

A review of landscape-scale habitat models of early life fish production

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Introduction

The identification of critical habitats (i.e., areas or volumes of water) for fish populations is essential for sustainable fisheries management. Limiting anthropogenic stressors in such habitats increases the sustainability of fish populations and their associated fisheries. The recognition that habitat protection is a critical component of sustainable fisheries management and conservation biology is reflected by policies in North America and elsewhere requiring the preservation of habitats critical to exploited and threatened fish populations (e.g., the United States' Sustainable Fisheries and Endangered Species Acts and the European Union's Common Fisheries Policy). These regulations provide an impetus for the identification (and subsequent protection) of critical habitats, but do not set clear criteria for defining such habitats. Most habitats are under-sampled, and thus critical habitats must be identified based upon a paucity of data. In addition, habitat value can be measured at a range of spatial and temporal scales, for various life-stages (eggs through adults), and can be quantified based upon data relating to abundances, growth and/or mortality rates. The appropriate spatial scale, life-stage, and population metric for evaluating habitat value will likely vary somewhat among populations and systems. However, in general the protection of habitats producing significant numbers of young fish should be prioritized, and for both theoretical and practical reasons, habitat value should be measured at a relatively coarse (i.e., landscape) spatial scale, based upon early life-stage production rates. Unfortunately, such rates are difficult to measure,

especially in open aquatic systems such as the pelagia of marine and large lacustrine systems. Thus, habitat models are necessary to overcome relatively sparse spatial data and integrate various data-types to obtain spatially-explicit estimates of production. In this chapter, I provide justification for the use of early life production rates to quantify habitat value in open systems, and present potential modeling approaches and considerations for generating landscape scale estimates of habitat-specific production rates.

Habitat Importance

The identification of critical habitats is complicated by a variety of factors, including limited data, high temporal and spatial variation, and the complexity of natural systems (Rose 2000). For many fish stocks there is a dearth of data. It is simply not possible to sample every habitat using traditional sampling methods. In addition, most fish stocks are characterized by high inter-annual variation in abundance, and the relative contribution of young fishes from particular habitat-types will often vary from year to year. Even if habitat-specific data can be obtained throughout a system over an extended time period, it is not obvious how such data may be used to quantify the relative value of particular habitats. Several authors have inferred the profitability of habitats from presence-absence or density data (e.g., Höök et al. 2001). However, if vital rates vary among habitats, then the presence or relative abundance of a fish life stage may reveal little regarding the ultimate yield of fish biomass or number of recruits from a habitat. The relative quality of a habitat for juvenile animals (e.g. young pre-recruited fish) has been hypothesized to be a function of habitat-specific mortality and growth rates (Werner

and Gilliam 1984). Houde (1997) related this idea to fish recruitment and suggested that the ratio of instantaneous mortality rate (M) to instantaneous growth rate (G) provides an index of recruitment potential, synonymous with instantaneous population production. If $M/G < 1$, the population production is positive (i.e., the biomass of a fish population within a habitat is increasing), and conversely if $M/G > 1$, the population production is negative. However, the utility of this index for assessing the ultimate importance of habitats is limited because M/G is expressed on a per unit basis (i.e. this index does not account for fish density or habitat area). The actual yield of recruits from a habitat is a function of M , G , the number of young fish in the habitat, and the relative size of the habitat (Figure 1.1). That is, if young fish in a specific habitat experience relatively high growth and survival rates (i.e. $M/G < 1$), but densities in the habitat are low or the habitat constitutes a relatively small area (or volume), then the contribution of this habitat to the overall fish population is likely limited. It is therefore necessary to differentiate between habitat quality and habitat importance for a fish population. The importance of a habitat should be judged by the actual contribution of recruits from the habitat.

In general, habitat management plans should prioritize the protection or rehabilitation of those habitats which currently or potentially produce significant numbers of early life stages. Early life stage densities, growth, survival and production rates can vary tremendously over space and time (Cowan and Shaw 2002). The majority of fish species are highly fecund, but experience very low survival during early life. Thus, relatively slight changes in early life stage vital rates can lead to dramatic changes in production, recruitment (to fisheries and adult populations), and ultimately stock size (Houde 2002). Hjort (1914) was the first to recognize the importance of early life

dynamics, and argued that the spatio-temporal overlap of patches of food and young fish was critical to prevent the starvation of these life stages. Other authors have expanded upon Hjort's ideas and have suggested that not only starvation (e.g., Houde 1975), but also predation (e.g., Luecke et al. 1990; Rice et al. 1997) and transport (e.g., Heufelder et al. 1982) are potential sources of mortality for young fish. Moreover, several researchers have demonstrated that mortality rates of young fish are directly related to growth rates (Ware 1975; Werner and Gilliam 1984; Houde 1987; Houde 1997). Slow growth during early life can prolong the time spent in a vulnerable size class. Regardless of the mechanisms, due to the highly fecund nature of most fish species, early life growth and survival rates (not stock size) are the primary determinants of recruitment success. Because these vital rates are likely to vary spatially (i.e., across habitats), the contributions of different habitats to adult fish populations also will vary.

The availability of habitats suitable for early life stages may limit overall population biomass (Minns et al. 1996). Further, such habitats often are particularly vulnerable to anthropogenic activities. Adults of many exploited fish species undertake spawning migrations towards shore or into rivers. Similarly, many young fish which emerge offshore subsequently migrate to coastal and estuarine nursery habitats. These migrations result in the early life stages of many fish species developing in habitats highly susceptible to anthropogenic-induced stressors, including eutrophication, exotic species introduction, hydrologic alteration, and contaminant discharge.

Fisheries Management and Habitat Importance

Current fisheries regulations and management strategies reflect the need to identify habitats producing large numbers of early life stages. In 1996, the U.S. Congress passed the Sustainable Fisheries Act (SFA; as a reauthorization of the Magnuson-Stevens Fishery Conservation and Management Act) requiring managers “to promote and protect essential fish habitat” (EFH), defining EFH as “those waters and substrates necessary to fish for spawning, breeding, feeding or growth to maturity.” The SFA is an important document for U.S. marine fisheries management in general, and for habitat management in particular. The SFA directs the National Oceanic and Atmospheric Administration’s (NOAA) National Marine Fisheries Service (NMFS) to provide guidance in the identification of EFH. On January 17, 2002, NOAA issued its final EFH regulations, which call for EFH identification based on analyses of available habitat information. Ideally, EFH should be identified based on information on production rates (i.e., habitat importance). However, NOAA’s regulations recognize that habitat-specific information on production rates is often not available, and thus identifies four levels of habitat data which may be used in identifying EFH. Level 1 is defined as “distribution data” such as presence or absence of a fish species or life stage in particular habitats; Level 2 is defined as “habitat-related density” data, including relative abundance data; Level 3 is defined as data on “growth, reproduction and survival within habitats;” and, Level 4 is defined as data on “production rates by habitats.” The regulations further direct managers to “strive to describe habitat based on the highest level of detail (i.e., Level 4).” In short, the NOAA regulations provide further impetus to obtain Level 4 data relating production of young fish to habitat.

Marine Protected Areas (MPAs) have recently received a great deal of attention as a management strategy for achieving a multitude of objectives, including maintaining biodiversity, protecting rare species and restoring ecological functions (e.g., Botsford et al. 1997; Conover et al. 2000; Jones 2002; Pauly et al. 2002; Lubchenco et al. 2003). In addition, MPAs can serve to enhance and sustain regional fisheries by serving as sources of recruits to surrounding areas. If this latter strategy is to succeed, MPAs must contain habitats which produce and hold or export significant numbers of young fish (e.g., Warner et al. 2000), and thus such habitats should be identified (Crowder et al. 2000). Multi-annual management plans are now being implemented whereby regulators annually adjust fishing pressure based on estimates of present and future stock size (e.g., E.U.'s new Common Fisheries Policy). Current stock size often can be estimated from catch rates, whereas future stock size (i.e., future recruitment to the fishery) must be estimated from fishery-independent surveys. By limiting pre-recruit monitoring to habitats identified as significant producers of young fish, managers can more effectively and efficiently gauge pre-recruit year-class strength, and can thereby annually adjust future fishing pressure to reflect anticipated future recruitment.

