributes into one model. Recent advances in GIS software and ease of use have provided greater opportunity to develop this approach.

There are very few examples in the literature where GIS have been used in an analysis role in fisheries research. The majority of studies utilize map analysis functions. Legault (1992) described a GIS used to evaluate the effects of shellfish closure zones on shellfish leases, aquaculture, and habitat availability in eastern Prince Edward Island. A high-end GIS (Computer Aided Resource Information System (CARIS)) was used in the analysis. The GIS was primarily used as a demonstration and mapping tool to evaluate shellfish closures. On the west coast of Canada, Environment Canada uses QUIKMAP to keep track of its shellfish closures and pollution sources. It is used mainly as an accounting and display tool (David Walker, Environment Canada, North Vancouver, B.C., pers. comm.). QUIKMAP is a desktop mapping package that does not have the ability to perform mathematical analyses on multiple attribute layers.

Fisheries and Oceans has also conducted a pilot project utilizing GIS (COMPUGRID) to organize the collection and management of experiential knowledge of marine resources acquired from field staff (J. Morrison, pers. comm., South Coast Division, DFO Nanaimo). This pilot project in subdistrict 25 (Nootka-Esperanza) mapped information on the distribution of fishery resource stocks, their associated fisheries and the relative importance of the geographic area or intensity of the fishery. The information was mapped on hydrographic charts (1:40,000) and converted to electronic

maps, supplemented by resource information databases and a narrative document. The information sketched on working copy hydrographic charts was interpreted and then digitized to develop the final electronic maps. For example, the depiction of bivalve beds was confined to intertidal areas, the depiction of herring spawning beds was made congruent to the low intertidal to shallow subtidal zone, and inlet wide applications of sea cucumbers were revised to exclude the deeper central inlet waters. This application of GIS logical function intelligence reflects an biological understanding of fishery resources and their habitats. However, this particular GIS does not enable analysis of map attributes.

The Department of Natural Resources of the state of Washington is carrying out an implementation plan to characterize nearshore habitats of Puget Sound (Mumford et al. 1992). The objective is to inventory and routinely monitor the distribution and types of marine and estuarine nearshore habitats of Puget Sound using the most cost-effective methods including remote sensing. The monitoring program uses ARC/INFO as the GIS product, which will allow analysis of the quantitative habitat data. This project incorporates remote sensing data into the data base.

The Environmental Protection Agency (EPA) of the United States has developed the Environmental Monitoring and Assessment Program (EMAP) which is designed to estimate on a regional basis, the status, changes, and trends in ecological indicators of estuarine resources (Hale et al. 1993). EMAP uses an information management system to process, store, analyze, and distribute data and information. The GIS used is ARC/INFO, and the analytical tools include C programs, Oracle RDBMS, and SAS. The GIS is used to calculate sample areas, validate station data, conduct spatial analyses, and graphically present the results.

Only one paper was identified in our review that could be considered relevant to linking fish-habitat models and GIS. Donovan et al. (1987) evaluated the use of a GIS to automate the application of habitat suitability index (HSI) models. The general modelling approach of HSI is to assign relative values to habitats depending on how well they provide the life requisites of the species being studied. The life requisite values were then combined to obtain a habitat suitability index for the specified area. The authors used a GIS as a source of habitat information for developing HSI models, and evaluated wild turkey nesting and brood-rearing habitat requirements. By basing HSI indices on geographical attributes, the authors found that the GIS was useful in evaluating the relative value of turkey nesting and brood-rearing habitat suitability. They state that "the effectiveness of the model is based on the ability to generalize wild turkey habitat requirements so that GIS-based variables adequately represent the life requisites of the species. For instance, traditional modelling would use stocking density and tree size as direct measures of forest suitability for turkeys, whereas, large area GIS-based models often require less specific

assumptions, such as the area of forest land, as a measure of habitat suitability". The authors also noted that modelling with coarse resolution GIS variables may be more difficult for species with narrow habitat requirements, and that unless specific requirements can be associated with GIS-measured variables, the success of modelling will be limited. Although Donovan et al.'s (1987) study dealt with turkey habitat, it does demonstrate the usefulness of GIS in ecological modelling and may be used as a prototype for developing a GIS-based nearshore fish-habitat model. Because of the limitations of HSIs, however, this particular approach may not be broadly applicable.

To sum up, the use of geographic information systems in fishery science is in its infancy. There are few studies that use little more than the mapping capabilities of GIS. Studies like Donovan et al. (1987) however, demonstrate that GIS has analysis capabilities with the potential to be used effectively in studying organism-habitat relationships. The recent rapid increase in analytical power and data storage capabilities of personal computers, and the ease of use of GIS software, will ultimately allow for the development of powerful management tools for assessing fish-habitat relationships in foreshore areas.

