FISH MOVEMENTS IN A PREDATOR-PREY AND FISHERIES MANAGEMENT CONTEXT

by

Olaf P. Jensen

A dissertation submitted in partial fulfillment of the requirements for the degree of

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[Signatures]

Signature, Dean of Graduate School
[Signature]
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ABSTRACT

FISH MOVEMENTS IN A PREDATOR-PREY AND FISHERIES MANAGEMENT CONTEXT

OLAF P. JENSEN

Under the supervision of Professor James F. Kitchell
at the University of Wisconsin-Madison

Electronic observations of fish movements have provided great insights into fish behavior at hourly to inter-annual time scales. Hydroacoustics and electronic tag technology, including radio, acoustic, and satellite archival tags, have developed rapidly in recent years. Data from these technologies have the potential to answer important ecological and management-oriented questions. Development of mathematical models to make use of these data has not kept pace with the development of these technologies. In this thesis, I develop models that use observations of fish behavior from hydroacoustics (Chapter II); radio, acoustic, and conventional (non-electronic) tags (Chapter III); and conventional and pop-up satellite archival tags (PSATs, Chapter IV and V) to answer questions related to predator-prey interactions and population dynamics. The results have important implications for our understanding of how fish manage trade-offs between predation risk and growth (Chapter II) and how we manage fish populations and trade-offs among competing fisheries (Chapters III – V).

I developed linked foraging, bioenergetic, and predation risk models to understand the implications of different diel vertical migration (DVM) strategies for coregonids (Coregonus
Coregonids face trade-offs. A DVM trajectory that places them in warm, well-lit, waters near the surface during the day would provide substantial growth benefits. It would also expose them to high predation risk by lake trout. At the other extreme, a deep and dark trajectory would greatly reduce predation risk, but would result in poor growth. Coregonids in the western arm of Lake Superior appear to follow an intermediate path that results in a low ratio of risk to growth.

In Chapter III, I develop a population model for taimen, *Hucho taimen*, in Mongolia. Little is known about taimen—the world’s largest salmonid—yet management decisions must still be made. A great challenge resides in developing taimen fisheries that provide large economic benefits, while protecting populations of this endangered species. I compared the economic and population consequences of two extremes: a 100% catch-release recreational fishery and a commercial fishery operating at maximum sustainable yield (MSY). The existing recreational fishery appears to have little impact on the population, while providing 20 to 30 times the economic benefit of a potential commercial fishery.

Recreational fisheries for striped marlin, *Kajikia audax*, off of Baja California, Mexico are in conflict with commercial longline fisheries that take this species as bycatch. Areas closed to longlining have been used to protect striped marlin; however, there is little analysis to suggest that closed areas are a useful management tool for highly mobile pelagic marine species. Using information from PSATs applied to striped marlin, I show that the current closed areas protect striped marlin during a large fraction of their time spent near Mexico (Chapter IV). A population dynamics model fit to striped marlin catch and effort from the Japanese longline fleet shows that past closures of Mexican waters allowed a rapid recovery. Recreational catch-release can also help protect this population, but the effect is not as large.
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Approved

James F. Kitchell
I am deeply indebted to Jim Kitchell for the guidance and opportunities that he has provided during my time as a Ph.D. student. Jim's contagious enthusiasm and endless well of ideas have been a true inspiration. From the moment I arrived in Madison, Jim made it clear that he expected great things, and that he would provide the resources, contacts, and big picture ideas to make those happen. He's always lived up to his end of that bargain and inspired me to do my best to live up to mine. The poor Greeks had to travel to Delphi for good advice. I've never had to do more than walk up to Jim's office.

To the extent that I've been able to meet Jim's high expectations, it's because of the excellent preparation that I had as a M.S. student with Tom Miller. Tom taught me the foundations of all the research skills that I use today. He also encouraged me to look into doing a Ph.D. at Madison with Kitchell, Carpenter, and Ives - some of the best advice I've ever received.

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My committee members: Steve Carpenter, Tony Ives, Volker Radeloff, and Jake Vander Zanden have provided a ton of great advice on everything from career directions to analysis of tag data. Their suggestions drove my thesis in a more productive direction, and their comments on drafts resulted in substantial improvements of these thesis chapters.
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CHAPTER I
INTRODUCTION

This thesis consists of three geographically and taxonomically separate analyses that share a few common themes, foremost among them, the importance of understanding fish movements. In this introduction, I provide some background regarding the study of fish movements from both a behavioral ecology and a fisheries management / fish population dynamics viewpoint. The link between these two viewpoints is that behavior, specifically fish movements, affects the vulnerability of fish to natural predators and fishing. Arena foraging theory offers a framework for this link, and I review these ideas briefly. Striped marlin are the taxonomic focus of Chapters IV and V. I provide a short overview of their stock status and fisheries to supplement the material contained in these chapters.