Importance of Spatial Scale

The spatial extent of fish populations and the management strategies directed towards such populations necessitate that habitat importance be quantified at relatively coarse spatial scales (i.e. a landscape perspective). For instance, although the optimal size for MPAs is debatable, it is likely that relatively large MPAs will be more effective (Walters 2000). Thus, to select appropriate locations for MPAs, managers should ideally utilize

estimates of landscape scale production rates. Similarly, several potentially deleterious anthropogenic impacts (e.g., eutrophication, exotic species introduction, hydrologic alteration, and contaminant discharge) will influence fish populations at a regional level. Thus, landscape scale analyses are necessary when prioritizing areas to protect from such stressors. Unfortunately, the majority of past studies relating fish and habitat have been conducted at fine spatial scales, and have related fish abundance to some local habitat variable (e.g., substrate, structure). Scaling up results of such studies to a landscape scale can be difficult. For example, an apparent positive relationship between a habitat variable and fish abundance may only reflect local aggregation and thus will not necessarily influence regional production. Ultimately, both landscape and local scale processes affect fish populations (Wiley et al. 1997). However, as human activities and potential management strategies will have regional impacts, measuring habitat importance at landscape scales should prove most useful for management purposes. Finally, as fish production is essentially an integration of several processes (e.g., foraging, growth, starvation, predation, movement), it is unrealistic to quantify production at very fine spatial scales. In particular, it is unrealistic to quantify production at fine spatial scales within relatively open systems, such as marine and lacustrine pelagic environments. Within such systems, there are often no clear horizontal boundaries between habitats, and fish likely disperse (both actively and passively) within these systems, necessitating some spatial integration in the horizontal dimension.

Methods for Measuring Habitat Importance

Methodologies for estimating the importance of habitats (particularly under-sampled habitats) are not well defined and will likely vary among populations and systems. In some cases, field and laboratory studies may be sufficient to estimate habitat-specific production and recruitment, but often such methods are not feasible. As an example, natural (e.g., chemical composition of otolith cores; Kennedy et al. 2002; Brazner et al. 2004) and artificial tags (e.g., Miller and Able 2002) may allow identification of natal habitats of individuals recruited to a fishery or adult population. However, artificial tagging of young fish may be impractical due to high handling-related mortality and the need for distinctive tags for each habitat type. Further, natural tagging analysis involves discrimination among natal habitats based on attributes conferred onto individuals due to unique physical and chemical environments. Such discrimination among habitats may be impossible if the physical and chemical characteristics of habitats are not sufficiently different, or if the number of habitats to be discriminated is high.

Alternatively, if young fish remain in a single habitat during their early development it may be appropriate to simply estimate late-season young-of-year (YOY) densities (i.e., once year-class strength has been set) in individual habitats in order to infer habitat importance. Basically, this approach involves sampling the population after early-life growth and mortality dynamics have had a chance to influence densities and size distributions within individual habitats. For example, fixed location (i.e. at river mouths) counts of out-migrating anadromous or potadromous juvenile fish can potentially generate estimates of the relative contribution of recruits by different river systems (e.g., Stables and Kautsky 2000). However, this method is realistically viable for only a small subset of populations and systems (e.g., anadromous fish). For most

populations, counting late-season YOY fish in every habitat is infeasible. More importantly, many young fish continuously move among habitats and in most systems there is no single fixed location where one can count individuals exiting a nursery habitat (especially in open systems).

Many of the factors mentioned above that limit the utility of field and laboratory methods and ultimately complicate the identification of important fish habitats can be overcome through modeling analyses. With models, one can estimate data for habitats that are under-sampled, simulate habitat-specific yields during years with limited empirical data, and integrate habitat-specific information on fish densities, movement, growth, and survival rates in order to quantify habitat importance. Historically, fisheries models have focused on the temporal dynamics of fish populations and production. However, with the development of analytical tools, such as Geographic Information Systems (GIS) and spatial statistics, and data collection tools, such as remote sensing and hydro-acoustics, spatially-explicit models allowing for habitat comparisons have become more prevalent (e.g., Nishida et al. 2001). In addition, habitat models can allow for forecasting the consequences of habitat degradation, rehabilitation and restoration on fish population production (e.g., Jones et al. 1996; Jones et al. 2003). With continued habitat alterations, such ecological forecasts will likely grow in necessity (Clark et al. 2002). Further, habitat models can potentially play a role in bridging the gap between the two schools of fish population models identified by Minns et al. (1996); 1) temporally dynamic models of fish populations and their harvest and 2) static analyses of fish and habitat linkages.

Models of Fish Production

I review some general approaches to quantify the importance of under-sampled habitats for single species within large, open systems. The appropriate approach will vary depending on the population of interest and the amount, quality, and type of data available. Habitats are also managed to enhance biodiversity, and models with this goal in mind will take different forms. Also, given that habitat modeling is necessary in large part due to lack of data, it seems unlikely that “broadening from the single species to the ecosystem, with its exponential increase in data needs, will help with quantitative forecasts” (Rose and Cowan 2003).

In defining the structure of landscape-scale, habitat-specific production models, there are essentially two primary issues. First, should the separate components of production (i.e. initial abundances, growth and mortality rates; see Figure 1.1) be represented within each modeled habitat, or should production be the only habitat-specific characteristic represented? I discriminate between these two general classes of models for generating habitat-specific estimates of production. One class (direct models of production) involves predicting fish production directly and then extrapolating production estimates across habitats. The other class (integrative models of production) involves extrapolating the components of production, and then integrating these extrapolated estimates to generate habitat-specific estimates of production.

The second issue relates to how to extrapolate either production or the components of production across habitats. The simplest approach for extrapolating across habitats involves estimating values (i.e., production or abundance, growth and mortality) in one area from measured values in surrounding areas. Such geostatistical

approaches make use of spatial trends in geographically-referenced measurements and the tendency for near measures to be more similar than distant measures (Figure 1.1). Although most geostatistical methods were not developed with fish populations in mind, these techniques have become increasingly prevalent within fisheries science (Rivoirard et al. 2000). Examples of geostatistical techniques include inverse distance weighting (IDW), triangular irregular networks (TIN), and kriging. Some geostatistical techniques (e.g., IDW and TIN) do not account for interpolation uncertainty, whereas others can. For instance, kriging involves fitting a spatial correlelogram to measured values, and then using this model to interpolate data. The error bound around an interpolated point is then a function of the goodness-of-fit of the correlelogram and the distances between the interpolated point and surrounding measured points.

Alternatively, population values in under-sampled areas can be inferred from one or more measurable (or readily estimated) covariates (Figure 1.1). Covariate methods can be based on statistically-derived relationships (e.g. regression equation relating fish abundance to temperature) or more mechanistic models (e.g. bioenergetics and foraging models predicting growth based upon temperature and prey density). These methods can take advantage of the fact that several potential covariates are measured at finer spatial scales and over larger areas than fish populations. For instance, relatively fine-scale satellite-derived measured of temperature and chlorophyll and drifter-derived measures of water currents can cover vast regions and even entire oceans (Dalton 2002; deYoung et al. 2004). In addition, observation networks have been established and are developing in various aquatic systems, including Great Lakes, Atlantic Ocean and Pacific Ocean (Gerwin 2002; Schrope 2002; <http://www.csc.noaa.gov/coos/>). These networks generally

target the measurement of physical, chemical, and lower trophic level biological variables, which should serve as useful predictors of fish population indices.