SUMMARY AND POSSIBLE APPLICATION OF GIS

In the preceding sections five major modelling approaches used to describe and evaluate relationships between abiotic and biotic attributes of foreshore habitats and properties of fish such as biomass, production, survival, etc. were reviewed. The five approaches are: 1) habitat classification systems, 2) fish-habitat models, 3) trophodynamic models, 4) energy flow models, and 5) geographic information systems. The following offers a brief perspective on the utility of each of the modelling approaches, and discusses a possible approach for assessing the productive capacity of fish in foreshore habitats of the Strait of Georgia, British Columbia.

Habitat classification systems offer a structured, user-defined framework for identifying and describing the type and distribution of foreshore habitats that are "critical" to fish. Thus the habitat manager has a tool to track interannual changes in habitat, catalogue the diversity of habitats, or identify the quantity of critical habitats. Fish-habitat models extend the utility of habitat classification systems by providing a quantitative approach for describing the possible functional relationships between abiotic (physical and chemical) attributes of critical habitats and properties of fish. However, the utility or success of a fish-habitat model ultimately depends on the structure of the model (either by fish species or by habitat), and on the mathematical approach, which is frequently limited by the quantity and quality of data available. Trophodynamic models extend the usefulness of fish-habitat models by offering the habitat manager a method to better understand and evaluate the relative importance of the more subtle effects

of habitat condition (e.g., biological factors such as predation) on fish properties. Ecosystem models combine an evaluation of both abiotic and biotic processes occurring in closely related habitats, and thus provide the manager with an holistic view of the foreshore ecosystem. GISs offer a method that can simultaneously consider several modelling approaches while utilizing the same spatial and non-spatial data sets. GISs offer the habitat manager a comprehensive tool for entering, storing, manipulating, analyzing and displaying extensive fish-habitat data sets, that can in turn be used to develop specific applications such as ecological models, or habitat classification systems to assess the productive capacity of foreshore fish habitats.

In the following, we describe how a GIS could be used as a general quantitative tool to assist habitat managers to evaluate and quantify fish-habitat relationships in foreshore habitats of the Strait of Georgia.

Before a specific GIS software/hardware system is selected it is necessary to explicitly identify and define the basic needs of the users, namely fish habitat managers and biologists. Users should develop a comprehensive list of current and perceived needs over the short and long term. Initially defining user needs follows the philosophy of making the GIS fit the data/analysis needs of the user. The needs of investigators that can be successfully addressed by a GIS are ultimately related to two considerations of geo-referenced and non-spatial data: 1) are abiotic and biotic data available that are pertinent to evaluating fish-habitat relationships?; 2) does the map scale of the geo-referenced data match the level of the questions being asked? Thus, the quality and quantity of existing geo-referenced and non-spatial data sets, relevant to foreshore areas of the Strait of Georgia should initially be identified and inventoried.

Once user needs and data availability or requirements have been explicitly defined and inventoried, three specific issues of choosing and implementing a GIS should be considered:

- a) The availability and quality of fish-habitat data is the most important asset when it comes to using a GIS to address user needs. Several key issues of data base development and management must initially be considered when choosing a GIS: e.g., data quality standards, database format or structure, data translators, and personnel to maintain the database.
- b) The next critical issue for choosing a GIS is to consider what analysis and mapping capabilities are required to utilize the available data to generate products that address user needs. For evaluating fish-habitat questions the GIS must have strong analysis capabilities such as map analysis and contouring. The GIS must also be able to use specific models for the area of interest. The GIS software must also have strong mapping capabilities, such as effective use of graphic layout and manipulation features, access to numerous output devices, and map

overlay functions. Not all GIS software packages have both adequate analysis and mapping capabilities (see reviews by Johnstone 1992a,b).

- c) The selection of the "appropriate" GIS software and hardware is highly related to the user defined database and analysis/mapping requirements. GIS selection must also include an evaluation of factors like ease of use, cost, technical support, and learning curve. The GIS should be able to accept downloaded data files from existing regional GISs to minimize duplication in costly database development. The B.C. Ministry of the Environment, for example, has developed a large database for use with a work station version of ARC/INFO. The GIS database has > 80 thematic layers (1:40,000 base maps with some 1:10,000 attribute maps) describing biophysical attributes of nearshore areas of the Strait of Georgia, west coast of Vancouver Island, and Queen Charlotte Sound (D. Howes, Ministry of Environment, Lands and Parks, pers. comm.). A similar GIS structure is used by the states of Washington and Oregon to characterize and classify foreshore habitats. The results of ARC/INFO may be down-loaded into a medium end GIS, ARCVIEW, that can be used on a PC.

In general, the majority of the habitat classification systems (HCS) reviewed above in section 2.0 are relatively complex, and do not specifically address the habitat requirements of foreshore fish species in the Strait of Georgia. However, a simple, consistent and biologically meaningful HCS might be developed using the geo-referenced data and analysis/mapping tools of a GIS. The approach could consider either the habitat requirements of individual fish species or requirements of fish assemblages in particular foreshore habitats. In either case, the criteria for classifying critical fish habitat needs to develop from an understanding of habitat function and how it relates to fish properties. Pacific herring, for example, require certain vegetation, water depths and substrate to spawn. Assuming that critical habitat data are available and geo-referenced, the GIS could produce maps describing the distribution and extent of spawning areas, and could classify the quality of herring spawn habitat for coastal areas. The maps would be constructed based on an interpretation of critical spawning habitat. The major assumption in this approach is that data describing the functional fish-habitat relationships are available. In situations where this information is absent, the habitat manager must have the necessary data collected, or take data from similar studies, or derive relationships from proxy or surrogate variables (e.g., substrate type, vegetation communities and fish distributions).