**Behavioral ecology of fish movements**

What is the best time for a fish to move from one habitat to another? This question has been asked at daily (diel vertical migration, DVM), seasonal, and developmental (ontogenetic niche shift) time scales. Predation risk and food availability often co-vary among the different habitats occupied by a fish. Changes in resource and habitat use are often abrupt and discrete, for example: nighttime movements to feed near the surface or the shore, anadromous fish moving from fresh water to marine environments, or juvenile fish switching from feeding on pelagic zooplankton to littoral invertebrates. Werner and Gilliam (1984), focusing on ontogenetic shifts, developed a fitness-based argument that fish should change resources (food and/or habitat) when such a shift minimized the ratio of risk to growth (μ/g). Similar arguments
about balancing risk and growth had already been applied to DVM of juvenile sockeye salmon (Eggers 1978), albeit with less mathematical detail. Clark and Levy (1988) applied a dynamic optimization model to the daily decision of whether and when to leave the relative safety of deeper water to forage in food and predator rich surface waters. The optimal decision depends on an individual’s current size relative to the size required to survive a future mortality bottleneck and the time until that bottleneck. Individuals that fall behind on the optimal growth curve must engage in more risky behavior, e.g., foraging near the surface at times outside of the “anti-predation window,” if they are to “make weight” (Mangel and Clark 1988).

These studies all assumed simple discrete shifts from habitat one to habitat two, with accompanying changes in resource levels and predation risk. Later behavioral optimization studies of fish movements compared observed movement patterns to space-time gradients of food availability, growth rate potential (essentially food availability modified by temperature effects on bioenergetic rates), and predation risk (e.g., Scheuerell and Schindler 2003).

**Fisheries management and fish movements**

In population ecology, the focus is typically on broad scale horizontal movements rather than DVM. Most early population dynamic models, and indeed most of the stock assessment models still used today, assumed closed populations, i.e., that immigration and emigration are zero. MacArthur and Wilson’s (1967) theory of island biogeography was one of the first high profile community models to focus specifically on immigration and emigration. Metapopulation models (Gilpin and Hanski 1991) apply the same idea at the population level. Here the stochastic balance between the local processes of birth and death is summarized in a single
extinction probability, and the stability of the metapopulation is determined by these extinction probabilities and recolonization rates.

Metapopulation models have not had a large effect on fish stock assessment and management despite the fact that metapopulation structure can have implications for optimal harvest strategies (Tuck and Possingham 1994). This is likely due partly to the inherent conflict between the metapopulation and the traditional unit stock concepts and partly to the fact that the assumptions of basic patch metapopulation models (Levins 1969) do not seem to hold for most managed fish stocks. First, the definition of a stock is determined by practical management considerations (e.g., management jurisdiction) as well as biological characteristics. Second, stock extinction is rare (Carlton et al. 1999), though perhaps not as rare as is commonly believed (Casey and Meyers 1998), at the time scales for which most management decisions are considered. Third, most fish do not live in habitats that can be easily divided into patch (the areas where sub-populations can exist) and matrix (the hostile area separating patches).

In contrast, fish movements have received a great deal of attention recently in models of the fisheries effects of marine reserves (areas closed to fishing). These models typically highlight the finding that reserves can have the greatest value as fishery management tools at intermediate levels of dispersal (Guénette et al. 1998). When dispersal is high, build-up of fishing effort outside of the reserve can effectively cancel benefits derived from improved survival within it. If dispersal is too low, there is no spillover, and the fishery as a whole receives no benefit from the build up of biomass within the reserve. Monitoring of fisheries adjacent to marine reserves supports these conclusions (Russ and Alcala 1996, Ebesamis and Russ 2005).
An ecosystem model of the central North Pacific (Martell et al. 2005) has shown that the impact of marine reserves also depends on the drivers of fish movements. In the case of random fish movements, larger reserves are required in order to achieve the same reduction in fishing mortality as movement rates increase. If emigration rate from a region is inversely proportional to “fitness” (a density-dependent function of growth and predation risk), however, greater movement rates give the opposite result (i.e., smaller reserves will suffice as movement rates increase). This effect is further magnified if, in addition to decreasing emigration rate in high fitness habitats, fish are also able to sense and follow fitness gradients. Of course, in an ecosystem model, what’s good for the predator is bad for the prey—densities of prey species and of juvenile predators decrease as reserves become increasingly effective at protecting adult predators from fishing.