Finally, a general method for estimating values in under-sampled areas involves a combination of geostatistical and covariate methods (Figure 1.1). Such interpolation of data can be based on both the spatial structure of the variable of interest and spatial measurements of a useful covariate (e.g., co-kriging and some Bayesian approaches; Su et al. in press). Population values in under-sampled areas are bound to be related to both habitat characteristics (i.e., physical, chemical and biological factors within the area of interest) and population values in surrounding areas. Models which predict population values based on both of these features should ultimately prove superior to those that only consider one. Unfortunately, these combined spatial covariate methods are presently underdeveloped and underutilized.

Direct Models of Production

If habitat-specific production can be directly estimated, then such estimates can be extrapolated to other habitats. Methods to extrapolate such estimates have not been extensively developed, but there is evidence that both geostatistical and covariate approaches may be successful. For instance, within-species year-class strength varies spatially (i.e., across stocks), with year-class strength of more proximate sub-stocks being more similar (Myers et al. 1995 and Myers et al. 1997). This suggests that there are identifiable spatial patterns in fish production which could be used to improve production estimates across habitats (Su et al. in press). On the other hand, Hilborn et al. (2003)

demonstrate that year-class strengths of nearby sub-stocks will not necessarily be highly correlated.

A multitude of models have been developed to index the overall, across-species productive capacity of habitats based on variables such as primary production (Oglesby 1977), mean depth (MD; Rawson 1952), total dissolved solids (TDS; Rawson 1951), morphoedaphic index (TDS/MD; Ryder et al. 1974), and benthos biomass (Matuszek 1978). In order to be of use for single species analyses, these models must discriminate among species. The presence of fish species other than the species of interest will no doubt affect the species-specific productive capacity of a habitat. Thus, it follows that single species models of production based on one or more measurable variables will likely be specific to regions within which the fish biota is fairly uniform.

Integrative Models of Production

Habitat models which integrate production components require measures of initial abundances and vital rates (growth and survival). These are often difficult to directly measure in all habitats of interest, and thus the first step in integrative production modeling will often involve the generation and extrapolation of estimates on initial abundances and vital rates. Here, I review some methods to extrapolate abundances and vital rates across habitats, and I draw upon my own experiences developing landscape-scale spatial relationships and models for steelhead (*Oncorhynchus mykiss*) in Lake Michigan in order to provide some examples.

Abundance rates

Compared to vital rates and production, habitat-specific abundances (or relative densities) of young fish are fairly straightforward to estimate using traditional techniques. Nonetheless, confounding factors such as patchy spatial distributions of young fish may result in considerable sample variance, and thus substantial effort (i.e. sampling a large volume, sampling over an extended time period, and/or repeated sampling) may be necessary to generate habitat-specific abundance estimates with suitable error bounds. The necessity for great effort often precludes estimation of abundances in all habitats within an area of interest, and models of abundance are therefore necessary to fill in information for under-sampled habitats. Geostatistical, covariate, and even spatial covariate techniques can be used to extrapolate measures of abundance. Geostatistical techniques for extrapolating values across space are essentially the same regardless of the type of value to be extrapolated (i.e., methods for extrapolating abundances are essentially identical to methods for extrapolating vital rates).

Covariate models of fish abundance can take several forms including regression analysis, path analysis, ideal free distributions, suitability indices and classification models. Covariate models also and can 1) involve covariates measured at coarse, landscape scales and/or fine, local scales; 2) fall on either end of a continuum between mechanistic and empirical models; and 3) include simple measures of static covariates or complex quantification of dynamic processes. The plethora of model types used to predict abundances in undersampled areas prevent a thorough review of all such types. However, it is worthwhile to distinguish among three general classes of covariate models: statistical continuous, theoretical continuous and categorical/index models. Statistical continuous models involve fitting a statistical relationship between fish abundance (or

density) and one or more continuous covariates (e.g., between egg abundance and macrophyte density). Most categorical and index models integrate measurements of multiple habitat characteristics in order to group or score the corresponding habitat based upon some defined criteria (e.g., hydrological and temperature classes, habitat suitability indices, instream flow incremental method). Habitat-specific densities are then predicted based on group or score. Thus, these models yield discontinuous estimates of abundance. However, given the uncertainties around estimates of abundance, continuous models may be a bit optimistic, and instead models which group or score habitats by incorporating a multitude of factors which likely influence fish distributions may be superior. The final class of covariate models, theoretical continuous models, does not rely upon statistical fits. An example is the Ideal Free Distribution (IFD; Fretwell and Lucas 1970), an optimality model which predicts that a group of organisms will distribute itself across space such that resource intakes of individual foragers will be equal. Thus, based upon the IFD, habitat-specific abundances could be predicted as a function of prey densities.

Recent analyses of steelhead distributions and growth rates in Lake Michigan are based upon comparing spatial patterns of angler catch rates of steelhead (indices of steelhead abundance) with spatially-explicit measures of temperature and prey densities at a 10×10 minute grid cell resolution (Figure 1.2; Höök et al. 2004 and Höök et al. in press). The analyses demonstrate the potential use of both geostatistical and covariate methods for extrapolating abundance estimates across habitats. A component of these analyses involved geostatistical, kriging algorithms to extrapolate acoustic measures of alewife densities to un-sampled grid cells (Figure 1.3). In addition, a relationship between steelhead densities and satellite-derived measures of surface temperatures was

developed (Figures 1.3-1.5). Although surface temperatures were not used to extrapolate steelhead densities across Lake Michigan, the strengths of these relationships suggest that such covariate-based extrapolation is feasible for this population (Figure 1.5).

Vital Rates

In practice, generating habitat-specific measures of vital rates (growth and mortality) is quite difficult, particularly in large ecosystems. Traditional methods of estimating growth and mortality rates require repeated population sampling (i.e., high effort), and if there is a high degree of movement, it may not be possible to generate spatially explicit measures with traditional methods. Models are therefore often necessary tools for first generating and subsequently extrapolating measures of vital rates. As with abundance, geostatistical, covariate, and even spatial covariate techniques can be used to extrapolate measures of vital rates. Geostatistical techniques for this purpose are essentially the same as for extrapolation of any measurements. In addition, covariate approaches are by far the most developed and employed method for estimating vital rates in under-sampled areas.

There are basically two covariate methods to extrapolate vital rates across habitats: empirical statistical methods and mechanistic models, as exemplified by bioenergetics models. There are also several theoretical models relating inter-specific differences in life-history traits and individual size to variation in growth and mortality (e.g., Pauly 1980). Because these theoretical models can be used to predict average vital rates for individual species, such models are they are of little use for predicting within-species variation in growth and mortality. However, theoretical models potentially can

be used to model one vital rate as a function of another. For instance, mortality rates of young fish are, in general, thought to be negatively related to size (Miller et al. 1988). Thus, if growth rates can be extrapolated across habitats as a function of some covariate, then mortality rates can potentially be inferred as a function of size (i.e., growth).