Fish habitat managers have to continue managing as data bases are built, and this information could be used in a GIS to develop empirically based predictive analytical tools of fish-habitat relationships. However, because of the shortcomings of fish-habitat data quality and quantity, and their statistical attributes, nonparametric probability density functions (pdf)

might also be developed to assess fish-habitat relationships in the Strait of Georgia. The use of predictive models like pdfs, within the GIS framework, will depend on the modelling capabilities of the GIS. It is presently unclear what possible logistic problems would be encountered when setting up pdf models in a GIS framework. These models are substantially more complex than the map analysis functions typically used and therefore modelling capabilities would have to be carefully considered before choosing a GIS.

The prediction of fish-habitat relationships is a present-day need for habitat managers, but prediction can only be refined and enhanced by understanding variability in the biological and physical realms, and their interactions. Combinations of empirical and mechanistic functions, in the form of an ecosystem model, could be developed to enhance the understanding of fish-habitat relationships. General analytical models such as Network Analysis (e.g., Asmus and McKellar, 1989) could be modified and used to evaluate energy flow among abundant organisms within critical habitats based on existing and literature data. Depending on the in-house modelling capabilities of the GIS, ecosystem models could be a part of the GIS and thus act as analysis tools. Alternatively, the ecosystem model may be operated externally of the GIS, and thus would use the GIS primarily as a data source. An effective approach might be for biologists to become directly engaged in the ecosystem modelling process. Users could contribute ideas about model formulation and structure, as well as participate in running the model and analyzing output (Korman et al. 1994). Because there are strong linkages and feedbacks between developing an understanding of system processes and enhancing predictive ability, the parallel hands-on approach of developing both predictive and ecosystem models in a GIS framework might be useful. The development of a GIS-based analytical system and data base for foreshore habitats in the Strait of Georgia is an ambitious undertaking. It may be more productive to develop a prototype system by choosing a location relatively rich in fish habitat data. This approach would eliminate many start-up problems that are likely to occur before tackling the whole Strait of Georgia. Users could meet and identify important questions or needs that should be addressed for the region, and then inventory existing geo-referenced and non-spatial data. A GIS would be selected based on data availability and requirements of the user group, but remaining cognizant of the future needs of the GIS to service larger areas. A classification system of fish habitats could be developed using existing data and a species-specific or a habitat suitability index modelling approach. Predictive models and ecosystem models could be simultaneously developed in-house or "linked" to the GIS for assessing and understanding fish-habitat relationships. Once the prototype system has been "fine-tuned" to user needs and data of the study region, it could be used as a template to expand to other areas of the Strait of Georgia. Breaking the task into smaller topics also greatly increases the likelihood of success in developing a GIS-based quantitative approach that can successfully evaluate fish-habitat relationships in the Strait of Georgia.

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Table 1. Habitat classification systems (HCS) identified in the literature search used to describe habitats in foreshore coastal regions.

Reference	Title	Major Classifiers	HCS Property
Harper et al. 1993.	A biophysical inventory of the coastal resources in the Gwaii Hanaas/South Moresby national park reserve.	substratum, exposure, biota, tidal zone	description
Brown 1993.	A classification system of marine and estuarine habitats in Maine: an ecosystem approach to habitats.	substratum, depth, energy level, salinity	description
Fox 1993.	Habitat classification for Oregon rocky shores.	scale, substratum,	description
Frith et al. 1993.	Review of habitat classification systems and an assessment of their suitability to coastal BC.	substrate, tidal zone, biota	description
LGL 1993.	Habitat classification scheme for the Southern Strait of Georgia oil spill atlas.	exposure, physical, salinity, biota	description
Pearsal et al. 1992.	An ecosystem classification and criteria for biodiversity conservation in the tropical insular Pacific.	salinity, substratum, tidal zone, slope, biota	description
Busch and Sly 1992.	The development of an aquatic habitat classification system for lakes.	flow, topographic, physical, substratum, vegetation	description
Hiscock and Connor 1991.	Benthic marine habitats and communities of Britain: the development of an MNCR classification.	physiographic, salinity, exposure, tidal flow, geology, biota, substratum	description
Simenstad et al. 1992.	Estuarine Habitat Assessment Protocol.	habitat type, feeding, reproduction, refuge, physiology, biota	description, function
Nature Conservancy 1991.	Marine classification hierarchy for the tropical western Atlantic.	salinity, substratum, vegetation	description
Dethier 1990.	A marine and estuarine habitat classification system for Washington State.	depth, substratum, energy level	description

Table 1. (Con't.)