**Arena foraging theory**

The focus on movements of adult fish at broad temporal and spatial scales may be misplaced since the single most important requirement for sustainable fisheries appears to depend on interactions among juveniles and their predators and prey at the scale of meters and minutes. For any fish population to be capable of withstanding harvest without crashing, it must exhibit a compensatory increase in natural survival rate when fishing mortality is applied. Typically such compensation is seen in juvenile survival rates. Arena foraging theory (Walters and Juanes 1993) offers an explanation for the compensatory response and also addresses the discrepancy between observed predator/prey stability and the predictions of Lotka-Volterra models.
The arena foraging concept posits that fish that are vulnerable to predation divide their time between refuge and foraging arena habitat. Refuge can take many forms: littoral habitat too shallow for predators, structural refuge in physically complex habitats such as weeds or rocks, depths where light levels impede predation, or dense schools that offer protection from predators. The key feature of refuges is that, while they provide protection from predators, they offer little in the way of foraging opportunities. Individuals must periodically leave the shelter of refuges to enter the foraging arena where prey are available, but predation risk is increased.

Walters and Korman (1999) show that foraging arena behavior leads directly to the phenomenon of nearly constant recruitment (in absolute terms) across a wide range of spawner biomass. Put another way, compensatory increases in juvenile survival allow a small number of eggs to develop into nearly as many recruits as result from a large number of eggs. This pattern is described in the widely used Beverton and Holt recruitment ($R$) function:

$$R = \frac{aS}{1 + bS}$$  \hspace{1cm} (1)

where $S$ represents the number or biomass of spawners (or eggs), $a$ is the slope of the stock recruitment curve at low spawner abundance and $b$ is a scaling factor that determines the maximum recruitment level. Walters and Korman (1999) derive $a$ and $b$ from arguments about how foraging time per individual should vary as a function of the total number of individuals if each individual forages for the amount of time required to reach some threshold size.

In addition to explaining recruitment compensation, foraging arena theory offers a solution to the “paradox of enrichment” (Rosenzweig 1971), i.e. the prediction that predator-prey models should develop dynamic instability as prey productivity increases. Arena foraging theory leads to a modification of basic Lotka-Volterra dynamics through the incorporation of exchange
rate parameters, \( v \) and \( v' \), that describe the instantaneous rates of movement of individuals into and out of the foraging arena, respectively. The total consumption rate of prey by predators \( (Q) \) in the foraging arena then becomes:

\[
Q = \frac{a v B_{\text{prey}} B_{\text{pred}}}{v + v' + a B_{\text{pred}}}
\]

where \( a \) is the Lotka-Volterra constant and \( B_{\text{prey}} \) and \( B_{\text{pred}} \) are the biomass of prey and predators, respectively (Walters and Martell 2004). High rates of flux into the vulnerable biomass pool \( (v) \) result in Lotka-Volterra dynamics, i.e., predation rates approximately equal to the random encounter rate \( a B_{\text{prey}} B_{\text{pred}} \); however, intermediate values of \( v \) give a saturating curve for the relationship between predation rate and predator density. This mathematical feature suppresses the instabilities that give rise to the paradox of enrichment. The existence of prey refuges may be a key factor for the creation and maintenance of biodiversity (Hixon and Beets 1993). Modifying the assumed exchange rate between such refuges and foraging arenas is also a key to creating stable ecosystems in models such as Ecopath with Ecosim (EwE, Walters et al. 2000).