Several authors have developed statistical relationships (primarily through regression analyses) between early-life vital rates and habitat characteristics (e.g., temperature, wind speed, prey density, latitude). Data to develop such relationships have come from laboratory treatments (e.g., Miller et al. 1990) and field sampling (e.g., Van der Veer et al. 2000). With regard to field data, two approaches have been used: 1) temporally relating system-wide average vital rates and habitat characteristics (e.g. Peterman and Bradford 1987; Shuter et al. 1998), and 2) spatio-temporally relating habitat-specific estimates of vital rates and habitat characteristics (e.g., Rutherford and Houde 1995). One should closely consider the source data when attempting to estimate vital rates within habitats based on statistical covariate relationships. For instance, biases may arise when scaling down relationships based on system-wide annual measures to finer habitat levels. Similarly, models of growth and mortality based on laboratory data may not readily translate to natural scenarios due to confounding effects such as density-dependence and interacting, uncontrolled habitat variables.

Another general method for estimating vital rates from covariates relies less on statistical, empirical fits and more on “first principles.” Combinations of such models can be used to estimate both habitat-specific growth and mortality rates. The most widely used vital-rate, mechanistic models are bioenergetics models (e.g., Kitchell et al. 1977), which estimate growth of individual fish as a function of food consumed, ambient

water temperature, and mass of fish. Specifically, these models estimate growth (G) on a daily basis,

$$(1) \quad G = C - (R + SDA + F + U)$$

where C is consumption, R is respiration, SDA is specific dynamic action, F is egestion, and U is excretion. In order to estimate growth rates with bioenergetics models, estimates of consumption are necessary. Such estimates can come from empirical relationships between prey density and consumption rates (i.e., functional responses) or more mechanistic foraging models.

Bioenergetics models also can be used to estimate mortality rates. Generally, there are two main sources of mortality for young fish, starvation and predation. When losses (R+SDA+F+U) in the above equation exceed consumption (C), an individual fish will lose weight (or energy density). If a fish loses sufficient weight, it will die of starvation. Thus, the same inputs used to estimate growth (consumption, temperature, and fish size) also can be used to estimate starvation mortality rates. In addition, bioenergetic analyses can be used to estimate consumptive demand of predators and mortality rates of prey. Several authors have used such an approach to make system-wide estimates of consumptive demand and mortality rates (Hewett and Stewart 1989; Brandt et al. 1991; Hartman and Margraf 1993). Walline et al. (2000) used a bioenergetics approach to generate spatially-explicit estimates of lavnun (*Acanthobrama terraesanctae*) consumption.

The Hook et al. (In press) analysis of steelhead growth potential in Lake Michigan did not make use of geostatistical methods to extrapolate vital rates across habitats. However, it did use a covariate approach to estimate steelhead growth rates throughout Lake Michigan based upon satellite-measured surface temperatures and extrapolated alewife densities (Figures 1.3-1.4). The covariate method was based upon an approach introduced by Brandt et al. (1992) whereby spatially explicit measures of water temperature and prey densities are integrated to generate a grid of spatially explicit estimates of fish growth rate potential (GRP). Under this approach, potential consumption within a particular volume of water (i.e., grid cell) is estimated with a foraging sub-model (as a function of temperature and prey density), and GRP within the same volume of water is estimated with a bioenergetics sub-model (as a function of potential consumption and temperature). Thus, the degree of spatial overlap between suitable temperatures and prey densities is the key determinant of GRP.

Practical Considerations and Future Work

In the sections above, I have presented very general frameworks for developing habitat production models. The details associated with implementing such models will be more complicated, and several alternative model forms are possible. Below, I identify five critical issues which should be addressed in constructing habitat production models. Also, I present some potential additional facets which could be incorporated into future habitat production modeling efforts in order to ultimately improve upon this modeling approach.

1) Biomass, Cohort, or Individual Level

Population ecology and fisheries models focusing on temporal dynamics have progressed from depicting populations as single entities (e.g., logistic and surplus production models) to depicting distinct cohorts and age-classes (e.g., Leslie matrix and catch-at-age models), and more recently depicting individual organisms (e.g., individual-based models, IBMs). Habitat production models similarly can represent populations within habitats at various levels of detail. Individuals in a habitat can collectively be characterized by a single value, representing either number of individuals (N_t) or the total biomass of individuals (B_t) within a habitat. Alternatively, individuals within a habitat can be grouped into temporal cohorts based on birth dates (e.g., daily, weekly). Discrete temporal cohorts can then be represented by single values (N_t or B_t). Finally, it is possible to model the experiences and subsequent modifications of separate individuals over time, and then integrate individual-level information to consider population-level processes. Individual-based models are a fairly novel approach for studying population dynamics (e.g., Huston et al. 1988; DeAngelis and Gross 1992). This modelling approach acknowledges that ecological interactions truly occur at the individual-level, and that several biological processes are more readily and realistically estimated for individuals compared to populations (e.g., temperature dependence of growth, prey selection). In addition, this modelling approach does not require the unrealistic assumption that all individuals within a population or cohort are identical. This flexibility to consider variation among individuals is particularly useful when modelling populations with highly size-dependent interactions (as is the case for most fish populations). The available data and controlling processes should dictate the population

level depicted within habitat models. Individual-based models may have the potential to realistically represent dynamics within a habitat. However, a plethora of data is necessary to parameterize such models and their implementation (i.e., the tracking of thousands of individuals) may require significant computer programming and processing. Thus, for a variety of reasons (e.g. available data, ease of analysis, simple dynamics) population biomass or cohort-based models may be preferable for certain systems. It is also feasible to use a combination of modelling approaches. For instance, egg development may be represented at a cohort level, while upon hatching larvae are tracked as individuals. Similarly, for large populations an individual-based approach can be used with each model individual actually representing a multitude of individual fish (e.g., Scheffer et al. 1995).

2) Spatial scale of analysis

Regarding the spatial scales of habitat production models there are two considerations, 1) how to define the size and boundaries of habitats, and 2) how to incorporate the multitude of sub-habitats contained within larger habitats. I argue above that production should be measured at a landscape scale, and thus model habitats should be quite large. As Wiens and Milne (1987) point out, one should choose a spatial scale of analysis based upon the particular organism and question of interest. I also argue that one should choose a spatial scale which allows for fairly clear discrimination among habitats.

The demarcation of habitats can be simple or complicated. When comparing riverine habitats, it is relatively simple to delineate and compare productivity among tributaries, river branches, or entire systems. It is more difficult to discriminate among

habitats in open systems. One option is an arbitrary approach whereby habitats of similar size are blocked off without heed to underlying physical, chemical and biological characteristics. For instance, habitats can be defined based upon latitudinal and longitudinal units (e.g., 10-minute by 10-minute areas; Höök et al. 2004). Alternatively, habitats can be defined such that variation in physical, chemical and biological characteristics is minimized within habitats and maximized among habitats. This latter approach increases the likelihood that production rates will vary significantly among the habitats analyzed.

A secondary issue of spatial scale is how to integrate the characteristics of sub-habitats contained within individual habitats. The simplifying assumption that habitats are functionally homogenous (e.g., Höök et al. 2003) can facilitate analyses, but can also potentially bias production estimates. For instance, Mason and Brandt (1996) demonstrated that the spatial scale at which GRP is estimated can dramatically influence mean GRP values within particular areas, and the degree of heterogeneity perceived within such areas. A relatively fine spatial scale is likely appropriate if the area of interest has a vertical dimension, because physical and biological features in marine and lacustrine systems can vary dramatically over short distances along the vertical axis. However, a coarser scale of analysis that allows for some integration across space is more appropriate when considering horizontal, regional differences throughout large systems. For instance, in developing a three-dimensional model for Atlantic menhaden (*Brevoortia tyrannus*) GRP throughout Chesapeake Bay, Luo et al. (2001) divided their environment into 4,000 cells, each approximately 5×10 km along the horizontal plane, but only 2 m deep.