Williams 1990.	Coastal/estuarine fish habitat description and assessment manual.	exposure, substratum,	description, function
Toole et al. 1987.	Habitat suitability index models: juvenile English sole.	prey, water quality	function
Levings et al. 1983.	Review of benthos of the Strait of Georgia and contiguous fjords.	depth, salinity, biota	description
Hunter et al. 1983.	A biophysical estuarine habitat mapping system for B.C.	tidal zonation, substrate, vegetation, salinity, anthropogenic	description
Cowardin et al. 1979.	Classification of wetlands and deepwater habitats of the United States.	substratum, vegetation	description

Table 2. Comparison of the classification levels used in the Cowardin et al. (1979) versus the Dethier (1990) hierarchical systems for foreshore coastal habitats (From Dethier 1990).

<u>Cowardin et al.</u>	<u>Dethier</u>
System: Marine vs Estuarine	System: Marine vs Estuarine
Subsystem: Intertidal vs subtidal	Subsystem: Intertidal vs subtidal
Class: Rocky shore Unconsolidated Aquatic bed Reef	Class: Consolidated Unconsolidated No category Reef Artificial
Subclass: Bedrock Rubble Cobble-gravel Sand Mud Organic	Subclass: Bedrock Hardpan Boulders Cobble Mixed-coarse Gravel Sand Mixed fine Mud Organic
No category	Energy/exposure
Modifiers (salinity, depth, etc.)	Modifiers
Dominance types	Characteristic species

Table 3. Hierarchy of habitat functions for fish and wildlife used in the Assessment Protocol for estuarine habitats of Puget Sound (from Simenstad et al. 1991).

<p>I. Reproduction</p> <p>A. General</p> <ol style="list-style-type: none"> 1. light 2. salinity 3. sound 4. temperature 5. turbidity 6. water/sediment quality <p>B. Elevation</p> <ol style="list-style-type: none"> 1. intertidal 2. subtidal 3. riparian <p>C. Substrate</p> <ol style="list-style-type: none"> 1. sediment 2. emergent vascular plants 3. macroalgae 4. riparian vegetation 	<p>III. Refuge and Physiology</p> <p>A. General</p> <ol style="list-style-type: none"> 1. light 2. salinity 3. sound 4. temperature 5. turbidity 6. water/sediment quality <p>B. Physical complexity</p> <ol style="list-style-type: none"> 1. bathymetric features 2. horizontal edges 3. vertical relief 4. water movement <p>C. Biological complexity</p> <ol style="list-style-type: none"> 1. macroalgae 2. emergent vascular plants 3. submergent vascular plants
<p>II. Feeding</p> <p>A. General</p> <ol style="list-style-type: none"> 1. carrion 2. detritus 3. gravelling 4. light 5. salinity 6. sound 7. temperature 8. turbidity 9. water/sediment quality <p>B. Plants</p> <ol style="list-style-type: none"> 1. microalgae 2. macroalgae 3. emergent vascular 4. submergent vascular <p>C. Invertebrate</p> <ol style="list-style-type: none"> 1. benthic 2. epibenthic 3. neustonic 4. terrestrial 	

Table 4. The three major types of models identified in the literature search, and their subsections discussed in the text.

1. Fish-habitat models

1.1 Mathematical approaches

- 1.1.1 ■ Index Models (e.g., HSI)
- 1.1.2 ■ Simple Qualitative Models (e.g., correlation)
- 1.1.3 ■ Complex Qualitative Models (e.g., ordination)
- 1.1.4 ■ Regression Models
- 1.1.5 ■ Probability Density Functions

1.2 Structural approaches

- 1.2.1 ■ Species-Specific Models
- 1.2.2 ■ Habitat-Specific Models

2. Trophodynamic models

- 2.1 ■ Predator-Prey Models
- 2.2 ■ Food-Chain Models

3. Energy/nutrient flow models

- 3.1 ■ Population Models
- 3.2 ■ Ecosystem Models

Table 5. Studies identified in the literature search that use or review index models to evaluate fish-habitat relationships.

Reference	Title of study
Levy 1993.	A review of habitat capability for salmon spawning and rearing.
Modde et al. 1991.	Use of a habitat-based stream classification system for categorizing trout biomass.
Heggenes et al. 1991.	Seasonal habitat selection and preferences by cutthroat trout (<i>Oncorhynchus clarkii</i>) in a small, coastal stream.
Nelson 1990.	Prospects for development of an index of biotic integrity for evaluating habitat degradation in coastal systems.
Hubert and Rahel 1989.	Relations of physical habitat to abundance of four nongame fishes in high-plains streams: a test of habitat suitability index models.
Kozel and Hubert 1989.	Testing of habitat assessment models for small trout streams in the Medicine Bow National Forest, Wyoming.
Smith et al. 1988.	Habitat value of natural versus recently transplanted eelgrass, <i>Zostera marina</i> , for the bay scallop, <i>Argopecten irradians</i> .
Wesche et al. 1987.	Modified habitat suitability index model for brown trout in southeastern Wyoming.
Angermeier and Schlosser 1987.	Assessing biotic integrity of the fish community in a small Illinois stream.
Crance 1987.	Habitat suitability index curves for paddlefish, developed by the Delphi technique.
Pajak and Neves 1987.	Habitat suitability and fish production: a model evaluation for rock bass in two Virginia streams.
Toole et al. 1987.	Habitat suitability index models: juvenile English sole.
Angermeier and Karr 1986.	Applying an index of biotic integrity based on stream-fish communities: considerations in sampling and interpretation.
Kistritz 1985.	Proposed method for the quantitative assessment of nearshore marine and freshwater aquatic habitat in coastal British Columbia.