**Striped Marlin**

Striped marlin are large, fast-growing, pelagic apex predators that are distributed throughout the tropical and subtropical waters of the Pacific and Indian Oceans. They are primarily harvested as bycatch in pelagic longline fisheries, although they are sometimes targeted in regions of high abundance such as the area off of Baja California Sur, Mexico (Kume and Joseph 1969). Diet studies (Arbitia-Cardenas et al. 1997, 2002) show that striped marlin are opportunistic predators that feed primarily on locally abundant epipelagic fish and cephalopods.
The stock structure and current status of striped marlin are both the subject of considerable debate. Early work based on morphometrics (Kamimura and Honma 1958) and more recent analysis of spatial catch per unit of effort (CPUE) patterns (Squire 1987, Squire and Suzuki 1990, Squire and Au 1990) suggest separate northern and southern stocks. Recent microsatellite DNA evidence further divides the population into distinguishable North Pacific (Taiwan, Japan, Hawaii, and California), Mexican, Ecuadoran, and Australian genetic groups (Graves and McDowell 1994, McDowell and Graves in press). Conventional tags offer no evidence against such regional differences; less than 8% of conventional tagged individuals moved more than 1,000 km (Bromhead et al. 2004). Time at large for tagged fish, however, has typically been short (90% of recoveries occurred within one year) and recapture rates are extremely low (average for all programs: 0.93%, Ortiz et al. 2003). Similar results have been reported for pop-up satellite archival tags (PSAT’s, Domeier 2006).

Stock assessments of striped marlin currently exist only for the Eastern Pacific Ocean (EPO, Hinton and Bayliff 2001, Hinton and Maunder 2003), although a Western Pacific assessment is underway (P. Kleiber, National Marine Fisheries Service, Honolulu Lab, pers. comm.). The EPO stock assessments, based on Deriso-Schnute delay-difference models (Deriso 1980, Schnute 1985, 1987), suggest that striped marlin biomass is at or above $B_{msy}$, the biomass that would produce the maximum sustainable yield, and that current biomass of striped marlin is between 47% and 70% of the unfished biomass. Earlier analyses of longline catch and effort data using simple surplus production models also concluded that striped marlin (or at least the northern stock) were not overexploited (Bartoo and Ueyanagi 1978, Suzuki 1990, Skillman 1990). Analysis of CPUE trends, however, suggest that overall the biomass of large pelagic predators in the tropical and sub-tropical Pacific has declined by approximately 80-85% (Myers...
and Worm 2003), and the raw CPUE (uncorrected for catchability changes) for striped marlin has declined by 93%. The analysis by Myers and Worm (2003) has been hotly contested by other stock assessment experts because they failed to adequately account for changes in catchability due to changes in gear and the spatial distribution of the fishery over the 50 year period (Hampton et al. 2005, Polacheck 2005), and their method of spatial averaging made unsupportable implicit assumptions about unfished regions (Walters 2003).

There is serious concern about striped marlin stocks in the Pacific both because of the uncertainty in their status and the high value of recreational fisheries for this species. Striped marlin are a primary target of recreational fisheries in Hawaii, California, Mexico, Costa Rica, Panama, Ecuador, New Zealand, and Australia. These fisheries are an important source of tourist revenue in many regions, and their annual economic impacts, where they have been estimated, are typically in the tens of millions of dollars. For example, Ditton and Stoll (2003) give an annual economic impact of $59 million for the billfish fishery in Baja California Sur, Mexico (assuming an impact multiplier of 1.5) plus an aggregate economic value (based on willingness-to-pay) of approximately $5 million.

Summary

Chapter II of this thesis focuses on the behavioral ecology of fish movements and trade-offs between predation risk and food availability using a simple pelagic food chain from Lake Superior as an example. Chapter III looks at the trade-offs between recreational catch-release and commercial harvest fisheries for taimen, Hucho taimen, in Mongolia. Chapters IV and V focus on the spatial distribution and population dynamics, respectively, of striped marlin.
In the past 10 years, the number of electronic tags placed on pelagic fish has increased dramatically. Most of the published analyses of electronic tag data to date, however, have simply shown the tracks of individuals and reported various summary statistics about the movement patterns. These data have not yet been used to guide the design of MPAs. Chapter IV describes a few key modifications to animal movement methods that make them more applicable to tracking data from pelagic animals. These methods are applied to conventional and electronic tag data from striped marlin to understand the spatial distribution of fish and fishermen.

Chapter V uses a population dynamics model to evaluate the efficacy of two policy actions: increasing releases of striped marlin in the recreational fishery and closing the Mexican EEZ to longline fishing. This chapter challenges the notions that for widely distributed, highly mobile fish such as striped marlin, management must occur through international agreements and marine protected areas would need to be unfeasibly large to have any benefit.


Kamimura, T., and Honma, M. 1958. A population study of the so-called Makajiki (striped marlin) of both northern and southern hemispheres of the Pacific. I. Comparison of external characters. Reports of the Nankai Fisheries Research Laboratory: 8-11.


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