3) Movement among and within habitats

Movement of individual fish among and within habitats can complicate estimation of habitat-specific production rates. One can simplify analyses by discounting movement among habitats and still generate realistic production estimates. However, it is clear that for most fish stocks, there is some movement among habitats during early life, and for the vast majority there is movement within habitats (e.g., among sub-habitats). Thus, if one strives for realism within habitat models, then movement should be incorporated. The inclusion of movement, however, limits the number of potential modelling approaches and can greatly increase model complexity. In order to account for movement within habitats it is necessary to discriminate among sub-habitats, and thus models which treat habitats as functionally homogenous are unsuitable. Also, since it is unlikely that all fish within a habitat or cohort change habitats simultaneously, models which separately track individuals (e.g., IBMs, and not population biomass or cohort models) are necessary to account for movement among habitats.

Actually incorporating movement into models can be difficult. Young fish can either move passively (e.g., eggs or early stage larvae drifting in currents) or actively (e.g., well-developed larvae or juveniles swimming effectively). Models of passive movement can be quite complex (e.g. Hinrichsen et al. 2002), but the underlying principles are relatively straightforward and involve established physical rules to account for the processes (e.g., water currents) which can transport passive objects of a certain size. Models of active movement on the other hand can be quite simple, but the underlying principles are complex (e.g., Tyler and Rose 1994). These models involve

depicting individual fish behaviors, which tend to be poorly understood. Fish have been hypothesized to choose locations based on a variety of biotic (e.g., food availability, refuge from predation, resource competition) and abiotic (e.g., temperature, salinity, oxygen concentration) factors. Ultimately, these factors relate directly or indirectly to growth, survival, and reproductive rates, and a more theoretical approach involves predicting fish distributions directly from estimated vital rates.

In general, tests of proposed models for how organisms choose their spatial location have yielded a mixture of support for and against such models. A variety of approaches have been employed to investigate the validity of the Ideal Free Distribution (IFD; Fretwell and Lucas 1970), including experimental manipulations (Grand and Dill 1997; Giannico and Healey 1999), and theoretical models (Kacelnik et al. 1992; Cartar and Abrahams 1997; Krivan 1997; Tyler and Hargrove 1997; Bernstein et al. 1999). These studies have both lent support to the validity of the IFD (Dill 1987) and demonstrated significant deviations from it (Abrahams 1986; Tyler and Hargrove 1997). Another theoretical model which also incorporates mortality for predicting fish distributions is Werner and Gilliam's (1984) μ/g rule. This rule argues that the fitness value of a habitat is a function of instantaneous growth (g) and mortality (μ) rates and that in order to maximize fitness, individuals should choose habitats during ontogeny whereby μ/g is continuously minimized. Ontogenetic habitat shifts observed in nature have been attributed to the μ/g rule (Werner and Hall 1988), and some experimental manipulations suggest that species distributions across habitats loosely adhere to the μ/g rule (Werner and Hall 1988). In contrast, other authors have suggested that the μ/g rule is too simple and should not hold for species placed under time constraints via fixed

generation times or size-dependent over-winter mortality (Ludwig and Rowe 1990; Aksnes and Giske 1990; Schindler 1999). Some authors have attempted to correlate bioenergetic growth rate potential with the spatial distributions of fish. Again, results have been equivocal. Nislow et al. (2000) observed that age-0 Atlantic salmon (*Salmo salar*) tended to occupy stream sites with positive GRP, rather than sites with negative GRP. On the other hand, Wildhaber and Crowder (1990), Tyler and Brandt (2001), and Höök et al. (in press) found that a bioenergetic integration of food and temperature was a relatively poor predictor of individual fish habitat choice.

4) Population feedback

Habitat models can explicitly or implicitly account for population feedbacks, such as density dependent processes, or essentially ignore such phenomena. It is easy to imagine that density dependent controls on growth and survival can influence the number of young fish produced within a habitat, but it is more difficult to actually estimate the degree of density dependence for particular populations and habitats (Rose et al. 2001). Further, densities of young fish in many habitats may be sufficiently low to render density dependent factors largely irrelevant (e.g., Rutherford et al. 2003), or such factors may primarily influence older life stages. Thus, in some cases it may be appropriate to avoid the modeling complexities associated with the incorporation of feedback processes by discounting such processes.

There are a variety of approaches through which population feedback mechanisms can be incorporated into habitat models. Mechanistic dynamic models which are updated continuously (or essentially continuously; e.g. daily) to reflect reciprocating responses of

model organisms and environment, should prove most useful for integrating feedback processes. Rose et al. (2001) point out that individual-based models may be particularly useful for considering density dependence, because unlike more aggregate models, IBMs overcome the estimation difficulties of a priori specification of quantitative form of density dependence.

5) Annual variation

Most past studies quantifying the relative value of habitats for fish populations have been conducted over short time periods (i.e. 1-3 years). However, some studies have directly demonstrated that the relative contribution of young fish from particular habitat-types can vary annually (e.g., Hilborn et al. 2003). It is likely that this phenomenon is common among fish populations. Most fish stocks are characterized by high inter-annual variation in year class strength, and often, year class strength is related to some environmental variables. For instance, recent analyses by Axenrot and Hansson (2003) and Madenjian et al. (in review) demonstrate that Baltic herring and Lake Michigan alewife year class strengths are related to climatic variation. Thus, since climate (i.e. temperature) drives temporal variation in fish production, it follows that climate may also drive spatial variation in production, and that the relative contribution of young fish from different habitats may vary annually.

Given that the relative contributions of young fish by different habitats will tend to vary annually, quantification of habitat importance should ideally reflect conditions during multiple years. Obtaining habitat-specific measures of fish abundance, growth and survival can be difficult during a single year, and obtaining such empirical measures

during multiple years may be unfeasible. Thus, models can be a useful tool for generating habitat-specific estimates of abundance and vital rates for years with sparse data. Ideally, such models should rely in part upon readily measurable variables (e.g. temperatures, river discharges) to estimate habitat-specific annual abundances and vital rates. This stipulation limits the type of modelling approaches for incorporating annual effects. The covariate type models outlined above, and in particular bioenergetics models may be useful for considering annual differences (e.g., Brandt et al. 2002). Ultimately, models can allow one to simulate how annual habitat-specific production may change as annual environmental conditions vary. By inputting the range of environmental conditions likely to occur over an extended time period (e.g. fifty years), one can consider which habitats, on average produce the majority of young fish.

Future Work

Landscape-scale models of early life fish production can potentially be useful in identifying important habitats for exploited and threatened fish populations. However, in order for such models to become robust fisheries management tools, a number of additional challenges must be overcome, including methods for model validation, accounting for the uncertainties associated with complex production models, directly linking fish production models with other trophic level models, and the accurate representation of three dimensional habitats. Perhaps most importantly, methods for validating habitat production models need to be developed. Unfortunately, the constraints of field and laboratory methods for identifying important habitats not only necessitate habitat models of fish production, but also serve to make validation of such

models difficult. Nonetheless, if individuals' natal habitats can be determined from natural (e.g., Kennedy et al. 2002; Brazner et al. 2004) or artificial tags (e.g., Miller and Able 2002), then a potential model validation involves comparing the relative importance of various habitats inferred from production models to the importance of habitats inferred from individual tags. Similarly, if there is evidence that young fish remain in a single habitat during their early development it may be appropriate to infer habitat importance by simply estimating late-season young-of-year (YOY) densities (i.e. once year-class strength has been set). Basically, this approach involves sampling the population after early-life growth and mortality dynamics have had a chance to influence densities and size distributions within individual habitats. For example, there is evidence suggesting that young Baltic herring (*Clupea harengus*) are fairly non-migratory (Hansson 1993; Hansson et al. 1997), and herring year-class strength is set late during the first year of life (Axenrot and Hansson 2003). Thus, it may be possible to validate production models for YOY Baltic herring by comparing model predictions with late-season YOY densities.