Table 6. Studies identified in the literature search that use simple qualitative approaches to evaluate fish-habitat relationships. Modelling approaches: cor: correlation analyses; ANOVA: analysis of variance. Fish properties: A: abundance, numbers, or density; G: growth; B: biomass; D: diversity; P: production; S: survival. Habitat variables: sal: salinity, tmp: water temperature; exp: exposure; tur: water turbidity; dch: discharge; veg: vegetation properties; z: depth; sub: substrate properties.

Reference	Title	Analysis	Habitat variable	Fish property
Rutz et al. 1993.	Shallow water as a refuge habitat for fish and crustaceans in non-vegetated estuaries: an example from Chesapeake Bay.	ANOVA	Z, pred, veg	A
Mgaya 1992.	Density and production of <i>Clinocottus globiceps</i> and <i>Oligocottus maculosus</i> (Cottidae) in tidepools at Helby Island, British Columbia.	ANOVA corr	Z, site	A, B, P
Worthington et al. 1992.	Effects of the shoot density of seagrass on fish and decapods: are correlation evident over larger spatial scales.	ANOVA corr	veg	A, D
Sogard and Able 1991.	A comparison of eelgrass, sea lettuce macroalgae, and marsh creeks as habitats for epibenthic fishes and decapods.	ANOVA	veg, site	A
Hettler 1989.	Nekton use of regularly-flooded saltmarsh cordgrass habitat in North Carolina, USA.	ANOVA	site	A, B, D
Bell and Westoby 1988.	Importance of local changes in leaf height and density to fish and decapods associated with seagrasses.	ANOVA	veg	A, D
Bennett and Griffiths 1984.	Factors affecting the distribution, abundance and diversity of rock-pool fishes on the Cape Peninsula, South Africa.	ANOVA corr	site,	A, B, D
Stoner 1983.	Distribution of fishes in seagrass meadows: role of macrophyte biomass and species composition.	ANOVA corr	veg	A, D

Table 7. Studies using relatively complex qualitative approaches to evaluate fish-habitat relationships.

Reference	Title of study
Gibson et al. 1993.	Seasonal and annual variations in abundance and species composition of fish and macrocrustacean communities on a Scottish sandy beach.
Tzeng and Wang 1993.	Hydrography and distribution dynamics of larval and juvenile fishes in the coastal waters of the Tanshui River estuary, Taiwan, with reference to estuarine larval transport.
Potter et al. 1993.	The fish fauna of a seasonally closed Australian estuary. Is the prevalence of estuarine-spawning species high?
Bell et al. 1992.	Variations in assemblages of fish associated with deep and shallow margins of the seagrass <i>Posidonia australis</i> .
Wilkins and Myers 1992.	Microhabitat utilisation by an assemblage of temperate Gobiidae (Pisces: Teleostei).
Baelde 1990.	Differences in the structure of fish assemblages in <i>Thalassia testudinum</i> beds in Guadeloupe, French West Indies, and their ecological significance.
Cyrus and Blaber 1987.	The influence of turbidity on juvenile marine fishes in estuaries. Part 1. Field studies at Lake St. Lucia on the southeastern coast of Africa.
Sogard et al. 1987.	Epibenthic fish communities on Florida Bay banks: relations with physical parameters and seagrass cover.
Potter et al. 1986.	Consistency of seasonal changes in an estuarine fish assemblage.
Moreno and Jara 1984.	Ecological studies on fish fauna associated with <i>Macrocystis pyrifera</i> belts in the south of Fuguian Islands, Chile.
Weinstein and Brooks 1983.	Comparative ecology of nekton residing in a tidal creek and adjacent seagrass meadow: community composition and structure.
Weinstein et al. 1980.	Multiple determinants of community structure in shallow marsh habitats, Cape Fear River estuary, North Carolina, USA.

Table 8. Studies identified in the literature search that use regression analyses to estimate fish-habitat parameters. Note that some of these studies also use approaches other than regression. For example Rice (1993) compares using both regression analysis and probability density functions to describe fish-habitat relationships.