However, for the majority of fish populations (especially populations in open systems) direct validations of production models based upon laboratory and field methods will be methodologically impractical if not infeasible. In such cases, it may nonetheless be possible and useful to test the validity of individual components of production of models (i.e. predictions of abundance, growth, mortality). For such testing, elasticity or sensitivity analyses can be used to determine which model components to focus upon. Perturbation of individual parameters within production models can help identify the degree to which slight estimation errors of individual parameters can translate into inaccurate estimates of relative habitat importance. Subsequently, efforts to validate

and improve parameter estimates should focus on those model components or individual parameters which have most influence on estimates of habitat importance.

Regardless of whether model and model component outputs can be validated, it is critical to account for and communicate the degree of uncertainty associated with model estimates. There is bound to be a great deal of uncertainty in models of habitat production because the data used to parameterize such models are themselves uncertain (due to measurement variability and limited data). In addition, data used as inputs for fully constructed models and pathways depicted in such models can further augment uncertainties. Finally, if habitat production models are to be used for forecasting, then model inputs must themselves be estimated (and not directly measured) thereby adding an additional level of uncertainty. Although it may ultimately be possible to limit some of these model uncertainties, the complexities associated with natural systems preclude the elimination of uncertainty, and thus future habitat modelling efforts should strive to both account for and communicate these uncertainties (e.g., Clark et al. 2001; deYoung et al. 2004).

Issues of how to couple the spatial and temporal dynamics of a fish population to the dynamics of its prey, predators and competitors are quite complicated. However, as fish populations do not exist in isolation, predictions of habitat production models should ultimately improve by simultaneously accounting for the dynamics of multiple trophic levels. Nonetheless, in practice the need to account for the dynamics of interacting trophic levels will depend on the processes to be depicted and the form of model. If a model is to mechanistically incorporate feedback mechanism, such as density-dependent growth and mortality, then it is likely necessary to track the dynamics of predators and

prey. Due to data limitations, biological distinctions, and desired spatio-temporal resolution, various types of models may be suitable for different trophic levels. In general, the “rhomboid modeling approach” presented by deYoung et al. (2004) is a useful framework to guide the spatial, temporal, and biological resolution appropriate for various trophic levels. This framework suggests that highest resolution is necessary at the trophic level of the population of interest, and that resolutions should decrease at progressively higher and lower trophic levels.

Humans generally manage aquatic environments as two-dimensional features (i.e. only the horizontal plane is considered). For instance, MPAs protect defined areas, not volumes. However, physical, chemical and biological features of marine and lentic systems can vary greatly and abruptly along the vertical axis, whereas variation along horizontal axes tends to be more gradual. Further, understanding both vertical distributions of potentially interacting populations and how physical and chemical factors (which also vary vertically) can adjust such interactions are critical to understanding and subsequently modeling the spatial dynamics of fish populations. Thus, spatial models of fish production should ideally explicitly depict the vertical dimension. This additional axis will of course add to the complexity and data needs of these models, and as less-complex, two-dimensional models are themselves likely to be data limited, the development and implementation of three-dimensional models may in many cases be impractical. Some past landscape-scale models of fish production have assumed that target species are primarily benthic (e.g., Chu et al. 2004) or occur along the surface (e.g., Höök et al. 2003) and have thus discounted the vertical dimension and considered environments as two-dimensional. For many fish populations, however, such simplifying

assumptions are not valid and thus three-dimensional models are likely more appropriate (i.e., Luo et al. 2001).

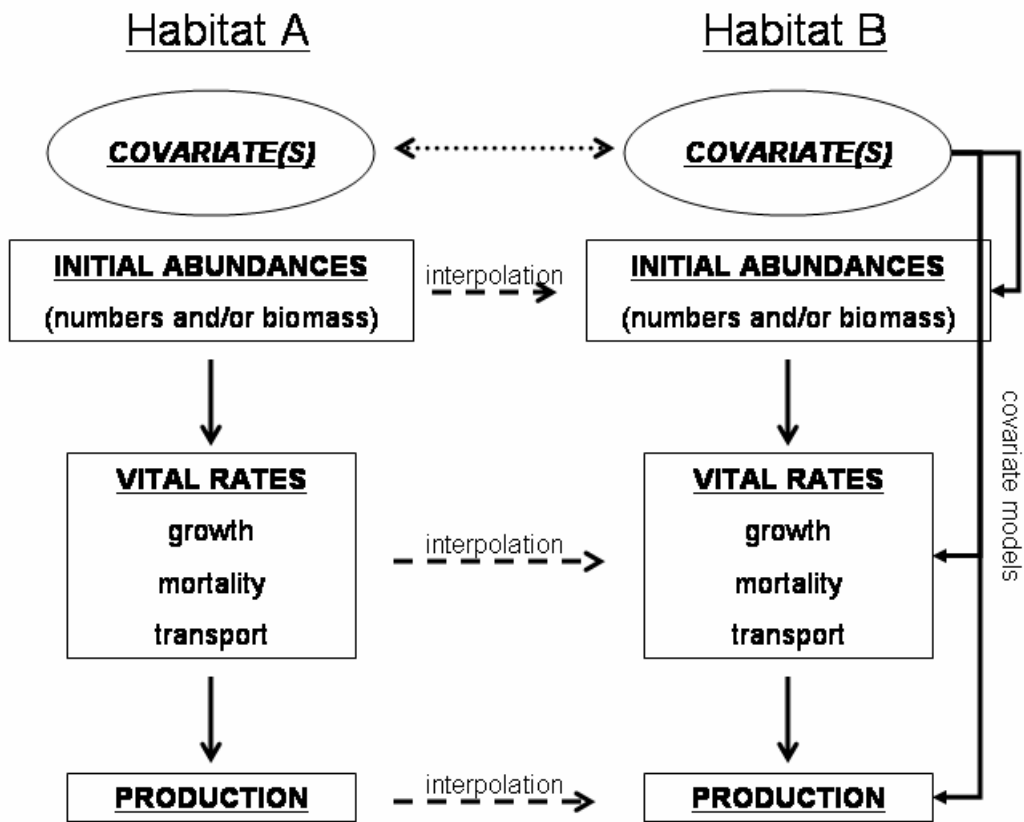


Figure 1.1) Conceptual diagram of how components of early-life fish production within a habitat (i.e. abundances, vital rates and production) may be extrapolated across habitats (from sampled Habitat A to un-sampled Habitat B). The initial abundances and biomass of young fish in a habitat are modified by vital rates to determine the ultimate production in the habitat. These components can be extrapolated across habitats based upon geostatistical techniques (only actual measures of abundances, vital rates and production in Habitat A are used to predict values in Habitat B), covariate methods (only covariate values are used to predict abundances, vital rates and production in Habitat B), or combined spatial-covariate methods (both measures of abundances, vital rates and production in Habitat A and covariate values, are used to predict abundances, vital rates and production in Habitat B).

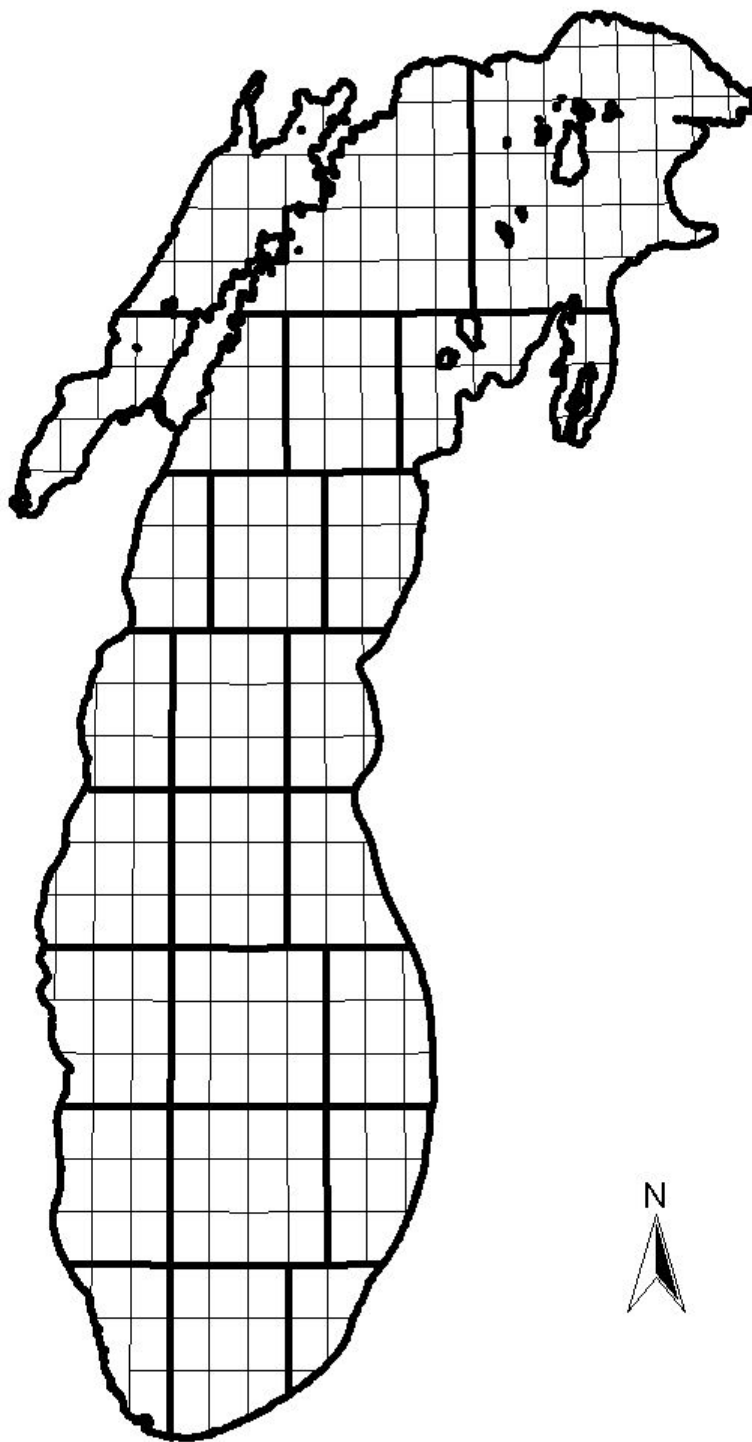


Figure 1.2) Lake Michigan divided into 273, 10-minute by 10-minute grid cells (thin lines) and 26, approximately 30-minute by 30-minute grid cells (bold lines).

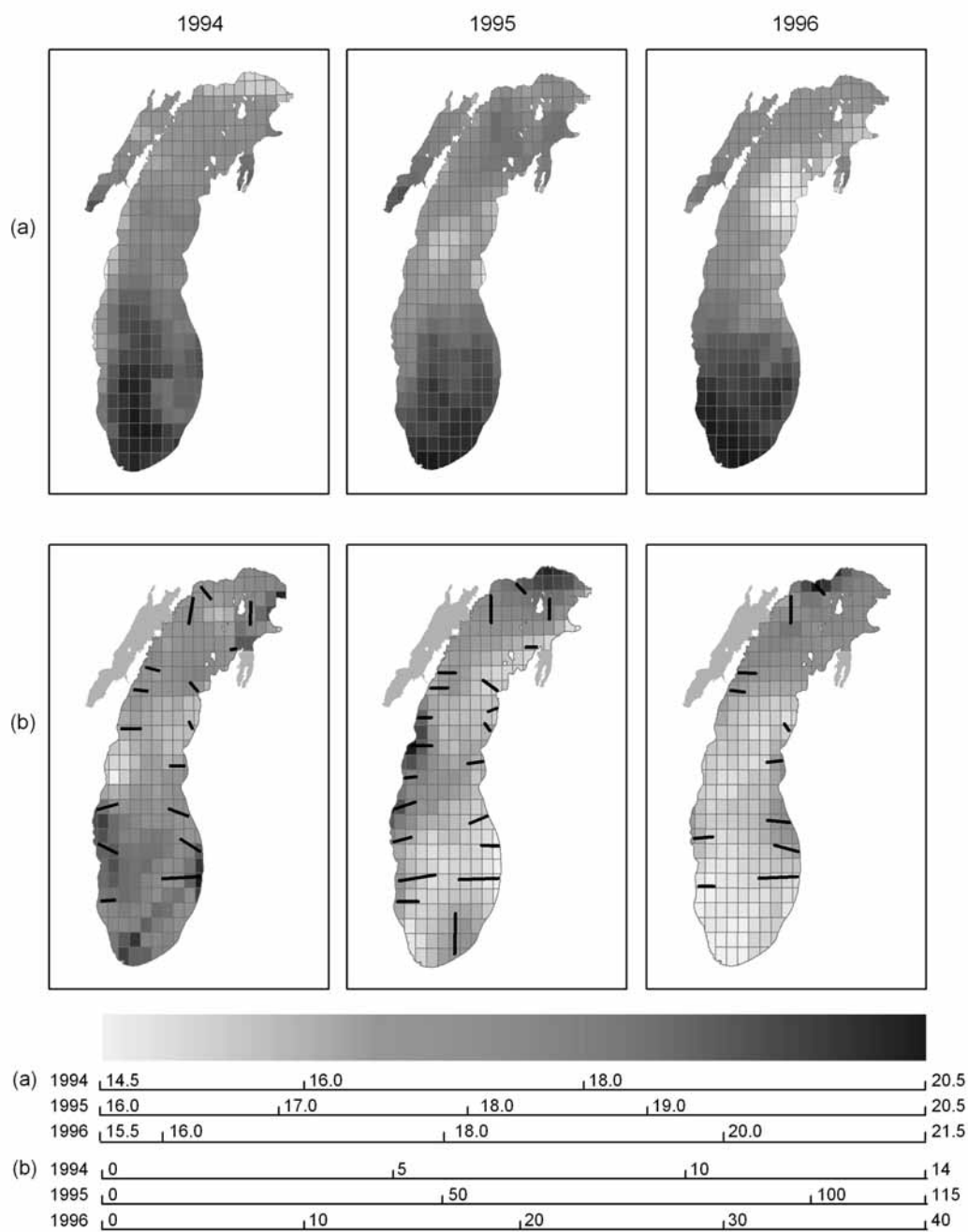


Figure 1.3) Lake Michigan September 1994-1996: a) Mean satellite-measured surface temperatures (°C) and b) USGS-GLSC acoustic transects (black points) and interpolated alewife densities summarized by 10-minute grid cells (kg ha⁻¹). Note that scales differ among years.