Reference	Title
Rice 1993.	Forecasting abundance from habitat measures using nonparametric density estimation methods.
Fechhelm et al. 1992.	Modelling of in situ temperature and growth relationships for yearling broad whitefish in Prudhoe Bay, Alaska.
Lubbers et al. 1990.	Variations in structure of estuarine fish communities in relation to abundance of submersed vascular plants.
Shirvell 1989.	Habitat models and their predictive capability to infer habitat effects on stock size.
Brown 1988.	Multivariate analyses of the role of environmental factors in seasonal and site-related growth variation in the Pacific oyster <i>Crassostrea giagas</i> .
Marais 1988.	Some factors that influence fish abundance in South Africa estuaries.
Cole and Cloern 1987.	An empirical model for estimating phytoplankton productivity in estuaries.
Sibert 1979.	Detritus and juvenile salmon production in the Nanaimo estuary: II. Meiofauna available as food to juvenile chum salmon (<i>Oncorhynchus keta</i>).
Naiman and Sibert 1979.	Detritus and juvenile salmon production in the Nanaimo estuary: III. Importance of detrital carbon to the estuarine ecosystem.

Table 9. Examples of foreshore species-specific habitat models identified in the literature search. Modelling approaches: ANOVA - analysis of variance; cor: correlation analyses; ord: ordination analyses; pca: principal components analysis; pdf: probability density function; poly: polynomial; slr: simple linear regression; mlr: multiple linear regressions. Habitat properties include temporal and spatial analysis. Fish properties are: A: abundance, numbers, or density; G: growth; B: biomass; D: diversity; P: production; S: survival, R: recruitment. Habitat variables: sal: salinity, tmp: water temperature; exp: exposure; tur: water turbidity; dch: discharge; veg: vegetation properties; z: depth; sub: substrate properties.

Reference	Species	Habitat/ Location	Analysis	Fish prop	Habitat variable	Sampling approach
O'Connell and Carille 1993.	Rockfish	demersal / Alaska	pdf	A	sub	time, space
Bologna and Steneck 1993.	Lobster	kelp beds / Maine	cor, ANOVA	A, D, B	veg, sub	time
McMahon and Holtby 1992.	Coho	estuary / BC	cor	A	sal, veg debris	time, space
Fechhelm et al. 1992.	White-fish	delta, Alaska	cor, mlr, poly	G	sal, tmp	space
Norris 1991.	Rockfish	nearshore / Washington	various	var	various	time, space
Kramer 1991.	Halibut	bay / California	cor	A, S, G	z	time, space
Castro and Cowen 1991.	Bay anchovy	estuary / NY	cor, ANOVA	A, G	veg, sub, tmp, sal	time, space
Schweigert et al. 1990.	Herring	nearshore / BC	model	B	veg	time, space
Deegan 1990.	Menhaden	estuary / Louisiana	cor, ANOVA	A, G, S	dch, tmp, sal, veg, z	time, space
Matthews 1989.	Rockfish	eelgrass, reef/ Wash.	ANOVA	A	sub, veg	time, space
Horne and Campana 1989.	Ground- fish	nearshore / Nova Scotia	pca, mlr, cls, ord	A	sal, tmp, sub, veg, z	space
Rogers et al. 1988.	English sole	estuary / Washington	cor	A, R	exp	time, space
Macdonald et al. 1987.	Coho, Chinook	estuary / BC	ord	A	sal, tmp	space

Table 9. (Con't.)

Levings et al. 1989.	Chinook	estuary / BC	cor	A		time, space
Stier and Crance 1985.	American shad	estuary / NY	model, HSI	A	tmp, z, dch, veg, sub	
Healey 1980.	Chinook	estuary / BC		G, A	sal, tmp	time, space

Table 10. Examples of fish-habitat models evaluating changes in properties of fish assemblages in coastal habitats. Modelling approaches: ANOVA - analysis of variance; cor: correlation analyses; cls: classification analyses; ord: ordination analyses; slr: simple linear regression; mlr: multiple linear regressions. Habitat properties include temporal and spatial analysis. Fish properties are: A: abundance, numbers, or density; B: biomass; D: diversity; P: production; S: survival, R: recruitment. Habitat variables: sal: salinity, tmp: water temperature; tur: water turbidity; dch: discharge; veg: vegetation properties; z: depth; sub: substrate properties.

Reference	Habitat/ Location	Analysis	Fish properties	Habitat variables	Sampling approach
Gibson et al. 1993.	beach/ Scotland	cor, cls, ord	A, D	tmp, sal	time
Neira et al. 1992.	estuary/ Australia	cor, cls	A, D	site, tmp	space, time
Kneib 1993.	saltmarsh/ Georgia	anova, slr	R, S	tmp, z	space
Marais 1988.	estuary/ S. Africa	mlr	A, B	tur, sal, site	space, time
Mgaya 1992.	tidepool/ BC	anova, cor	A, B, P	z, site	space, time
Bell et al. 1992.	seagrass/ Australia	pca, cls, anova	A, D	z, sub	space, time
Worthington et al. 1992.	seagrass/ Australia	cor, anova	A, D	veg	space, time
Ferrell and Bell 1991.	seagrass/ Australia	anova, cor, cls	A, D	site	space
Lubbers et al. 1990.	estuary/ Maryland	cor	A, B, D, P	veg	space, time
Loneragan and Potter 1990.	estuary/ Australia	cor, cls anova	A, D	sal, tmp	space, time

Table 10. (Con't.)

Allen and Barker 1990.	subtidal creeks/ S. Carolina	anova	A, R	site, sal	space, time
Abou-Seedo et al. 1990.	mud flat/ Kuwait	anova	A, B, D	site, tur, tide	space
Bell and Westoby 1988.	seagrass/ Australia	anova	A, D	veg	space
Sogard et al. 1987.	mudbanks/ Florida	ord, cls, mlr	A, D	veg, z, sub	space
Rozas and Odum 1987.	marsh/ Virginia	anova	A, D, R	veg, site	space
Moyle et al. 1986.	marsh/ California	cor, pca	A, D	tmp, sal, dch	time
Potter et al. 1986.	estuary/ UK	cls, ord	A	tmp, sal, dch	time
Weinstein and Brooks 1983.	seagrass/ Virginia	cls, ord, cor	A, D	site	space
Orth and Heck 1980.	eelgrass/ Maryland	cor	A, D	veg, tmp	time
Allen and Horn 1975.	lagoon/ California	cor	A, D	tmp	time

Table 11. Trophodynamic models identified in the literature search.

Reference	Title of study
Walters and Post 1993.	Density-dependent growth and competitive asymmetries in size-structured fish populations: A theoretical model and recommendations for field experiments.
Hall and Raffaelli 1991.	Food-web patterns: Lessons from a species rich web.
Peters and Schaaf 1991.	Empirical model of the trophic basis for fishery yield in coastal waters of the eastern USA.
Sullivan and Moncreiff 1990.	Edaphic algae are an important component of salt marsh food-webs: evidence from multiple stable isotope analyses.
Beamesderfer et al. 1990.	Management implications of a model of predation by a resident fish on juvenile salmonids migrating through a Columbia River reservoir.
Asmus and Asmus 1990.	Trophic relationships in tidal flat areas: To what extent are tidal flats dependent on imported food?
DeAngelis 1988.	Strategies and difficulties of applying models to aquatic populations and food webs.
McQuaid and Branch 1985.	Trophic structure of rocky intertidal communities: response to wave action and implications for energy flow.
Smith et al. 1984.	Community and trophic organization of nekton utilizing shallow marsh habitats, York River, Virginia.
Naiman and Sibert 1979.	Detritus and juvenile salmon production in the Nanaimo Estuary. III. Importance of detrital carbon to the estuarine ecosystem.
Evans 1983.	Production, predation and food niche segregation in a marine shallow soft-bottom community.
Livingston 1982.	Trophic organization of fishes in a coastal seagrass system.

Table 12. Nutrient/energy flow models identified in the literature search.

Reference	Title of study
Baird and Ulanowicz 1993.	Comparative study on the trophic structure, cycling and ecosystem properties of four tidal estuaries.
Cockcroft and McLachlan 1993.	Nitrogen budget for a high-energy ecosystem.
Deegan 1993.	Nutrient and energy transport between estuaries and coastal marine ecosystems by fish migration.
Wetzel and Hopkins 1990.	Coastal ecosystem models and the Chesapeake Bay program: Philosophy, background and status.
Du Preez et al. 1990.	Bioenergetics of fishes in a high-energy surf-zone.
Keizer et al. 1987.	Cumberland basin ecosystem model: Structure, performance and evaluation.
Childers and McKellar 1987.	A simulation of saltmarsh water column dynamics.
Wickens and Field 1986.	The effect of water transport on nitrogen flow through a kelp-bed community.
Bennett 1984.	A population energy budget for <i>Clinus superciliosus</i> L., with an assessment of the role of resident fish as predators in the intertidal zone.
Wulff and Field 1983.	Importance of different trophic pathways in a nearshore benthic community under upwelling and downwelling conditions.
Valiela and Kistritz 1980.	Dependence of salmon on Fraser estuarine marsh ecosystems: a simulation analysis.

Table 13. Studies identified in the literature search that discuss geographical information systems.

Reference	Title of Study
Donovan et al. 1987.	Use of Geographic Information Systems to develop habitat suitability models.
Hunsaker et al. 1991.	Spatial models of ecological systems and processes: the role of GIS.
Kapetsky et al. 1987.	A Geographical Information System and satellite remote sensing to plan for aquaculture development: a FAO - UNEP/GRID cooperative study in Costa Rica.
Aronoff 1993.	Geographic Information Systems: a management perspective.
FAO of the United Nations. 1989.	Geographical Information Systems and remote sensing in inland fisheries and aquaculture.
Ricketts 1992.	Current approaches in Geographic Information Systems for coastal management.
Burrough 1986.	Principles of Geographic Information Systems for land resources assessment.
Legault 1992.	Using a Geographic Information System to evaluate the effects of shellfish closures on shellfish leases, aquaculture and habitat availability.
Johnstone 1992a.	Selection of preferred high-end and low-end GIS products for DFO, revision 1.4.
Johnstone 1992b.	High-level user requirements for Geographical Information Systems for DFO, revision 1.0.
Hale et al. 1993.	A comprehensive data and information management system for estuarine monitoring.
Mumford et al. 1992.	Implementation plan for the characterization of Puget Sound nearshore habitats.
Simpson 1992.	Remote sensing and Geographic Information Systems: implications for global marine fisheries.
Fox 1993.	Habitat classification for Oregon rocky shores.