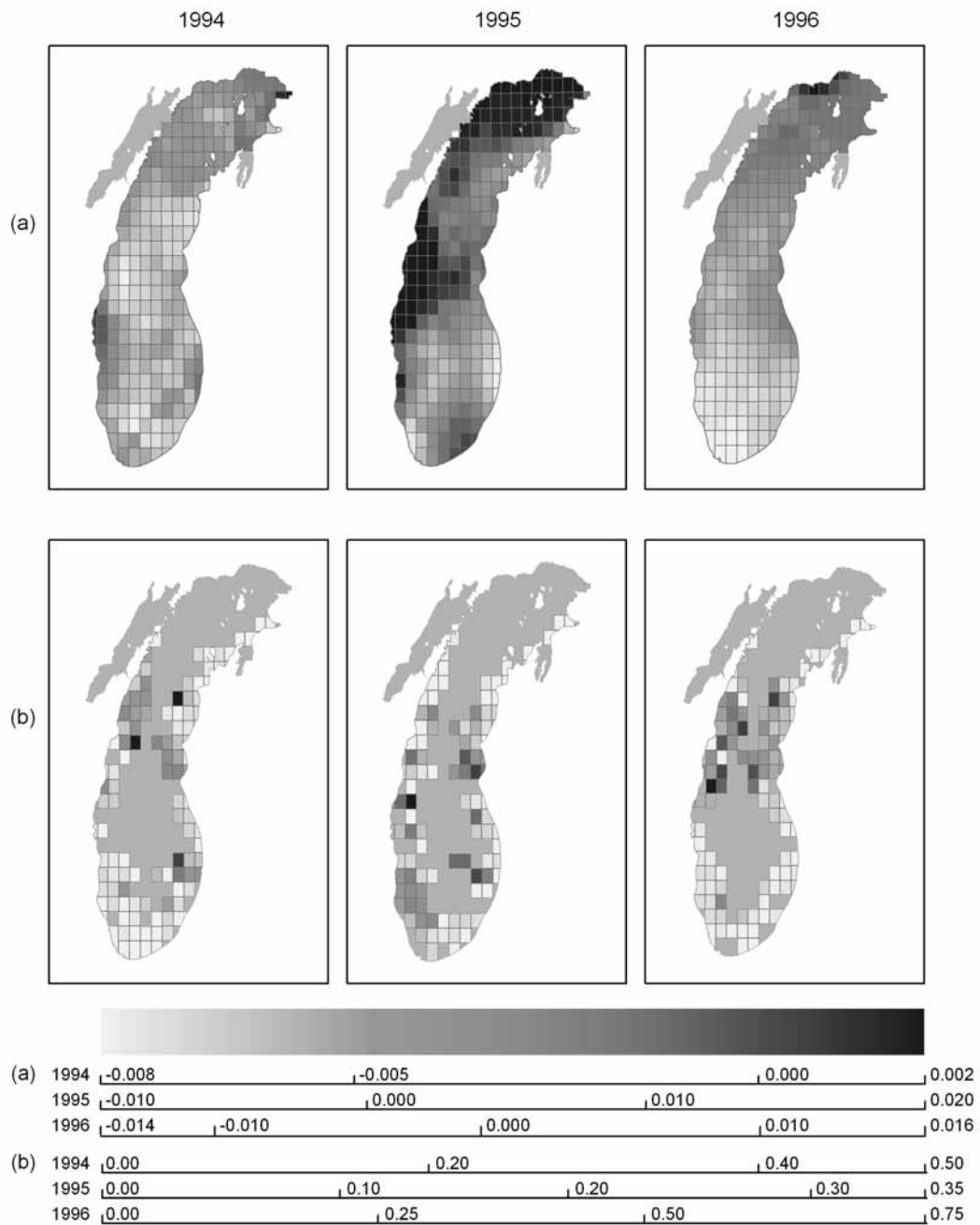


Figure 1.4) a) Growth rate potential (GRP; g g⁻¹ d⁻¹) of a 3.5-kg steelhead and b) Average catch per unit effort (CPUE; number caught per angler hour) within Lake Michigan, 10-minute grid cells during September 1994-1996. Note that scales differ among years.

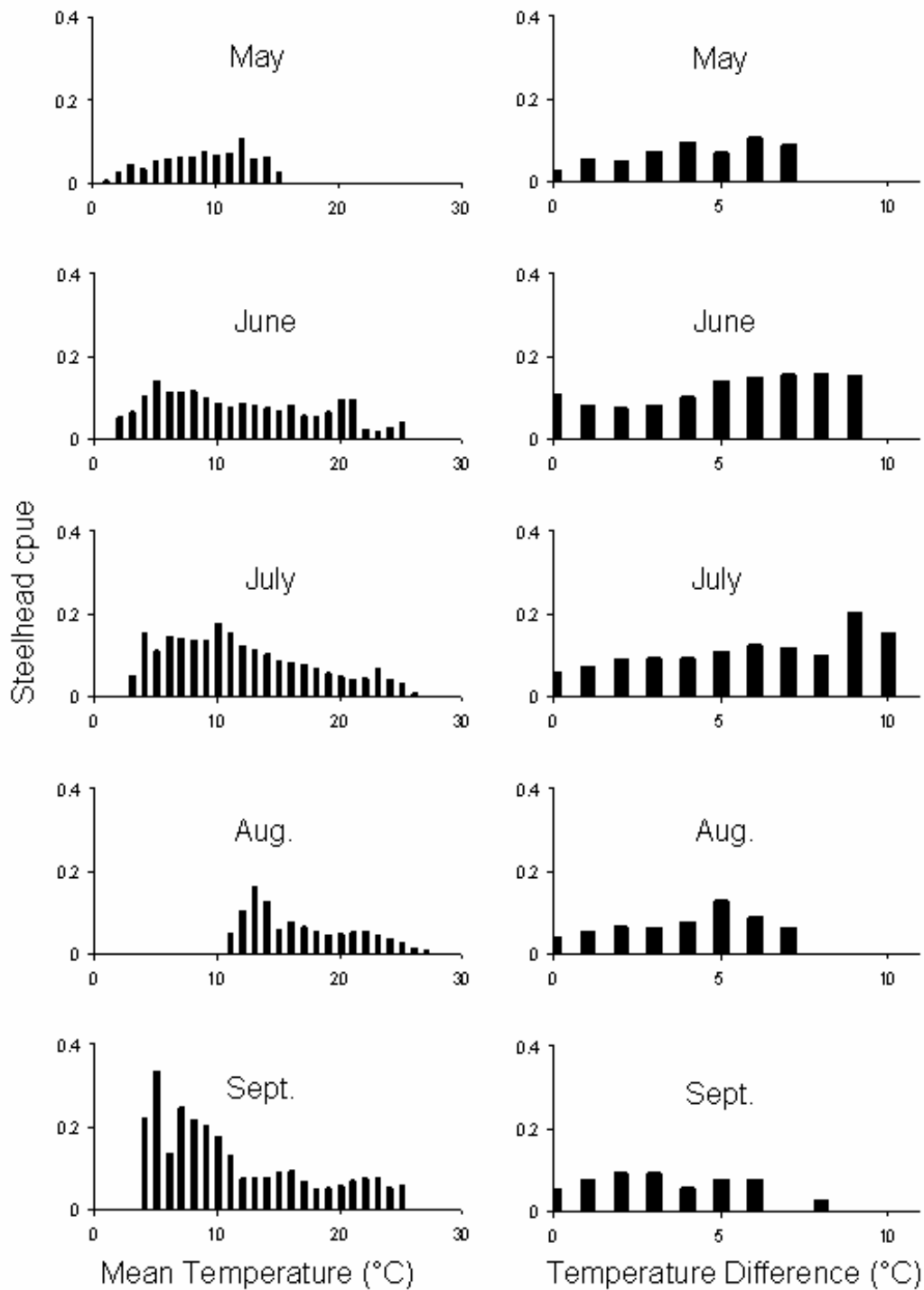


Figure 1.5) Mean steelhead catch-per-unit-effort (cpue) in 1°C temperature bins in Lake Michigan, 1992-1997. Each bar in the five left plots represents the mean cpue among all cells (1992-1997) with the corresponding mean daily temperature. Each bar in the five right plots represents the mean cpue among all cells (1992-1997) with the corresponding daily temperature difference.

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