Appendix 1.

List of key words/phrases used to search AQUAREF, WAVES, and ASFA computer data bases.

- 1) GIS or geographic* information system*
- 2) energy flow or (marine and model) and (primary produc* or consumer or predator)
- 3) model* and survival and (larva* or juvenile)
- 4) fish and (wave or current) and (survival and productivity)
- 5) marine and environment and (shallow or coast* or estuar* or intertidal) and (habitat or model*)
- 6) habitat and fish* (survival or productivity) and marine or tidal or intertidal or nearshore or estuar*)
- 7) habitat* and marine and (management or classification* or map* or model)
- 8) habitat* and fish* and marine and (nearshore or coast* or estuar* or benthic or intertidal or tidal or shallow)

Appendix 2.

Overview of advantages and disadvantages of nearshore habitat classification systems discussed in Frith et al. (1993).

Reference	Advantages	Disadvantages
Cowardin et al. 1979.	<ul style="list-style-type: none"> - habitats classified using substrate or vegetation data - hierarchical system - biological data can be included 	<ul style="list-style-type: none"> - extensive field work required - system not complete for all habitat types - lack of physical energy as classifier
Dethier 1990.	<ul style="list-style-type: none"> - extension of Cowardin - widely applied to Pacific coast - based on descriptive physical criteria - addresses both intertidal and subtidal habitats - diagnostic and associated biota listed for each habitat 	<ul style="list-style-type: none"> - combined habitats not considered - no recognition of repetitive associations across shore - estuarine/marine division difficult to apply
Demarchi et al. 1990.	<ul style="list-style-type: none"> - hierarchical system - combines physical and biological criteria - physical and vegetative parameters have been recorded for many areas of B.C. 	<ul style="list-style-type: none"> - parameters used to define levels subjective - can not be applied to coastal or marine areas
Harper et al. 1993.	<ul style="list-style-type: none"> - data collected from remote sensing - multi-level structure allows for flexibility in selecting level of display - applicable over large areas 	<ul style="list-style-type: none"> - physical classification used to infer biological communities - distinction between habitat types often vague or arbitrary - across shore classification too detailed and not cost effective for large applications - system not hierarchical
Hiscock and Connor 1991.	<ul style="list-style-type: none"> - based on species assemblages - collects both physical and biological data in detail - system designed for area similar to BC 	<ul style="list-style-type: none"> - requires detailed field surveys - impractical for large expanses of coastline

Appendix 2. (Con't.)

Hunter et al. 1983.	<ul style="list-style-type: none"> - uses aerial photos and field data - physical parameters chosen as modifiers for biota distributions 	<ul style="list-style-type: none"> - biological data not collected for species occupying habitats surveyed - require extensive modification to be applied to other non-estuarine habitats
LGL Limited 1993.	<ul style="list-style-type: none"> - shore units combine exposure, physical shore features and biological components - use percent cover and cover distribution 	<ul style="list-style-type: none"> - overlap between habitat groups makes it difficult to combine data hierarchically - criteria to define break points for shore units not given - grouping of habitat types questionable
Pearsal et al. 1992.	<ul style="list-style-type: none"> - data requirements are general and thus suitable for large areas - hierarchical system - upper levels are global and allow for expansion to other geographic regions 	<ul style="list-style-type: none"> - physical habitat criteria general and poorly reflect ecosystem units - physical habitat parameters not good indicators of processes that effect species distributions - use of individual biota to identify ecosystem not likely to reflect abundance and diversity of all species in each community
Busch and Sly 1992.	<ul style="list-style-type: none"> - similar to Cowardin et al. 1979 - hierarchical system - system has a shoreline component based on substrate type - system flexible and additional modifiers like wave energy or species can be added - system can be monitored by remote sensing to subdivision level 	<ul style="list-style-type: none"> - no method of classifying habitats based on biological community is provided - shoreline not distinguished from shallow coastal zone - habitat characteristics at class level require manual surveys - system designed for lakes and cannot be applied to marine systems without modifications

Appendix 2. (Con't.)

Nature Conservancy 1991.	<ul style="list-style-type: none"> - related to Cowardin et al. 1979 - system hierarchical - lower levels include physical and biological criteria for habitat categorization - provides high degree of detail for subtidal habitats 	<ul style="list-style-type: none"> - imprecise classification criteria - no explicit consideration of energy - intertidal zone poorly represented - system not amenable to remote observations - system limits scale of application to < 1:20 000
Williams 1990.	<ul style="list-style-type: none"> - system developed for BC - ecosystem level provides easy mechanism for sorting shore units - developed for DFO habitat policy - biological components relevant to management purposes 	<ul style="list-style-type: none"> - developed for small areas only - criteria for shore units not given - too complicated as divided shore unit into three cross shore zones - physical and biological components treated separately and thus habitat cannot be mapped as a discrete unit - biological units not habitat units

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